

Direct and maternal (co)variance components and genetic parameters for growth and reproductive traits in the Boran cattle in Kenya

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Abstract Direct and maternal (co)variance components and genetic parameters were estimated for growth and reproductive traits in the Kenya Boran cattle fitting univariate animal models. Data consisted of records on 4502 animals from 81 sires and 1010 dams collected between 1989 and 2004. The average number of progeny per sire was 56. Direct heritability estimates for growth traits were 0.34, 0.12, 0.19, 0.08 and 0.14 for birth weight (BW), weaning weight (WW), 12-month weight (12W), 18-month weight (18W) and 24-month weight (24W), respectively. Maternal heritability increased from 0.14 at weaning to 0.34 at 12 months of age but reduced to 0.11 at

24 months of age. The maternal permanent environmental effect contributed 16%, 4% and 10% of the total phenotypic variance for WW, 12W and 18W, respectively. Direct-maternal genetic correlations were negative ranging from -0.14 to -0.58 . The heritability estimates for reproductive traits were 0.04, 0.00, 0.15, 0.00 and 0.00 for age at first calving (AFC), calving interval in the first, second, and third parity, and pooled calving interval. Selection for growth traits should be practiced with caution since this may lead to a reduction in reproduction efficiency, and direct selection for reproductive traits may be hampered by their low heritability.

Keywords Kenya Boran cattle · (co)variance components · Genetic parameters · Growth traits · Reproductive traits

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Introduction

The Kenya Boran cattle constitute the largest proportion of *Bos indicus* breeds kept primarily for beef production in the arid and semi arid lands (ASALs) of Kenya. They are preferred to other *B. indicus* and *B. taurus* breeds due to their higher reproductive, productive and adaptability performance in similar conditions. Due to these potentials, this breed is being used in performance improvement programmes of other indigenous and exotic cattle for beef and milk production (Demeke et al. 2004)

The primary emphasis of the selection programme for the Kenya Boran is to improve growth and reproductive performance. Animals are selected by physical appraisal on their growth and body condition and thereafter on their reproductive performance. This mode of selection is highly subjective; nevertheless, its use is due to paucity of estimates of genetic and phenotypic parameters especially correlations between growth and reproductive traits (Burrow 2001). Accurate estimates of variance components and genetic and phenotypic parameters are influenced by how well the factors such as structure of the data, population history and the mode of inheritance of traits being analysed are accounted for (Maniatis and Pollott 2003).

Growth and reproductive performance are influenced by direct additive genetic effects. In addition, growth performance is influenced by effects attributed to the dam (maternal effects) (Albuquerque and Meyer 2001). In tropical breeds, maternal effects are often omitted during genetic evaluation due to data limitations. Where these effects are of importance, but omitted, genetic parameters are biased upwards (Dodenhoff et al. 1999; Maniatis and Pollott 2002a) and realised selection-efficiency reduced. In few studies where maternal effects have been accounted for in tropical beef breeds, studies have been based on data derived from research station where data collection is fairly consistent (Demeke et al. 2003, Wasike et al. 2006). However, studies of maternal effects based on field data in which direct-maternal correlation have been accounted for are scarce. There is the need to examine maternal effects holistically to accurately account for the various sources of variation in growth performance.

Knowledge of the magnitude of the (co) variance components for growth and reproductive traits in tropical beef cattle though critical is scanty. Therefore, the complete covariance structure of these traits needs to be estimated. Even in case of inadequate pedigree information and data, some attempt at estimating genetic (co) variance components and genetic parameters is better than no attempt. Therefore, the focus in this study was to provide preliminary estimates necessary for the establishment of a breeding programme for the Kenya Boran cattle based on quantified parameter estimates, which would be improved as more performance and pedigree data becomes available. The aim of this study was to estimate direct and maternal additive genetic (co) variance components and genetic parameters trends

for growth and reproductive traits in the Boran cattle breed in Kenya.

