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Genetic evaluation of growth and reproductive performance of the Kenya Boran cattle

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A thesis submitted to the Graduate School in partial fulfilment of the requirements for the Master of Science Degree in Animal Production (Animal Breeding option) of Egerton University.

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DECLARATION AND APPROVAL

1. DECLARATION

This thesis is my original work and has not, wholly or in part, been presented for an award of a degree or diploma in any other University.

Signed: _____

Wasike Chrilukovian Bwire

Date: 4th JULY 2006

2. APPROVAL

This thesis has been approved for final submission with our approval as University supervisors.

Signed: _____

Prof. Dr. A. K. Kahi

Date: 23rd JUNE 2006

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Dr. J. M. K. Ojango

Date: 5th July 2006

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ACKNOWLEDGEMENTS

I wish to sincerely appreciate several institutions and persons who in one way or another opened doors and answered my incessant questions in the quest for knowledge that culminated in the successful completion of this study. I thank Egerton University's Graduate School and Department of Animal Sciences for offering me the opportunity to pursue postgraduate studies. I am indebted to Delamere Estates and Kenya Agricultural Research Institute (KARI) for allowing me to use their data and facilities in the course of this work.

I am grateful to my supervisors, Prof. Dr. A.K. Kahi and Dr. J. M. K. Ojango for their technical advise, guidance, professional supervision, inspiration and unlimited support during the entire study period. I thank you for nurturing an attitude of scientific professionalism, keen interest, selflessness, patience and tolerance in me. A perfect blend of professional and social concern you showed during my study period made even bleak ends shine, for this I say thank you. I appreciate Dr. W. Pitchford's technical advice in development of random regression models.

I am greatly indebted to Ev. Dr. P. Onjoro whose timely financial assistance enabled me to register for this study programme. The unwavering kind support from Mr. C. Wangula, Dr. B. D. Odhiambo, Rev. Frs. L. Ekissa and A. Lincen and Mr. G. K. Musumba are highly appreciated. I thank my fellow postgraduate students for the moral support; great thanks to Deyie, Bett and Rewe for the brotherly support you gave me following the demise of my dad. The constant presence and support from Ms. Christine Nagwala was a chocolate chip in my life; thank you very much.

My appreciation goes to the Managing Director of Delamere Estates Mr. C. B. Chirchir, Livestock Manager SoySambu Ranch, Mr. R. Munuve, Centre Director KARI, Lanet, Mr. K.R.G. Irungu and the Head of Livestock section Mr. D. Indetie, for making the environment on the farms conducive for my research. I also acknowledge the assistance that the staff on these farms granted me during the data collection period.

For the good health, mental stability, physical strength and the gift of life, I say thank you to **God Almighty**.

DEDICATION

This work is dedicated to

my parents Mr. Joackim W. Omadwa (late) and Mrs. Catherine A. Omadwa

and

my siblings Adikinyi, Odeba, Omadwa and Maria for their great sacrifice, ceaseless prayers, support and encouragement.

Isando yomuinda nasuba chindolo nobuinda bwaye, khubira Nasaye orio mubwari bwao.

ABSTRACT

The Kenya Boran cattle constitute the largest proportion of single breed population of cattle raised for beef production in the Arid and Semi-arid Lands (ASAL) of Kenya. Records on growth and reproductive performance were used to estimate genetic and phenotypic parameters using various univariate, multivariate and random regression models and to examine genetic and environmental trends in performance. Sex, age of the animal, parity of dam and year-season effects were the main environmental effects that influenced birth weight (BW), weaning weight (WW), 12month weight (12W), 18month weight (18W) and 24month weight (24W). Reproductive performance, i.e. age at first calving, (AFC), pooled calving interval (CI) and calving intervals in parities 1 (CI1), 2 (CI2) and 3 (CI3) were affected by herd-year-season of birth and calving, and age at birth and calving. Direct heritability estimates from univariate analyses of growth traits were 0.34, 0.12, 0.19, 0.08 and 0.14 for BW, WW, 12W, 18W and 24W, respectively. Maternal heritability estimates were 0.14, 0.34 and 0.11 for WW, 12W and 24W, 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, 0.00, 0.15 and 0.00 for AFC, CI, CI1, CI2 and CI3, respectively. Direct heritability estimates from multivariate analyses were 0.36, 0.40, 0.38, 0.21 and 0.17 for BW, WW, 12W, 18W and 24W, respectively. The genetic correlations between growth traits were positive (0.36 to 0.94). The genetic correlations between reproductive traits were negative (-0.18 to -0.30). The genetic correlation between AFC and WW was positive (0.72). From random regression (RR) analysis, estimates of direct heritability and permanent environmental variance as a proportion of phenotypic variance ranged from 0.11 to 0.33 and 0.18 to 0.83, respectively. Genetic correlations were positive (0.10 to unity) but declined with increase in lag between the age points. The pattern was similar for permanent environmental correlation, which ranged from -0.13 between the early and later age points, to unity between later ages. Phenotypic correlation was 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. Effective genetic evaluation of Kenya Boran cattle should consider environmental sources of variation while fitting both direct additive and maternal effects for growth, and direct additive effects for reproductive traits. Higher rates of genetic change in growth traits are feasible when RR models are used in the evaluation rather than the conventional finite models.

