

# Genetic evaluation of growth of Kenya Boran cattle using random regression models

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**Abstract** Data consisting of 18 884 weight records collected from 1273 Boran cattle from birth to 24 months of age were used to estimate covariance functions and genetic parameters for growth of Boran cattle using random regression (RR) models under a situation of small herd size and inconsistent recording. The RR model fitted quadratic Legendre polynomials of age at recording for additive genetic and permanent environmental effects. Genetic variance increased from birth, reaching an asymptotic value at

455 days and was maximum at 525 days of age after which it gradually dropped. Permanent environmental variance increased throughout the trajectory. Estimates of temporary environmental variance were heterogeneous across ages. Direct heritability and permanent environmental variance as a proportion of phenotypic variance fluctuated greatly during the early ages but later stabilized at intermediate to later ages; the estimates ranged from 0.11 to 0.33 and from 0.18 to 0.83, respectively. Genetic correlation estimates were positive, ranging from 0.10 to unity. The estimates declined with increasing in lag between the age points. Phenotypic correlation pattern was erratic between early ages, negatively low ( $-0.02$ ) between the extreme data points and moderate to highly positive ( $>0.50$ ) between intermediate and later points, with prominent spikes along the diagonal. It is concluded that RR models have potential for modelling growth of Boran cattle, notwithstanding conditions of small herd sizes and inconsistent recording.

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Parameter estimates

## Abbreviations

ASAL arid and semi-arid lands  
CF covariance function  
EBV estimated breeding value  
RR random regression  
SRM simple repeatability model

## Introduction

Kenya Boran cattle constitute the highest proportion of the single-breed population of cattle raised primarily for beef production in large-scale commercial beef production systems (commercial ranches) in the arid and semi-arid lands (ASAL) of Kenya. The breed is popular because of its high beef output and reproductive performance compared with other indigenous breeds and high adaptive performance compared with exotic beef breeds (Okeyo *et al.*, 1998; Indetie *et al.*, 2000a,b).

Inconsistent recording of small selected groups from the larger herds and overlapping age categories when weights are recorded characterize growth performance recording in the tropical commercial beef production systems. For instance, some ranches in Kenya wean Boran calves on average at 9 months while others wean at 7 months (Wasike *et al.*, 2007). In Ethiopia, the average weaning age of Boran calves is 8 months (Haile-Mariam and Kassa-Mersha, 1995). After weaning, animals tend to be selected on the basis of their body condition determined by visual appraisal rather than actual weight. Genetic evaluation and performance comparison between animals in similar production environments is thus difficult and selection to improve growth performance is based on individual animals' phenotype.

Growth in Boran cattle has been described using univariate and multivariate models, in which each individual weight measured at a particular age was considered a different trait assuming constant variances between ages (Haile-Mariam and Kassa-Mersha, 1995; Demeke *et al.*, 2003; Wasike *et al.*, 2007). In these analyses, the ages describing the traits were predefined to certain landmarks, e.g. weaning weight (270 days), yearling weight (360 days) and final weight (600 days), which vary between farms depending on management objectives. Because the ages at actual weighing rarely fit the defined trait, adjustment of the weights is made to the closest landmarks and weights that fall well off the landmark ages are discarded (Nobre *et al.*, 2003b). Consequently, there is loss of information following elimination of some animals in the evaluation and a reduction in accuracy of estimates due to pre-adjustments (Jamrozik *et al.*, 2000; Tier and Meyer, 2004).

Growth of animals to maturity follows a prescribed trajectory and performance is measured by repeatedly

recording weight as the animal grows, which constitutes longitudinal data. Random regression (RR) models based on covariance function methodology are used in evaluation of longitudinal data (Albuquerque and Meyer, 2001; Meyer, 2001a; Fischer *et al.*, 2004b). This is because the model provides an efficient method of evaluating traits that change with time owing to their ability to account for the temporal variation in addition to allowing for data interpolation and efficiency of data utilization (Kirkpatrick and Heckman, 1989). The models present a flexible means of estimating (co)variances between the ages without adjustment of the ages, thereby minimizing the errors due to approximations, and provide estimates for the particular ages when the measurements were taken (Fischer *et al.*, 2004a,b; Meyer, 2004).

Despite their versatility, RR models have not been used to a great extent in genetic evaluation of growth performance in tropical beef cattle. The models have been used in evaluation of growth in breeds such as Nellore and Bonsmara (Albuquerque and Meyer, 2001; Nobre *et al.*, 2003a,b; Nephawe, 2004; Albuquerque and Meyer, 2005). No attempts have been made to evaluate growth in Boran cattle using RR models; this is partly due to small sizes of recorded herds and inconsistent performance recording in beef ranches in the ASAL of Kenya. The objective of this paper was to estimate covariance functions and genetic parameters for growth in Boran cattle in a small herd using RR models and to examine the applicability of the estimates in selection for growth in the large-scale commercial ranches.

## Material and methods

### Data source

Data on growth performance of Kenya Boran cattle were made available by a national beef research station located in Nakuru district approximately 150 km north-west of Nairobi, Kenya. This farm maintains both research and stud herds of Boran cattle registered with the Kenya Studbook and is a member of the Kenya Boran Cattle Breeders' Society. The animals are raised under production conditions and practices typical in large-scale commercial beef production systems in the ASAL, thus presenting a good stereotype to describe the commercial ranching

conditions. The station is located at the interface of Agro Ecological Zones (AEZ) 3 and 4 and receives an average annual rainfall of 800 mm. The animals are reared in AEZ 4, since this is where all the grazing fields are located. The hottest and driest months are January and February.