Material and methods

Data source

Data on growth and reproduction performance of the Kenya Boran cattle were made available by a large-scale commercial ranch and a national beef research station located in Nakuru district approximately 140 km and 150 km northwest of Nairobi, Kenya, respectively. These farms maintain stud herds registered with the Kenya Studbook and are members of the Kenya Boran Cattle Breeders' Society (KBCBS). The large-scale commercial ranch is located in Agro-Ecological Zone (AEZ) 4, classified as typical ASAL and borders Lake Elementaita. The farm receives an average annual rainfall of 770 mm and the diurnal temperature ranges from 14° to 26°C. The national beef research station is located at the interface of AEZ 3 and 4 and receives an average annual rainfall of 800 mm. In this station, animals are reared in AEZ 4 since this is where all the grazing fields are located. The rainfall pattern on both farms is bimodal. The long rains fall in March to June while short rains come in September and October. The two rainy seasons are separated by dry seasons. The hottest and driest months in both farms are January and February.

Management of animals

Cattle on both farms were raised on natural pastures composed of mainly *Themeda triandra* with scattered acacia tree cover at varying density. Cattle on the research station grazed during the day and were "kraaled" at night next to station offices. On the ranch, animals were divided into small herds (average herd size of 150 cattle) and kept in pasture fields for 24 hours. Both farms practiced the cow-calf system. On the research station, calves were weighed and identified within 48 hours of birth while on the ranch they were not weighed but identified and their births recorded during weekly farm runs. Calves were weaned when they were 7 and 9 months of age on the research station and ranch, respectively. On both farms at weaning, all calves were weighed. Bull calves not selected for breeding were castrated and raised as beef steers. Weaners were herded together away from

the older stock until 18 months of age, when heifers were dispersed to various breeding herds.

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 KBCBS standards were culled. The selection intensity 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 in 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 in 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. The bull to cow ratio in the ranch was 1:50 while that on research station was 1: 60. Breeding bulls were replaced when their daughters attained the breeding age. On both farms, disease management was mainly prophylactic via the control of ecto- and endo-parasites. However, specific treatment was given when any disease occurrence was reported. Routine vaccinations were carried out for endemic diseases such as Foot and Mouth Disease, Theileriosis, Lumpy Skin Disease, Contagious Bovine Pleura-pneumonia (CBPP) and Bovine Pasteurellosis.

Data and traits

Data on growth and reproduction performance were collected from 1989 to 2004. Data were edited for consistency of pedigree information and correct dates of birth, calving and weighing. Records with anomalies in pedigree information and dates were discarded. Also discarded were records of animals with age at first calving (AFC) less than 640 and greater than 1827 days and calving interval (CI) less than 303 and greater than 884 days. A final data set comprised of 4502 records for analyses of growth traits and 2681 records for analyses of reproduction traits. The growth traits analysed included birth weight (BW, kg), weaning weight (WW, kg), 12-month weight (12W, kg), 18-month weight (18W, kg) and 24-month weight (24W, kg) obtained from the beef research station. Among the growth traits, only records on WW were analysed from the commercial ranch. The reproductive traits consisted of AFC and pooled calving interval (CI). In addition, CI in the first three parities (CI1, CI2 and CI3) were also considered as separate traits. The pedigree and data structure, and summary statistics for each trait are presented in Tables 1 and 2.

Statistical analysis and modelling

The GLM procedure of GENSTAT-Discovery edition (GENSTAT 2003) was used in the development of the fixed effects model for the traits considered. Fixed effects that significantly influence growth and reproductive performance were included in the subsequent univariate animal model analyses. The effects included in the model for the analysis of growth traits were sex (2 classes), parity of the dam (5 classes), year-

Table 1 Pedigree structure of the data (after pruning) used in the analysis of growth and reproductive traits

