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ESTIMATES OF GENETIC PARAMETERS FOR GROWTH OF KENYA BORAN CATTLE USING RANDOM REGRESSION MODELS

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Abstract
Data consisting of 18 884 weight records collected from 1 273 Boran cattle from birth to 24months of age were used to estimate 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. Direct heritability and permanent environmental variance as a proportion of phenotypic variance fluctuated during the early ages but stabilised at intermediate to later ages; the estimates ranged from 0.11 to 0.33 and 0.18 to 0.83, respectively. Genetic correlation estimates were positive ranging from 0.10 to unity. The estimates declined with increase 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. Conditions of small herd sizes and inconsistent recording notwithstanding, RR models have potential to model growth of Boran cattle.

Introduction
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 (Demeke et al., 2003; Wasike et al., 2006). Growth follows a prescribed trajectory and performance is measured by repeatedly recording weight as the animal grows, this constitutes longitudinal data. To minimise the loss of information and reduction in the accuracy of parameter estimates associated with univariate and multivariate models, random regression (RR) models based on covariance functions methodology are used in evaluation of longitudinal data. The advantages of RR models over univariate and multivariate models are well articulated in literature. They include ability to allow for easy interpolation between ages at which recording took place, accurate prediction of selection response and more efficient use of the data (Kirkpatrick and Heckman, 1989; Albuquerque and Meyer, 2001).

Inconsistent recording of small selected groups from the larger herds and overlapping age categories when weights are recorded characterise growth performance recording in commercial beef production systems in Kenya. Random regression models may seem a better alternative to univariate and multivariate models under such circumstances. However, the models have not been used in evaluation of growth data in beef ranches in the Arid and semi-arid land (ASAL) of Kenya. The objective of this paper was to estimate genetic parameters for growth in Boran cattle RR models under situations of small data sizes and inconsistent recording.

Material and methods
Data source
Data on growth performance of the Kenya Boran cattle were made available by the national beef research station of KARI-Lanet located in Nakuru district, Kenya. A detailed description of the farm and management of the animals is presented in Wasike et al. (2006). Data consisted of weights recorded once a month from birth to 24 months of age on the Kenya Boran cattle born between 1989 and 2003. Weights were clustered in age-classes of 0-2days (birth weight), 3-35days, 36-70days, 71-105days…701-735days to cover the first 24month growth trajectory from birth due to high variability in ages at weighing. There were 22 age classes in total. All the data were checked for consistency of pedigree information and correct dates of birth and weighing. Only animals that had at least 3 weight records within their first 24-month life were retained for analyses. A final data set for analysis after editing comprised 18,884 records from 1,273 animals. The distribution of weight records among age points and average weights at various age intervals with their standard errors are presented in Figure 1
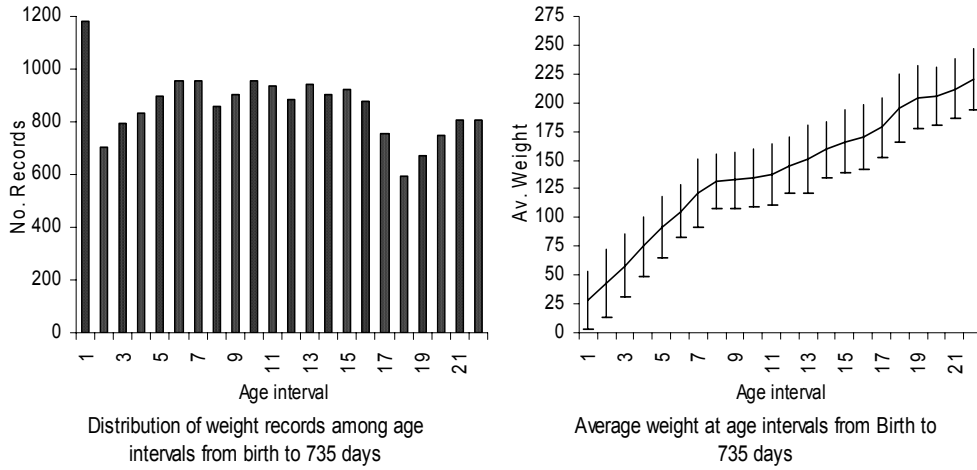
Fig 1. Distribution of weight records among age intervals and average weights at various age points from birth to 735 days

Data analyses

The fixed effects fitted in the model that was used to determine the best order of polynomial fit for the fixed regression to model the mean population curve included effects of sex, parity of the dam and the year month of weighing. Orthogonal (Legendre) polynomial of age at recording (in days) of order 4 was used in the fixed part of the model. All the effects were fitted as polynomial functions of age. A RR model fitting animal genetic and permanent environmental effects as the only random effects was used in genetic evaluation of growth. Third order orthogonal (Legendre) polynomial of age at recording (in days) best described the covariance between the RR coefficients in the model. The covariance between the coefficients were estimated using DFREML programme (Meyer, 2000). The general model used was:

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

where y_{ijk} denote 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 standardised age k (-1 to +1) at recording, $\Phi_m(a^*_{ijk})$ is the mth legendre polynomial of age, β_m are the fixed regression coefficients to model the population mean, α_{im} and γ_{im} are the im-th 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 ε_{ijk} is the random residual effect, which was considered independently distributed with heteroscedastic error variance.