A detailed description of the farm and management of the animals has been presented by Wasike and colleagues (2007). Briefly, the animals are kept on natural pasture with sporadic mineral supplementation under a 12 h grazing regime. Pasture availability is seasonal and depends on availability of rainfall. Calves are born all year round and the cow–calf system of calf rearing is practised. Weaning is done at 7 months of age and weaners are kept on pastures separate from the older stock up to the age of 18–24 months, when they are dispersed into various herds. The selected heifers are introduced to the breeding herds at the age of 20–24 months. Bulls selected for breeding are used from the age of 36 months. Heifers not selected for replacement of stud cows form a research herd, while bulls not selected for breeding are sold off.

## Data

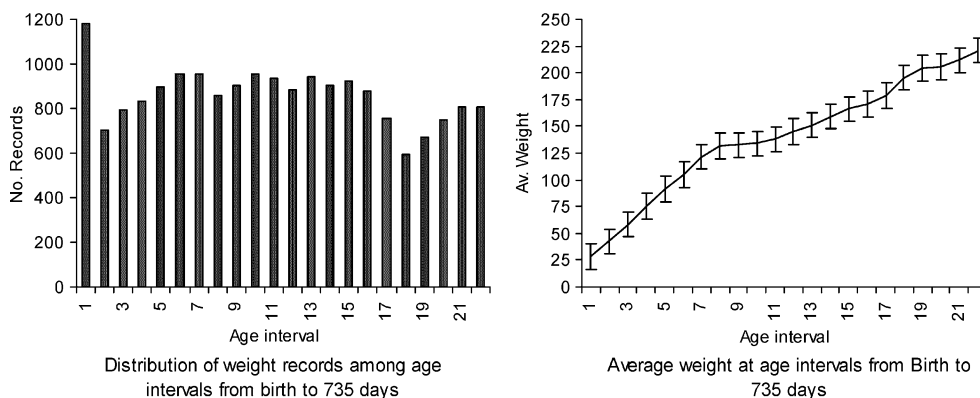
Data consisted of weights recorded once a month from birth to 24 months of age for Kenya Boran cattle born between 1989 and 2003. Dates of weighing within a month were highly variable, resulting in very high variability in ages (in days) at weighing. To carry out the analyses, weights were clustered in age-classes of 0–2 days (birth weight), 3–35 days, 36–70 days, 71–105 days, ..., 701–735 days to cover the first 24-month growth trajectory from birth. There were 22

age classes in total. All the data were checked for consistency of pedigree information and correct dates of birth and weighing. Records with anomalies in pedigree information and dates were discarded. An animal was required to have one record per age class such that if the animal had all the weight records the total number of observations would be 22 weight records. Only animals that had at least three weight records within their first 24 months of life were retained for analyses. The highest number of records per animal in the data was 21. From an initial 20 210 weight records the final data set for analysis after editing comprised 18 884 records from 1273 animals. The distributions of weight records among age points and average weights at various age intervals with their standard errors are presented in Fig. 1.

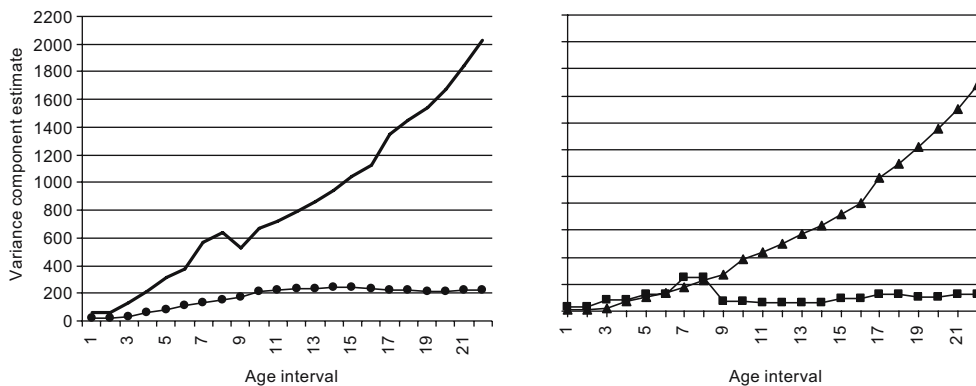
## Analyses

Preliminary fixed-effect analyses were carried out using GENSTAT (2003) to determine the factors that significantly influence growth. Effects of sex, parity of the dam, and the year/month of weighing influenced growth significantly. These effects constituted the fixed-effects model that was used to determine the best order of polynomial fit for the fixed regression to model the mean population curve. An orthogonal (Legendre) polynomial of age at recording (in days) of order four was the highest significant order of fit and was therefore used in the fixed part of the model. All the effects were fitted as polynomial functions of age.