	Trait ^a									
	BW (kg)	WW (kg)	12W (kg)	18W (kg)	24W (kg)	AFC (days)	CI (days)	CI1 (days)	CI2 (days)	CI3 (days)
pedigree structure										
No. animals in pedigree file	2116	8674	2116	2116	2116	8674	8674	8674	8674	8674
No. sires	23	81	21	21	21	45	45	45	41	35
No. dams	349	1010	301	248	264	259	259	259	146	79
No dams with progeny records	349	1010	301	245	260	254	254	254	143	79
Ave. No. offsprings/ dam	2.29	3.46	1.95	2.11	1.93	8.55	8.55	5.43	7.19	8.51

^a BW, birth weight; WW, weaning weight; 12W, 12-month weight; 18W, 18-month weight; 24W, 24-month weight; AFC, age at first calving; CI, pooled calving interval; CI1, calving interval in parity one; CI2, calving interval in parity two; CI3, calving interval in parity three.

Table 2 Number of records in the data, summary statistics and effects fitted in the analysis of growth and reproductive traits

	Trait ^a									
	BW (kg)	WW (kg)	12W (kg)	18W (kg)	24W (kg)	AFC (days)	CI (days)	CI1 (days)	CI2 (days)	CI3 (days)
Data structure										
No. records	1147	4502	888	761	761	2681	2681	1886	1886	1225
Summary statistics										
Mean	27.9	184.6	145.4	178.8	220.9	1187.7	476.9	496.6	460.1	442.6
SD	4.9	41.6	30.2	39.1	43.3	191.5	99.8	134.3	131.4	119.9
CV (%)	17.4	22.5	20.7	21.9	19.6	16.1	20.9	27.1	28.6	27.1
Effects ^b										
Sex	*	*	*	*	*					
Parity	*	*	*	*	*					
Year-season of birth	*	*								
Year-season of weaning			*	*	*					
Herd-year-season of birth		*				*	*	*	*	*
Herd-year-season of calving							*	*	*	*
Age at weighing			*	*	*					
Age at calving							*	*	*	*

^a BW, birth weight; WW, weaning weight; 12W, 12-month weight; 18W, 18-month weight; 24W, 24-month weight; AFC, age at first calving; CI, pooled calving interval; CI1, calving interval in parity one; CI2, calving interval in parity two; CI3, calving interval in parity three.

^b * indicates that the effect was fitted.

season of birth (22 classes), year-season of weaning (22 classes) and age at weighing as a covariable. For BW and WW, year-season of weaning and age at weighing were omitted while for 12W, 18W and 24W, year-season of birth was omitted in the model since they did not significantly influence the traits. For the analysis of reproductive traits, the effects included in the model were herd-year-season of birth (40 classes), herd-year-season of calving (40 classes) and age at calving as a covariable. For AFC, herd-year-season of birth was the only fixed effect while, for CI in each parity, herd-year-season of birth, herd-year-season of calving and age at calving as a covariable were the only effects fitted. Herd-year-season of birth was fitted during the multiple trait analysis of WW and reproductive traits since data from both farms were used. The effects fitted in the analysis of each trait are presented in Table 2.

The years of birth were from 1989 to 2003 while the years of calving were from 1992 to 2003. Each year consisted of two seasons; the wet season which comprised the months of March, April, May, June, September and October and the dry season comprising of January, February, July, August, November and

December. Parity effect was grouped into five classes with any calving recorded in parity five and above being grouped under parity five.

Estimates of (co) variance components and genetic parameters for growth traits were obtained using the ASREML programme (Gilmour et al. 2001) fitting univariate animal models. The following six models were fitted:

$$\text{Model 1} \quad \mathbf{y} = \mathbf{Xb} + \mathbf{Z}_1\mathbf{a} + \mathbf{e} \quad (1)$$

$$\text{Model 2} \quad \mathbf{y} = \mathbf{Xb} + \mathbf{Z}_1\mathbf{a} + \mathbf{Z}_3\mathbf{c} + \mathbf{e} \quad (2)$$

$$\text{Model 3} \quad \mathbf{y} = \mathbf{Xb} + \mathbf{Z}_1\mathbf{a} + \mathbf{Z}_2\mathbf{m} + \mathbf{e} \quad (3)$$