Parameters estimated in RR analysis were the **K** matrices containing variances and covariances between the RR coefficients. The covariance function for the random effects were obtained by pre- and post-multiplying **K** by a matrix containing orthogonal polynomials (**Φ**) 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 **Φ**. For additive genetic this would be explained by the expression

G₀= ΦKΦ′

and applies to permanent environmental effects as well.

Results

Estimates of direct heritability and permanent environmental variance as a proportion of phenotypic variance are presented in Figure 2. Direct heritability estimate was 0.30 at birth, fluctuated but on a declining trend until 0.23 at age interval 7 (210days) after which it slightly increased to 0.33 at interval 9 (280days) 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 (70days) (<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.
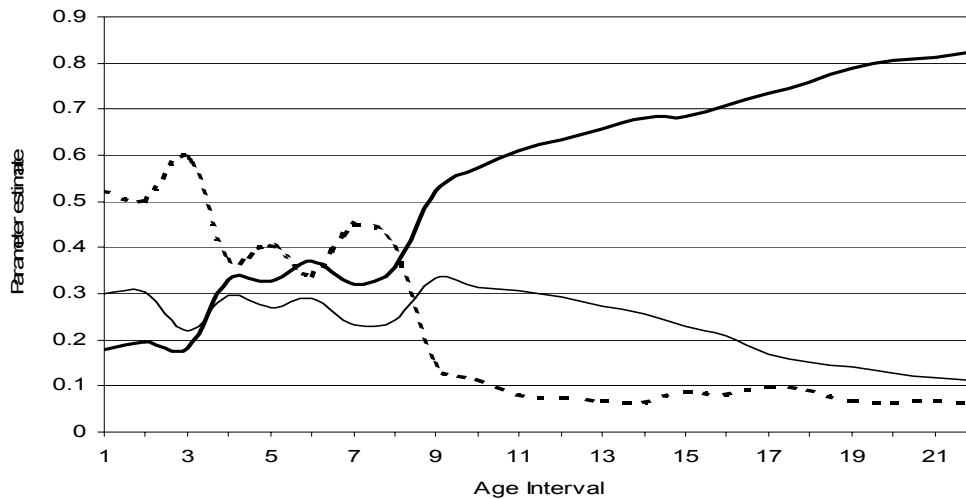

Fig 2. Estimates of direct heritability (⎯) and permanent environmental variance as a proportion of phenotypic variance (⎯) and temporary environmental variance as a proportion of phenotypic variance (   )

Estimates of additive genetic and permanent environmental correlations between the ages are presented in Table 1. Genetic 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 (71days) onwards. There was a decrease in estimates as the lag between the age points increased. Permanent environmental correlations between age interval 1 (birth weight) and weights at age interval 7 (176days) to age interval 22 were small and negative. The correlation between weights at other ages followed a similar pattern as the additive genetic correlations.

Phenotypic correlation between weights at different ages (Figure 3) followed a similar pattern as permanent environmental correlations with low estimates between birth weight and other weights. The estimates ranged from -0.018 between weight at birth and weight at interval 19 (630days) to 0.93 between weight at interval 21 (666days) and interval 22. There were more prominent spikes along the diagonal of the correlation graph at early ages than later ages.

Breeding value estimates for fifteen sires with more than 20 progeny each are presented in Figure 4. Estimated breeding values for sires varied significantly across age points and between sires. This implies that no meaningful selection has been carried out on these animals for growth from birth to 2 years.

Discussion
The relatively lower estimates of heritability and permanent environmental variance as a proportion of phenotypic variance (Figure 2) during early developmental stages (from birth to age interval 7) could be attributed to the fairly uniform environment provided by the Boran dams to their calves. The higher heritability estimates from birth to age interval 3 (70days) indicates that this phase of growth is under additive genetic influence, this is however subdued by the environmental influence arising mainly from the maternal effects (suckling) thereafter. After withdrawal of maternal environment at weaning, the additive growth potential was undermined by the strenuous production environment resulting in reliance of the animals on maternal environment conferred earlier for growth later in life.

High heritability between age interval 8 (211days) and 11 (350days) was of interest for selection purposes. At these age intervals, a high rate of response would be achieved when selection is carried out given the high heritability estimates and relatively low proportions of environmental influence than later ages. Heritability estimates reported here are within the range of estimates reported by Wasike et al. (2006). Estimates of heritability depicted growth as a low to moderately heritable trait. Reliability between weight records at early ages as predictors of weight at older ages was low. However, weights from intermediate ages upward, could

reliably predict one another. As a result, positive response to selection in later ages would be achieved if selection was based on intermediate ages.