A random regression model fitting animal genetic and permanent environmental effects as the only random effects was used in genetic evaluation of



**Fig. 1** Distribution of weight records among age intervals and of average weights at various age points from birth to 735 days

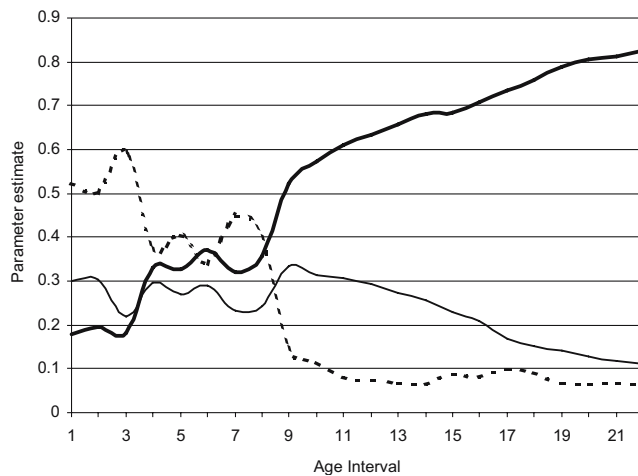


**Fig. 2** Estimates of direct genetic (●), phenotypic (—), permanent environmental (▲) and temporary environmental (■) variances

growth. Analyses fitting different orders of polynomial fit for the random effects were carried out in order to determine the most parsimonious model to describe the data. A third-order orthogonal (Legendre) polynomial of age at recording (in days) best described the covariance between the RR coefficients in the model. All the available pedigree information was used in the building of the relationship matrix (**A**) for evaluation of the additive genetic effects. The covariances between the coefficients were estimated using DFREML program (Meyer, 2000a). The general model used was as follows:

$$y_{ijk} = f_{ijk} + \sum_{m=0}^k \beta_m \Phi_m(a^*_{ijk}) + \sum_{m=0}^{k_{a-1}} \alpha_{im} \Phi_m(a^*_{ijk}) + \sum_{m=0}^{k_{c-1}} \gamma_{im} \Phi_m(a^*_{ijk}) + \varepsilon_{ijk} \quad (1)$$

**Fig. 3** Estimates of direct heritability (—) and permanent environmental variance as a proportion of phenotypic variance (—) and temporary environmental variance as a proportion of phenotypic variance (---)



where  $y_{ijk}$  denotes  $i$ th record for animal  $j$  at age  $k$ ;  $f_{ijk}$  is a set of fixed effects including the covariable age at weighing;  $a^*_{ijk}$  is the standardized age  $k$  ( $-1$  to  $+1$ ) at recording;  $(\Phi_m(a^*_{ijk}))$  is the  $m$ th Legendre polynomial of age;  $\beta_m$  are the fixed regression coefficients to model the population mean;  $\alpha_{im}$  and  $\gamma_{im}$  are the  $i$ mth-order RR coefficients for the direct additive genetic and direct permanent environmental effects, respectively;  $k_{a-1}$  and  $k_{c-1}$  are the corresponding order of fit for each effect; and  $\varepsilon_{ijk}$  is the random residual effect, which was considered independently distributed with heteroscedastic error variance. For the standardized age, the  $m$ th polynomial was given by:

$$\Phi_m(a^*_{ijk}) = \frac{1}{2^m} \sqrt{\frac{2m+1}{2}} \times \sum_{r=0}^{m/2} (-1)^r \binom{m}{r} \binom{2m-2r}{m} (a^*_{ijk})^{m-2r} \quad (2)$$

**Table 1** Estimates of variance components and genetic parameters for growth from a simple repeatability model

Trait	Parameter <sup>a</sup>					
	$\sigma_a^2$	$\sigma_{pe}^2$	$\sigma_e^2$	$\sigma_p^2$	$h^2 \pm SE$	$c^2 \pm SE$
Body weight	240.46	240.42	369.64	850.52	0.28±0.037	0.28±0.30

<sup>a</sup> $\sigma_a^2$ =additive genetic variance,  $\sigma_{pe}^2$ =permanent environmental variance,  $\sigma_e^2$ =temporary environmental variance,  $\sigma_p^2$ =phenotypic variance,  $h^2$ =heritability;  $c^2$ =permanent environmental variance as a proportion of phenotypic variance.

where  $r$  is an index number needed to determine the  $m$ th polynomial.

Parameters estimated in RR analysis were the  $\mathbf{K}$  matrices containing variances and covariances between the RR coefficients. The covariance function for the random effects were obtained by pre- and post-multiplying  $\mathbf{K}$  by a matrix containing orthogonal polynomials ( $\Phi$ ) pertaining to a set of specific ages directly from the data by REML. This resulted in estimated matrix for the random effect for the specific ages defined by  $\Phi$ . For the direct additive genetic effect, the matrix notation of the equation to estimate variance components was

$$\mathbf{G}_0 = \Phi \mathbf{K} \Phi' \quad (3)$$

and applied to direct permanent environmental effect as well. Random regression coefficients pertaining to different random effects were assumed uncorrelated throughout.

Analysis of growth was also done considering growth as a repeated measure using a simple repeatability model (SRM). The model used to describe variables was of the form:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Za} + \mathbf{Wpe} + \mathbf{e} \quad (4)$$

where  $\mathbf{y}$  is a vector of observations;  $\mathbf{b}$ ,  $\mathbf{a}$  and  $\mathbf{pe}$  are vectors of fixed, additive genetic and permanent environmental effects, respectively;  $\mathbf{e}$  is a vector of temporary environmental effects; and  $\mathbf{X}$ ,  $\mathbf{Z}$  and  $\mathbf{W}$  are incidence matrices relating observations to fixed, additive genetic and permanent environmental effects, respectively.