with $\text{cov}(\mathbf{a}, \mathbf{m}) = 0$

$$\text{Model 4} \quad \mathbf{y} = \mathbf{Xb} + \mathbf{Z}_1\mathbf{a} + \mathbf{Z}_2\mathbf{m} + \mathbf{e} \quad (4)$$

with $\text{cov}(\mathbf{a}, \mathbf{m}) = \mathbf{A}\sigma_{am}$

$$\begin{aligned} \text{Model 5 } \mathbf{y} &= \mathbf{X}\mathbf{b} + \mathbf{Z}_1\mathbf{a} + \mathbf{Z}_2\mathbf{m} + \mathbf{Z}_3\mathbf{c} + \mathbf{e} \\ &\text{with } \text{cov}(\mathbf{a}, \mathbf{m}) = 0, \text{var}(\mathbf{c}) = \mathbf{I}_{\text{NC}}\sigma_c^2 \\ &\text{and } \text{var}(\mathbf{e}) = \mathbf{I}_n\sigma_e^2 \end{aligned} \quad (5)$$

$$\begin{aligned} \text{Model 6 } \mathbf{y} &= \mathbf{X}\mathbf{b} + \mathbf{Z}_1\mathbf{a} + \mathbf{Z}_2\mathbf{m} + \mathbf{Z}_3\mathbf{c} + \mathbf{e} \\ &\text{with } \text{cov}(\mathbf{a}, \mathbf{m}) = \mathbf{A}\sigma_{\text{am}}, \\ &\text{var}(\mathbf{c}) = \mathbf{I}_{\text{NC}}\sigma_c^2 \text{ and } \text{var}(\mathbf{e}) = \mathbf{I}_n\sigma_e^2 \end{aligned} \quad (6)$$

where \mathbf{y} is a vector of observations on the specific trait of the animal; \mathbf{b} , \mathbf{a} , \mathbf{m} and \mathbf{c} are vectors of fixed effects including covariables, direct additive genetic effects, maternal additive effects and maternal permanent environmental effects, respectively; \mathbf{X} , \mathbf{Z}_1 , \mathbf{Z}_2 and \mathbf{Z}_3 are corresponding incidence matrices relating the effects to \mathbf{y} ; \mathbf{e} is the vector of residual error. \mathbf{A} is the numerator relationship matrix; \mathbf{I} is the identity matrix. NC is the number of dams, n is the number of animals in the analysis including parents without records, σ_{am} is the direct additive genetic by maternal genetic covariance and σ_c^2 and σ_e^2 are the maternal permanent environmental and residual error variances, 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. Likelihood ratio test were conducted to determine the most suitable model for each growth trait in a univariate analysis. A model was considered suitable when it increased the likelihood significantly on chi-square distribution with degrees of freedom equivalent to the difference between the number of variance components in the competing models.

Analysis of reproductive traits was done using model 1 in which direct additive genetic effect was fitted as the only random effect. Attempts to fit the other models were not successful due to the scope of data available.

Results

From the likelihood ratio tests, the ‘best’ model for BW did not include maternal effects (Model 1). The appropriate models for WW, 12W and 18W and 24W had maternal effects and were Models 6 and 4, respectively. Estimates of variance components and genetic parameters from “best” models for growth traits and from model 1 for reproductive traits are shown in Table 3. The direct heritability estimate for BW was 0.34. For WW and 12W, maternal genetic effects accounted for a higher proportion of total variation than direct additive genetic effects. At 18W and 24W, direct additive genetic effects accounted for a higher

Table 3 Estimates of variance components and genetic parameters^a with their S.E from univariate analyses using the “best” models for growth traits and Model 1 for reproductive traits