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LIST OF ABBREVIATIONS

AEZ	Agro ecological zone
AFC	Age at first calving
AM	Simple animal model
AMM	Maternal animal model
ARMM	Maternal repeatability animal model
ASAL(s)	Arid and semi arid land(s)
BW	Birth weight
CF	Covariance function
CI	Calving interval
EBV	Estimated breeding value
KBCBS	Kenya Boran Cattle Breeders' Society
KSB	Kenya Studbook
LRC	Livestock Recording Centre
PEV	Prediction error variance
REML	Restricted maximum likelihood
RR	Random regression
SEAZ	Small East African zebu
SRM	Simple repeatability model
WW	Weaning weight

CHAPTER ONE

GENERAL INTRODUCTION

The livestock sector in Kenya contributes between 10 to 12 percent of the national GDP (FAO, 2005), however specific estimates on the contribution of beef to the country's GDP are not available. The beef consumed in the country is derived from both *Bos indicus* and *Bos taurus* breeds. Kenya Boran cattle constitute the largest proportion of the population of *Bos indicus* breeds kept in the semi-arid areas of Kenya, primarily for beef production. However, other cattle genotypes that serve as sources of beef in the country include the Small East African zebu (SEAZ), *B. taurus* breeds such as the Hereford, Simmental, Charolais, Angus, their crosses and culled stock from the dairy cattle herds (Trail et al., 1984; Mwandotto et al., 1988; Indetie et al., 2000a). The Kenya Boran cattle are preferred to the *B. taurus* breeds by commercial ranchers due to their relative adaptability to the tropical production environment, which facilitate their greater ability to survive, grow and reproduce in the semi-arid conditions. These characteristics have been achieved following generations of natural and artificial selection in conditions of high ambient temperature, poor feed quality and high pathogen incidences that typify the Kenya's Arid and ASAL and low input production systems (Davis, 1993; Herlocker, 1999; Mpofu, 2002; Okomo-Adhiambo, 2002). Breed comparisons involving the Boran and its crosses, Angus, Charolais, Hereford, Limousine and South Devon have shown the superiority of Kenya Boran cattle for survival under tropical conditions (Gregory et al., 1984; Mwandotto et al., 1988; Said et al., 2001). Due to these potentials, this breed is recommended for use in performance improvement of other indigenous and exotic cattle for beef production in the tropics (Trail et al., 1984; Indetie et al., 2000a).

Beef in Kenya is produced under pastoral and commercial beef ranching systems, which are pasture-based (Peeler and Omore, 1997). In pastoral systems, the SEAZs and their crosses with the Boran are kept in a bid to minimise risks associated with deaths due to starvation and diseases, and are used for both milk and meat production. In commercial ranching systems, the Kenya Boran and *B. taurus* breeds are kept to maximise profit from sale of beef. Ranchers keep records of performance of their cattle, which are used when selecting for improved growth, fertility and partly survival performance (Irungu and Ouda, 2001). Production objectives and selection criteria in commercial ranching systems are however varied and therefore influence animal beef output between ranches, and subsequent beef cattle

performance under different conditions (Okeyo et al., 1998). Rewe (2004) developed alternative breeding objectives for the genetic improvement of the Kenya Boran cattle and emphasised the need for a more co-ordinated beef breeding programme. Despite the ranchers' efforts to improve beef productivity in the country, the industry is threatened by a high human population growth rate of 3%, grazing land conflicts between the ranchers and pastoralists, and inter-generation inheritance of land, resulting in continued subdivision of land into smaller pieces that cannot support extensive beef production (Bebe et al., 2002). The efforts of ranchers require bilateral support through implementation of good breeding programmes and legislation to enhance sustainable quality beef production (Prettejohn and Retief, 2001).