## Results

### Variance component estimates

Estimates of additive genetic, permanent environmental, temporary environmental and phenotypic variance obtained using RR model are presented in Fig. 2. Additive genetic variance gradually increased from birth through age interval 15 (490 days) when it reached maximum then slightly decreased to the end of the trajectory. Permanent environmental variance was high and increased with age throughout the growth period. Temporary environmental variance on the other hand was low at birth, gradually increased with age up to age interval 8 (245 days) after which it decreased until interval 9 (280 days) and remained low to the end of the trajectory. Phenotypic variance

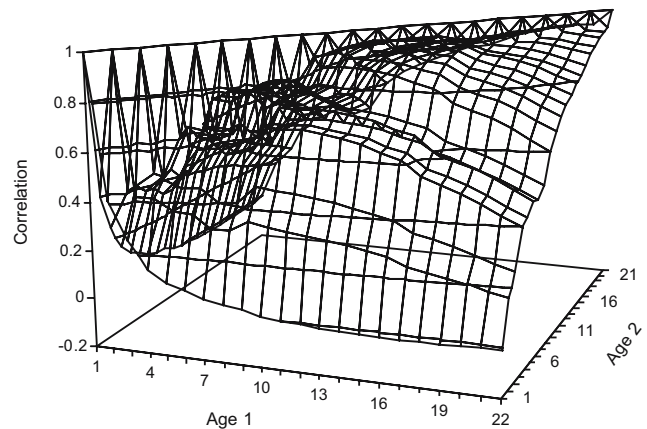
**Table 2** Estimates of variances (diagonal), covariances (below diagonal) and correlations (above diagonal) between RR coefficients and eigenvalues ( $\lambda$ ) of the coefficient matrix when order of fit ( $k$ )=3

Effect	0	1	2	$\lambda$
<i>Additive genetic</i>	277.44	0.70	-0.71	309.18
	70.63	36.46	-0.15	26.62
	-60.50	-4.66	25.96	4.06
<i>Permanent environmental</i>	797.93	0.92	-0.16	1 049.16
	437.60	286.48	0.22	58.75
	-22.82	18.92	25.90	2.40

**Table 3** Additive genetic correlation (below diagonal) and permanent environmental correlation (above diagonal) between weights taken at various age points from birth to 735 days

Age interval	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	
1	1.00	0.78	0.47	0.16	0.08	0.03	-0.01	-0.03	-0.06	-0.09	-0.10	-0.11	-0.11	-0.12	-0.12	-0.13	-0.13	-0.13	-0.13	-0.13	-0.13	-0.13	-0.13
2	0.88	1.00	0.92	0.73	0.68	0.64	0.61	0.58	0.56	0.51	0.49	0.47	0.46	0.44	0.42	0.40	0.35	0.33	0.31	0.29	0.26	0.24	0.24
3	0.67	0.94	1.00	0.95	0.92	0.89	0.87	0.85	0.83	0.80	0.78	0.76	0.73	0.71	0.69	0.66	0.60	0.57	0.54	0.51	0.48	0.44	0.44
4	0.37	0.76	0.94	1.00	1.00	1.00	0.98	0.97	0.96	0.94	0.92	0.91	0.89	0.87	0.84	0.82	0.76	0.73	0.70	0.66	0.63	0.59	0.59
5	0.29	0.70	0.91	1.00	1.00	1.00	0.99	0.99	0.98	0.96	0.95	0.93	0.91	0.90	0.87	0.85	0.80	0.76	0.73	0.70	0.67	0.63	0.63
6	0.23	0.66	0.88	0.99	1.00	1.00	1.00	1.00	0.99	0.97	0.96	0.95	0.93	0.92	0.90	0.87	0.82	0.79	0.76	0.73	0.70	0.66	0.66
7	0.19	0.63	0.86	0.98	0.99	1.00	1.00	1.00	1.00	0.98	0.98	0.96	0.95	0.93	0.92	0.90	0.85	0.82	0.79	0.76	0.73	0.70	0.69
8	0.16	0.60	0.84	0.97	0.99	1.00	1.00	1.00	1.00	0.99	0.98	0.98	0.96	0.95	0.93	0.91	0.87	0.84	0.82	0.79	0.76	0.73	0.72
9	0.12	0.58	0.83	0.97	0.99	0.99	1.00	1.00	1.00	1.00	0.99	0.98	0.97	0.96	0.95	0.93	0.89	0.87	0.84	0.81	0.78	0.75	0.75
10	0.11	0.56	0.81	0.96	0.98	0.99	0.99	1.00	1.00	1.00	1.00	1.00	0.99	0.98	0.97	0.96	0.93	0.91	0.88	0.86	0.83	0.81	0.81
11	0.11	0.55	0.80	0.95	0.97	0.98	0.99	0.99	1.00	1.00	1.00	1.00	1.00	0.99	0.98	0.97	0.94	0.92	0.90	0.88	0.86	0.83	0.83
12	0.10	0.54	0.79	0.94	0.96	0.98	0.98	0.99	0.99	1.00	1.00	1.00	1.00	1.00	0.99	0.98	0.96	0.94	0.92	0.90	0.88	0.86	0.86
13	0.10	0.53	0.78	0.93	0.96	0.97	0.98	0.98	0.99	0.99	1.00	1.00	1.00	1.00	1.00	0.99	0.97	0.96	0.94	0.92	0.90	0.88	0.88
14	0.10	0.53	0.77	0.92	0.94	0.96	0.97	0.97	0.98	0.99	0.99	1.00	1.00	1.00	1.00	1.00	0.98	0.97	0.96	0.94	0.92	0.90	0.88
15	0.10	0.52	0.76	0.91	0.93	0.94	0.95	0.96	0.97	0.98	0.99	0.99	1.00	1.00	1.00	1.00	0.99	0.98	0.97	0.96	0.94	0.92	0.90
16	0.11	0.52	0.75	0.89	0.91	0.93	0.94	0.95	0.95	0.97	0.98	0.98	0.99	0.99	1.00	1.00	1.00	0.99	0.98	0.97	0.96	0.94	0.92
17	0.13	0.50	0.71	0.84	0.86	0.87	0.88	0.89	0.90	0.92	0.93	0.95	0.96	0.97	0.98	0.99	1.00	1.00	1.00	1.00	0.99	0.98	0.97
18	0.14	0.49	0.68	0.79	0.81	0.83	0.84	0.85	0.86	0.89	0.90	0.91	0.93	0.94	0.96	0.97	1.00	1.00	1.00	1.00	1.00	0.99	0.98
19	0.16	0.47	0.64	0.74	0.76	0.77	0.78	0.79	0.81	0.84	0.85	0.87	0.89	0.91	0.93	0.95	0.98	1.00	1.00	1.00	1.00	1.00	0.99
20	0.18	0.45	0.59	0.67	0.69	0.70	0.71	0.73	0.74	0.77	0.79	0.81	0.83	0.86	0.88	0.92	0.96	0.98	1.00	1.00	1.00	1.00	1.00
21	0.19	0.42	0.53	0.59	0.60	0.61	0.63	0.64	0.65	0.69	0.71	0.73	0.76	0.79	0.82	0.85	0.92	0.95	0.98	0.99	1.00	1.00	1.00
22	0.21	0.38	0.46	0.50	0.50	0.51	0.52	0.54	0.55	0.59	0.61	0.64	0.67	0.70	0.74	0.77	0.86	0.90	0.94	0.97	0.99	1.00	1.00