Trait ^b	σ_a^2	σ_m^2	σ_c^2	σ_e^2	σ_p^2	h^2	m^2	r_{am}	c^2	h_T^2
BW	7.7			15.2	22.9	0.34±0.05				0.34
WW	64.26	73.6	83.5	324.9	528.6	0.12±0.04	0.14±0.09	-0.25	0.16±0.09	0.14
12W	129.2	224.6	29.4	379.4	664.4	0.19±0.07	0.34±0.15	-0.58	0.04±0.09	0.14
18W	82.0	38.3	104.8	872.7	1090.0	0.08±0.08	0.04±0.10	-0.14	0.10±0.09	0.08
24W	207.3	158.7		1162.9	1434.0	0.14±0.05	0.11±0.13	-0.52		0.10
AFC	1264.3			29847.2	31110.0	0.04±0.06				0.04
CI	26.1			8930.2	8956.0	0.00±0.04				0.00
CI1	0.0			15538.5	15540.0	0.00±0.05				0.00
CI2	2391.8			13066.7	15460.0	0.15±0.09				0.15
CI3	0.0			12213.9	12210.0	0.00±0.10				0.00

^a σ_a^2 , additive genetic variance; σ_m^2 , maternal genetic variance; σ_c^2 , maternal permanent environmental variance; σ_e^2 , residual error variance; σ_p^2 , phenotypic variance; h^2 , direct heritability; m^2 , maternal heritability; r_{am} , direct- maternal genetic correlation; c^2 , maternal environmental variance as a proportion of phenotypic variance; h_T^2 , total heritability.

^b BW, birth weight; WW, weaning weight; 12W, 12-month weight; 18W, 18-month weight; 24W, 24-month weight; AFC, age at first calving; CI, pooled calving interval; CI1, first calving interval; CI2, second calving interval CI3, third calving interval.

proportion of total variance than maternal genetic effects. Maternal genetic effects were lowest at 18W.

Maternal environmental effects were most evident at weaning (0.16). There was a decline in the magnitude of the estimates of maternal permanent environmental variance as a proportion of total variance with age. Direct-maternal genetic correlations were negative for all growth traits analysed using models that allowed for a direct-maternal genetic covariance (models 4 and 6). The estimates ranged from -0.14 for 18W to -0.58 for 12W. Estimates of total heritability (h_T^2) were highest (0.14) for WW and 12W among traits analysed by models with maternal effects.

Additive genetic effects accounted for a very small proportion of total variation in reproductive traits. Estimates of the residual error variance were high. This resulted in very low heritability estimates for the reproductive traits that ranged from 0.00 for CI to 0.15 for CI2. Notable was the difference in variance component estimates between CI and its constituents CI1, CI2 and CI3, which arises from the highly variable data sizes in the constituent traits.

Discussion

The results indicate that BW in Kenya Boran cattle is influenced by direct additive genetic effect alone and maternal effects did not account for any variation in BW (Table 3). Maternal effects at birth are generally as a result of the prenatal maternal environment and cytoplasmic effect (Maniatis and Pollott 2002b). The lack of maternal influence on BW could be an indicator that the Kenya Boran dams exhibit little variability in the uterine environment provided for their offsprings during embryonic development to cause pronounced maternal effects at birth.

At weaning, maternal effects were more pronounced. Maternal permanent environmental effects was higher than direct and maternal genetic effects indicating that obtaining robust calves at weaning is highly dependent on the post natal environment provided by the dam. The ability of the Kenya Boran dams to provide a good pre-weaning environment for their calves has been alluded to in other studies (Rege et al. 2001). The estimate of direct heritability for WW (0.12) from from this study was lower than estimates of 0.24 and 0.25 reported by Haile-Mariam and Kassa-Mersha (1995), and Maiwashe et al.

(2002) for Boran and South African Bonsmara cattle, respectively.