Table 1–Additive genetic correlation (below diagonal) ad permanent environmental correlation (above diagonal) between Weights taken at various age point 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
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
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
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
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
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
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	0.69
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	0.72
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
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
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
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
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
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
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
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
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	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	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	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	0.99	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
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
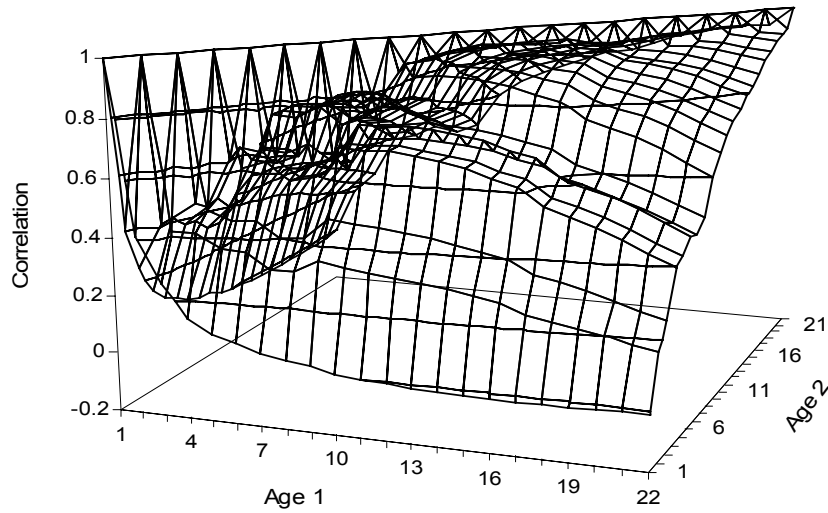
Fig 3: Phenotypic correlations between weights at various age points along the trajectory
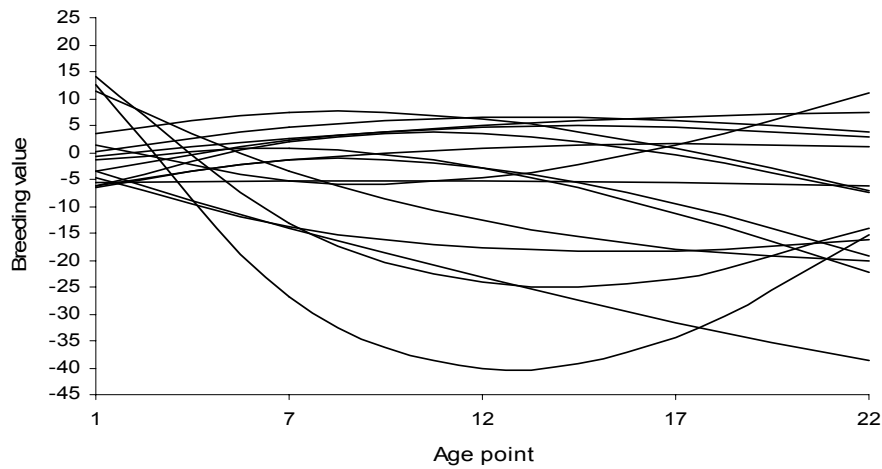

Fig 4:Estimated breeding values for fifteen sires with more than 20 progeny each

The estimates of genetic correlation between early and later 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. On the other hand correlations between intermediate ages and later ages were high implying pleiotropy and thus selection for heavier animals at 2 years could be done based on weight at intermediate age. The pattern of genetic correlations between ages was similar to those reported in beef cattle (Meyer, 2005). The correlation between later weights increased due to their dependence on the previous weights

Negative and low permanent environmental correlation estimates between very early and later ages imply that better environmental conditions during birth of the animals would have a little negative effect if any on later growth of the animal. However, environmental effects on weight at intermediate ages would more likely influence performance at later ages. Therefore it would be important to control the strenuous post weaning conditions which Boran weaners are subjected to avoid depressed performance later in life.

Phenotypic correlation patterns in Figure 3 indicate 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. The

5

observed spikes along the diagonal of the plot of phenotypic correlations depict inflation of phenotypic variance caused by measurement error variance.

The variability in the breeding values between sires and across age points (Figure 4) depict differences in the growth patterns of offspring of the various sires. The values also indicate that little or no selection for growth has occurred in the herd. Sires with high and very low EBVs at birth tended to have below average EBVs at 24 months. As an initial measure, selection of sires based on an aggregate breeding value for the growth curve would be a more effective mode of selection than EBVs at particular ages.

Conclusions
This study shows the potential of RR models to model growth of Boran cattle even when recorded herds are small and recording inconsistent. There is a large scope for selection to alter growth patterns of the Boran cattle in the ASAL. The estimates from this study could be used to effectively select for growth in Boran cattle on the commercial ranches. Further research is however needed to examine the optimal number of records that could adequately provide information for reliable and accurate estimation of genetic parameters.

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