**Fig. 4** Phenotypic correlations between weights at various age points along the trajectory



increased through out the trajectory. There was, however, a drop in variance estimates at age interval 9 after which it increased again.

Estimates of variance components from the SRM are presented in Table 2. Unlike in RR analysis where variance components varied with age, a constant variance between weights at all points was assumed in SRM. As a result, single estimates of variance components for the whole growth curve were obtained.

#### Proportions of phenotypic variance

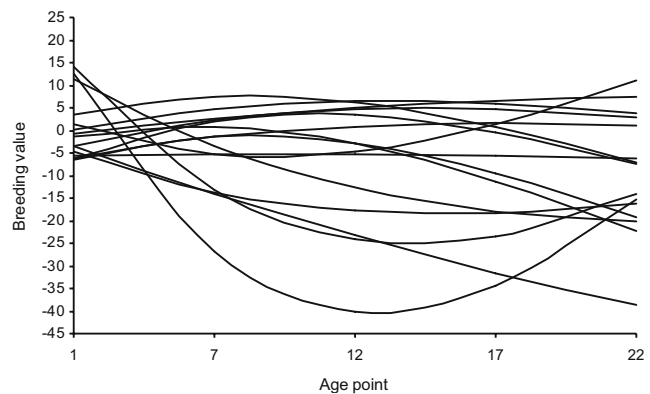
Estimates of direct heritability and permanent environmental variance as a proportion of phenotypic variance from RR analysis are presented in Fig. 3. Direct heritability estimate was 0.30 at birth, fluctuated, but on a declining trend, to 0.23 at age interval 7

(210 days), after which it increased slightly to 0.33 at interval 9 (280 days) then decreased monotonically to 0.11 at age interval 22 (735days). Permanent environmental effect as a proportion of phenotypic variance was low from birth to age interval 3 (70 days) (<0.2), increased to 0.33 at interval 4 where it remained constant to interval 7, after which it increased throughout to 0.83 at age interval 22 (735 days). Estimates of heritability and permanent environmental variance as a proportion of phenotypic variance from SRM are presented in Table 1. These estimates, though equal, had different standard errors ( $0.28 \pm 0.037$  and  $0.28 \pm 0.30$ , respectively).

#### Covariance functions

Estimates of covariance function (CF) for additive genetic and permanent environmental effects and their

**Fig. 5** Estimated breeding values for 15 sires with more than 20 progeny each



corresponding correlations and eigenvalues are presented in Table 2. The variance of RR coefficients were highest at  $k=0$  (constant) and lowest at  $k=2$  (quadratic). Estimates of permanent environmental variance were higher than additive genetic variance for both the intercept and linear coefficients. For both effects, correlation estimates between the intercept and linear coefficient were positive and high. The corresponding correlations between the intercept and the quadratic coefficients were negative and high for additive genetic effects, and low for permanent environmental effects. The first eigenvalues of the coefficient matrices explained 91% and 94.5% of the total additive genetic and permanent environmental variance, respectively. The second eigenvalues accounted for 7.8% and 5.3% of the total variation in the two random effects, while the third eigenvalues explained 1.2% and 0.20% of the variation, respectively.

#### Additive genetic, permanent environmental and phenotypic correlations

Estimates of additive genetic correlations between the ages are presented in Table 3. Correlations between adjacent ages exhibited an increasing pattern as the animals aged. The estimates ranged from 0.10 between birth and later age points to unity (1.00) between adjacent older ages. Estimates of correlations between weight measures were high ( $>0.50$ ) from age interval 4 (71 days) onwards. There was a decrease in estimates as the lag between the age points increased.

Estimates of permanent environmental correlation between the ages are presented in Table 3. The correlation between age interval 1 (birth weight) and other ages was peculiar in that small and negative estimates were observed between weights at this age and weights at age interval 7 (176 days) to age interval 22 (735 days). Permanent environmental correlation between weights at other ages followed a similar pattern as the additive genetic correlations. The correlation ranged from  $-0.13$  between age intervals 1 (birth) and intervals 16–22, to unity (1.00) between several adjacent intermediate and older ages.