The negative direct-maternal genetic correlation (-0.25) estimated for WW indicates an antagonistic relationship between these components for this trait. This has an implication on selection response such that selection for growth performance would be less effective if direct additive genetic effects alone are considered. The estimate was similar to average genetic correlation (-0.25) reported in a review by Koots et al. (1994) from nine studies on beef cattle. Different estimates have been reported for this parameter ranging from highly negative estimates (-0.54) (Maiwashe et al. 2002) to positive estimates (0.10) (Demeke et al. 2003). The differences between estimates may be attributed to the differing levels of genetic variation between populations. Omitting the direct-maternal genetic covariance in analyses where maternal effects are important therefore would result in an upward bias in estimates of direct and maternal heritability (Bijma 2006).

The low direct heritability for 12W (0.19) could be due to the stressful environment under which the animals were kept since environmental stress highly affects the magnitude of additive genetic variance for different traits (Demeke et al. 2003). Maternal genetic effects were more evident at 12W than any other age. The higher maternal additive effects from WW to 12W could be due to effects of post weaning stress, which suppressed direct additive genetic growth potential of the calf. Maternal environmental effects were most evident until weaning and calves from dams with a good maternal ability tended to pick up much better to 12W. In sheep, studies have found evidence of post weaning body weights with significant carryover maternal effects (Maniatis 2000).

The negative direct-maternal genetic correlation (-0.58) for 12W indicate that daughters of the Kenya Boran dams with high maternal ability would tend to provide an inferior maternal environment to their offspring. Similarly, negative estimates were reported by Haile-Mariam and Kassa-Mersha (1995) and Norris et al. (2004) in the Boran cattle in Ethiopia and Nguni cattle in South Africa, respectively.

The estimate of direct heritability for 18W (0.08) was low. The data available for this trait was limited (Table 2) resulting in high residual error variance estimates. On the ranches studied, 18W was not keenly monitored since selection of animals was mainly at weaning and

at 24 months when the animals were to be introduced to the breeding herds. Variance due to maternal effects was greater than additive genetic variance with maternal environmental variance accounting for the greatest proportion of phenotypic variance. Results from other studies on tropical beef cattle have reported negligible maternal effects at 18W (Haile-Mariam and Kassa-Mersha 1995; Demeke et al. 2003)

The direct heritability estimate for 24W was higher than the corresponding maternal heritability indicating waning of maternal influence on growth performance at 2 years. The value for direct heritability was lower than the mean of 0.44 reported by Lôbo et al. (2000) from fifteen studies on beef cattle.

Direct-maternal genetic correlation at 24W was high and negative (−0.52). There are two main causes of highly negative estimates of direct-maternal genetic correlation. Either due to existence of true genetic antagonism between the components or overestimation of the parameters arising from small datasets and of poor structure (Wasike et al. 2006). Given the data size considered in this study, highly negative estimate of direct-maternal genetic correlation could be attributed more to the data characteristics than true genetic antagonism. Higher estimates have however been reported elsewhere in literature on tropical beef cattle (Burrow 2001). Maniatis and Pollott (2003) observed inflated estimates of direct-maternal genetic correlation in their analyses of sheep data due to inability to disentangle the interdependence between the two genetic components.

The heritability estimates for reproductive traits were low. The very low estimates of heritability obtained in this study could be attributable to the high phenotypic variance arising from large environmental variation. This therefore implies that much of the improvement in reproductive traits could be attained by improvement of production environment rather than selection, as suggested by other authors (van der Westhuizen et al. 2001). In a review on genetic parameters for beef cattle in the tropics, average heritability estimates for AFC and CI of 0.31 and 0.11, respectively, were reported (Lôbo et al. 2000).

Conclusions

This study has shown that genetic progress is possible for all growth traits. Apart from BW, maternal effects

influenced the performance of the other growth traits. These effects should therefore be accounted for in genetic analyses of growth traits, by fitting it as either a genetic or a permanent environmental effect or both. Given the low heritability estimates obtained, effective improvement in reproductive performance of Kenya Boran cattle could be achieved by improving the production conditions. This however should not be construed to mean that genetic selection is not important. The estimates of variance components and genetic parameters presented in this study are important as initial estimates, but would later be updated as more data are collected and analysed once the breeding programme is in place.

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