Phenotypic correlation between weights at different ages (Fig. 4) followed a similar pattern as permanent environmental correlations. Phenotypic

correlation estimates were low between birth weight and other weights. The estimates ranged from  $-0.018$  between weight at birth and weight at interval 19 (630 days) to 0.93 between weight at interval 21 (666 days) and interval 22 (735 days). Correlation estimates between weights at younger ages were lower than estimates between weights at older ages. Prominent among the phenotypic correlations were the spikes along the diagonal of the correlation graph that were more prominent at early ages than later ages (Fig. 4).

#### Estimates of breeding values

Breeding value estimates for 15 sires with more than 20 progeny each are presented in Fig. 5. Estimated breeding values (EBVs) for sires varied significantly across age points and between sires. This implies that little selection has been carried out on these animals for growth from birth to 2 years.

## Discussion

#### Variance components

Estimates of variance components for the range of ages presented in Fig. 2 show varying patterns between and within the components. The increase in additive genetic variance from birth to an asymptotic value between age intervals 10 (281 days) and 14 (455 days) implies that response to selection would be greatest if selection were based on weight taken at the asymptotic age rather than other growth points. A similar pattern was reported on growth of Nelore cattle (Albuquerque and Meyer, 2001). Boran cattle are raised in the ASAL environment with no feed supplementation. Low permanent environmental variances during early stages of growth were a result of the good mothering ability of the Boran dams, which buffered the calves against the harsh environmental conditions, thus producing more uniform pre-weaning growth. After weaning (age interval 8), the spiralling permanent environmental variance throughout the growth curve was due to the post-weaning stress that the animals underwent, particularly during the first two months after weaning. This persisted because of the dependence of later weights on early weights.



This implies that nutritional intervention at these two months post-weaning would greatly reduce permanent environmental variance at later ages. The continuous increase in the permanent environmental variance throughout the trajectory and an increase in the gradient at later age points were also reported in growth of Angus cattle (Meyer, 2005a).

Most of the additive genetic variance estimates from RR analysis were lower than those from the SRM apart from the highest estimate obtained at age interval 14 (455 days), which was equivalent to the SRM estimate. On the other hand, permanent environmental variance estimates from RR model were higher than those from SRM. The higher estimates could be attributed to increase in accuracy due to higher precision in partitioning of the component sources of variation.

Estimates of temporary environmental variance, though low, varied with age. This indicates that the assumption of homogenous variance adopted in the univariate repeatability model would result in bias in genetic evaluation, particularly of younger animals (Nephawe, 2004). The estimates were generally lower than those from SRM, which further depicts enhanced accuracy of estimation when RR models are used. The estimates reported in this study were lower than those reported by Nobre and colleagues (2003a); however, the pattern of variation was similar to that reported on Nelore cattle (Albuquerque and Meyer, 2001).

Phenotypic variance increased throughout the growth trajectory. This was due to the additive effect of the ever-increasing permanent environmental variance attributable to the production environmental conditions that animals had to endure. A similar pattern was observed in the analysis of phenotypic variation of monthly weights of Australian beef cattle (Meyer, 1999).

Parameter estimates from RR models are highly influenced by order of polynomial fit. Owing to this, estimates of additive genetic variance from this study differed from reports on Bonsmara cattle (Nephawe, 2004), while phenotypic variance estimates in Australian beef cattle (Meyer, 2000b) fluctuated more than in the present study owing to the high orders of polynomial fitting that were used by the two authors, resulting in increased flexibility of the polynomial function that led to wiggly estimates.

## Variance proportions

The relatively lower estimates of heritability and permanent environmental variance as a proportion of phenotypic variance (Fig. 3) during early developmental stages (from birth to age interval 7) could be attributed to the fairly uniform environment that the Boran dams provided for their calves, as a result of which a more uniform growth was achieved and much of the phenotypic variation was due to the measurement error variances. Withdrawal of maternal environment at weaning implies the animal has to depend on its inherent growth potential (direct additive genetic effect). However, owing to the strenuous production environment, the additive growth potential was undermined, resulting in reliance of the animals on maternal growth potential conferred earlier in growth for growth later in life. This explains the continuous increase in permanent environmental effects throughout the growth curve. The higher heritability estimates than permanent environmental variance as a proportion of phenotypic variance from birth to age interval 3 (70 days) indicates that this phase of growth is under additive genetic influence; this is subdued, however, by the environmental influence arising mainly from the maternal effects (suckling) thereafter. High heritability between age intervals 8 (211 days) and 11 (350 days) was of interest for selection purposes. At these age intervals, high rate of response would be achieved if selection were carried out given the high heritability estimates and relatively low proportions of environmental influence than at later ages. Heritability estimates reported here are within the range of estimates reported by Wasike and colleagues (2007) using multivariate model on a larger data set. However, the present study reports lower estimates of heritability than those reported elsewhere in beef cattle (Albuquerque and Meyer, 2001; Arango *et al.*, 2004; Meyer, 2005a).

A negative but complementary relationship between genetic and permanent environmental variance was evident as these effects tended to balance each other. Opposite patterns were reported in a study to evaluate growth performance in beef cattle in the United States (Arango *et al.*, 2004). The opposite pattern observed in the present study was due to the persistently increasing permanent environmental

variance emanating from high environmental influence on performance of Boran cattle compared to the US beef cattle, in which environmental influence on their performance is greatly controlled and thus the animal's inherent growth potential is expressed to a larger extent.

Orthogonal polynomials have been reported to have poor mathematic properties for modelling growth at extreme data points on the trajectory, which influence parameter estimates at these points. Fluctuations in estimates of heritability and permanent environmental variance as a proportion of phenotypic variance during the early ages could be attributed to these deficiencies. Arango and colleagues (2004) made similar observations in evaluation of growth of beef cattle. Meyer (2001b), Albuquerque and Meyer (2005) and Meyer and Kirkpatrick (2005) recommended the use of parametric methods to overcome this limitation of the orthogonal polynomial functions. Cubic splines gave better estimates than orthogonal polynomials at the extreme ages in evaluation of growth in pigs and Australian Angus cattle (Huisman *et al.*, 2002; Meyer, 2005b).

Estimates of heritability and permanent environmental variance as a proportion of phenotypic variance from SRM fell within the range of RR estimates. The heritability estimates depict growth as a low to moderately heritable trait. On the other hand, estimates of repeatability indicate low reliability of weights at early ages as predictors of weights at older ages. However, weights from intermediate ages upwards could be reliable predictors of one another. As a result, positive response to selection at later ages could be achieved if selection were based on intermediate ages.

#### Covariance functions

The covariance and correlation structure between RR coefficients observed in this study indicates strong relationship between the intercept and the linear and quadratic coefficients. This study found higher covariances and correlations between the RR coefficients for the permanent environmental effects than for additive genetic effects. This was due to the high environmental influence on growth performance of the animals in the ASAL. This contrasted with other results on beef cattle raised under fairly favourable production environments (Arango *et al.*, 2004; Albuquerque

and Meyer, 2005; Meyer, 2005a). Eigenvalues and corresponding eigenfunctions determine the rate of change in the mean growth trajectory due to selection (Kirkpatrick *et al.*, 1990; Lewis and Brotherstone, 2002). The high estimate of the leading eigenvalue of the additive genetic coefficient matrix in this study (Table 2) indicates that selection on the basis of the corresponding eigenfunction would result in a rapid response. On the other hand, response to selection associated with the second and third eigenvalues would be slow as each accounts for very little additive genetic variation. This was also observed in studies evaluating growth of beef cattle in the tropics (Albuquerque and Meyer, 2001; Meyer, 2001a, 2005a). A similar explanation would be applicable to the eigenvalues and functions associated with the permanent environmental effects in the context of effect of environmental changes and corresponding response in growth performance. Plots of eigenfunctions (not presented) had a negative slope. A straight line parallel to the age axis indicates that selection at any age results in an equal response across all ages (Lewis and Brotherstone, 2002). The negative slope observed in this study indicates that selected animals would reach mature weight relatively late, which is a hint that little progress would be achieved when selecting to improve growth rate. Selection to alter the growth pattern of Boran cattle would yield little given the proportion of variation explained by the quadratic eigenvalue.

#### Correlations

Genetic correlation between birth weight and other weights was low, which implies the possibility of selection to increase weight at older ages without causing much change in birth weight. Low estimates of genetic correlation between early and older weights suggest a difference in genetic control of weight at these sets of ages. This has implications for potential to select on the shape of the growth curve, as an animal may be above average weight at younger ages but may be below average at older ages and vice versa (Fischer *et al.*, 2004b). On the other hand, correlations between intermediate ages and later ages were high, implying pleiotropy, and thus selection for heavier animals at two years could be done based on intermediate weights. The pattern of genetic correlations between ages was similar to that reported in beef

cattle (Albuquerque and Meyer, 2001; Arango *et al.*, 2004; Meyer, 2005a). In addition, correlations between weights at younger ages were lower than between weights at older ages. Weights at later ages depend on earlier weights and therefore, with time, the correlation between later weights increases since they are more dependent on the previous weights (Huisman, 2002; Fischer *et al.*, 2004b). Estimates reported in this study were lower than those reported for Boran cattle using multivariate analysis (Wasike *et al.*, 2007). It should, however, be noted that in the multivariate analysis a simple animal model was used.

Correlation patterns for permanent environmental effects between ages were similar to genetic correlations. Negative and low correlation estimates between very early and later ages imply that better environmental conditions during birth of the animals would have only a small or no negative effect on later growth of the animal. However, environmental effects on weight at intermediate ages are more likely to influence performance at later ages, as depicted by the moderate to high positive correlation between intermediate and later age intervals. Correlations between older ages were close to unity, indicating that environmental effects affecting growth performance in older ages were more less the same. Similar results were reported by Arango and colleagues (2004). Therefore, it is important that the strenuous environmental conditions to which Boran weaners are subjected be controlled to avoid depressed performance later in life.

Phenotypic correlation patterns, though somewhat erratic between early ages and negatively low between extreme ages, were moderately to highly positive between intermediate and later ages. This implies that animals that had better growth performance during early stages of growth would not necessarily perform better at later growth stages. However, animals that had higher weights at intermediate ages could reliably be anticipated to have higher weights at later ages. Similar patterns were observed in growth of Bonsmara cattle (Nephawe, 2004). The observed spikes along the diagonal of the plot of phenotypic correlations depict inflation of phenotypic variance caused by measurement error variance. Similar results were reported in earlier studies of growth in beef cattle (Kirkpatrick *et al.*, 1994; Meyer, 1999; Arango *et al.*, 2004). The estimates between intermediate and later ages were within the range of

those estimated using multivariate analysis (Wasike *et al.*, 2007).

#### Estimated breeding values

Estimated breeding values for sires varied across age points and between sires. The variability in the breeding values between sires depicts the differences in the growth patterns of the Boran cattle as a result of lack of selection in the herd. This shows variation in ranking of animals as they grow such that animals with good genetics at birth will not necessarily have good genetics at the end of the growth trajectory. Therefore, using aggregate breeding value for the growth curve would be a more effective mode of selection than EBVs at particular ages. This is similar to the results reported for growth in sheep (Lewis and Brotherstone, 2002). The advantage of the RR model is its ability to estimate breeding values for the whole trajectory as long as there are animals with records at the extreme data points even when the animals to be evaluated do not have the records at the reference points. In addition, each record of performance will be used in the evaluation process at its point of recording. There is therefore no restriction on recording time.

#### Conclusions

Results from this study show the potential of RR models to model growth of Boran cattle when herd sizes are small and recording is inconsistent. It should, however, be noted that some other advantages of RR were forgone in order to obtain reliable estimates owing to the high imbalance in the data structure. Because of this imbalance, other random effects such as maternal effects could not be investigated. This should be exploited as recording infrastructures improve and records become more available. Results from RR models vary greatly with the order of polynomial fit; as a result there should always be pre-evaluation to obtain the order of fit that best describes the data, thus allowing the most parsimonious model to be fitted. Selection to alter the growth pattern of Boran cattle is feasible given the information provided by the principal components. This is of interest to the beef industry, where selection for specific objectives can be achieved. There is need

to examine the optimal number of records that could adequately provide information for reliable estimation of genetic parameters by RR models given the economic implications of performance recording. It is also important to examine the effects of additional information on the accuracy of estimated breeding value from RR models.

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### Évaluation génétique de la croissance de bétail Boran au Kenya en utilisant des modèles de régression aléatoire

**Résumé** – Des données consistant en 18 884 enregistrements de poids recueillis auprès de 1273 têtes de bétail Boran de la naissance à 24 mois d'âge ont été utilisées pour estimer les fonctions de covariance et les paramètres génétiques de croissance du bétail Boran en utilisant des modèles de régression aléatoire (RR) sous une situation de petite taille de troupeaux et d'enregistrements irréguliers. Le modèle RR a adapté des codes polynomiaux quadratiques de Legendre à l'âge à l'enregistrement pour la détermination des effets génétiques additifs et environnementaux permanents. La variance génétique a augmenté depuis la naissance, atteignant une valeur asymptotique à 455 jours et un maximum à 525 jours d'âge après quoi, elle a progressivement diminué. La variance environnementale permanente a augmenté tout le long de la trajectoire. Les estimations de la variance environnementale temporaire ont été hétérogènes à travers les âges. La variance de l'héritabilité directe et la variance environnementale permanente à titre de proportion de la variance phénotypique ont fluctué considérablement durant les âges précoces mais se sont stabilisées plus tard à des âges intermédiaires à plus avancés ; les estimations se sont situées à entre 0.11 et 0.33 et 0.18 à 0.83 respectivement. Les estimations de la corrélation génétique ont été positives allant de 0.10 à une unité. Les estimations ont

diminué avec l'augmentation du retard entre les points d'âge. Le schéma de corrélation phénotypique a été irrégulier entre les âges précoces, négativement bas ( $-0.02$ ) entre les points de données extrêmes et modérés à hautement positif ( $>0.50$ ) entre les points intermédiaires et avancés avec des pics proéminents le long de la diagonale. Il en a été conclu que le modèle RR avait malgré tout le potentiel de modéliser la croissance du bétail Boran, les conditions de petites tailles de troupeaux et un enregistrement irrégulier.

### Evaluación genética del crecimiento del ganado Boran de Kenia utilizando modelos de regresión de efectos aleatorios

**Resumen** – Se utilizaron datos consistentes en 18884 registros de peso recogidos de 1273 reses de ganado Boran, desde el nacimiento a los 24 meses de edad, para estimar las funciones de covarianza y los parámetros genéticos para el crecimiento del ganado Boran, utilizando modelos de regresión de efectos aleatorios (RR, en inglés) en una situación de tamaño de rebaño pequeño y registros no regulares. El modelo RR se ajustaba a polinomios de Legendre cuadráticos de edad al registrar los efectos genéticos aditivos y ambientales permanentes. La varianza genética aumentaba a partir del nacimiento, alcanzando un valor asintótico a los 455 días y un máximo a los 525 días de edad, después de lo cual decrecía gradualmente. La varianza ambiental permanente aumentaba a través de toda la trayectoria. Las estimaciones de la varianza ambiental temporal resultaron heterogéneas a través de todas las edades. La heredabilidad directa y la varianza ambiental permanente como proporción de la varianza fenotípica fluctuaba enormemente durante las edades más tempranas pero luego se estabilizaba en edades intermedias a más avanzadas; las estimaciones variaban de 0.11 a 0.33 y de 0.18 a 0.83, respectivamente. Las estimaciones de la correlación genética fueron positivas variando de 0.10 a la unidad. Las estimaciones declinaban al aumentar el lapso entre los puntos de edad. La pauta de correlación fenotípica fue errática entre las edades más tempranas, negativamente baja ( $-0.02$ ) entre los puntos de datos extremos, y de moderada a altamente positiva ( $>0.50$ ) entre los puntos intermedios y posteriores con picos importantes a lo largo de la diagonal. Se concluye que los modelos RR poseen potencial para representar el crecimiento del ganado Boran; a pesar de las condiciones empleadas de tamaños de rebaños pequeños y registros no regulares.