In Kenya, a centrally organised breeding programme to facilitate genetic improvement of beef cattle is lacking. Selection of beef cattle by most of the commercial beef producers tend to be based on "age for weight" and physical appraisal. With the persistent dry conditions, a proportion of the producers are opting to breed for improved fertility rather than increased weight (C. B. Chirchir, Personal Communication). An efficient beef production system is one in which animals are selected for traits that influence profitability based on accurately estimated performance parameters (Rumph et al., 2002). This ensures improvement of animal performance without adversely affecting the profitability of the system. Fertility and growth traits are important in beef production because they directly influence the rate of off–take (Davis, 1993). These two categories of traits form the basis of Kenya Boran performance evaluation and selection. Survival traits are of importance within the strenuous tropical production conditions where the environment greatly influences performance. Unlike fertility and growth traits, these traits are not emphasised in performance recording, evaluation and selection programmes and tend to be selected for as correlated traits (Davis, 1993).

Performance evaluation involves estimation of genetic and phenotypic parameters in the populations of interest, and evaluation of trends for genetic improvement purposes (Musani and Mayer, 1997; Ebangi et al., 2000; Plasse et al., 2002). The efficiency of a genetic improvement programme is dependent on animal selection, using precise and accurate estimates of performance parameters for prediction of breeding values (Burrow, 2001). Environment specific estimates obtained by appropriate analytical models yield greater accuracy and are more efficient when applied in tropical beef breeding programmes (Davis, 1993). However, due to limitations in availability of animal records, accurately quantified performance parameter estimates for various traits on indigenous cattle under varied production systems are limited. As a result, there is limited use of performance parameter estimates in beef cattle selection programmes.

Animal model evaluations of performance of the tropical beef cattle in Africa have been performed mostly considering single trait analysis, and to a lesser extent multi-trait analysis (Haile-Mariam and Kassa-Mersha, 1994,1995; Demeke et al., 2003). In many of these analyses, the relationships between traits in different categories were not considered and maternal effects were ignored. Omitting maternal effects result in an upward bias of direct heritability estimates (Meyer, 1992; Rumph et al., 2002). As a result, there is slow genetic progress due to sub-optimal selection decisions arising from errors and biases in parameter estimates (Hazel et al., 1994). Multi-trait models are based on the assumption of constant variances with covariances between the traits in the analysis. They are therefore suitable for analysis of traits that exhibit static variances in their data structure e.g. fertility traits. However, growth traits change over a trajectory (time). Consequently, multi-trait models assuming constant variances do not adequately describe the covariance structure of their data. This can be done using covariance functions (CF) that account for changing variances and correlations between measurements over time (Meyer, 2000b; Nobre et al., 2003b). In addition, CF can be used to model the fluctuations in growth patterns of animals raised in the ASALs that result from compensatory growth following dry periods. This methodology remains unexploited in beef production systems in Africa despite its ability to handle longitudinal data with missing records, which are typical of the recording systems in the tropics.

1.1. Objectives

The overall objective of this study was to evaluate direct and maternal effects on growth and reproductive performance of the Kenya Boran cattle in arid and semi-arid areas of Kenya. The specific objectives were:

1. To estimate direct and maternal (co)variance components of growth and reproductive traits in Kenya Boran cattle using genetic models accounting for different random effects.
2. To estimate covariance functions for growth in Kenya Boran cattle from birth to 720 days of age using random regression models.
3. To examine the genetic and environmental trends in the growth and reproductive traits of the Kenya Boran cattle.

1.2. Hypotheses

H_O There was no difference between direct and maternal (co) variance components of growth and reproductive traits of the Kenya Boran cattle estimated using different genetic models.

H_O There was no difference in the genetic and phenotypic parameters estimated for growth traits of the Kenya Boran cattle at certain age points along the growth trajectory using random regression models.

H_O Prior breeding programmes and management practices did not confer improvement in performance of Kenya Boran cattle populations over the years.

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CHAPTER TWO

LITERATURE REVIEW

2.1. Traits of economic importance in beef production

Beef cattle performance is generally described by reproduction, production, carcass and survival traits (Burrow, 2001; Hearnshaw et al., 2002). The economic impact of these traits on a beef production enterprise is examined by considering their effects on profitability of the enterprise. These traits are related and therefore breeding programmes incorporating all the trait categories would be more effective than those considering a particular trait category (Mackinnon et al., 1991). Selection for improvement of these traits in a production system is influenced by the production environment, ease of expression and market conditions (Mackinnon et al., 1991; Davis, 1993).

2.1.1. Productive traits

These are described by growth performance of an animal at various stages of the growth curve and directly influence profitability in beef production systems (Newman and Coffey, 1999). They include all growth characteristics measured as live weight. The expression of these traits is dependent on the animal's inherent growth ability and production environment (Mackinnon et al., 1991; Davis, 1993). Productive traits influence various aspects of production, ranging from maintenance requirements to cull-cow value, and therefore directly affect revenue in beef production. These traits directly influence carcass (Pariacote et al., 1998) and reproductive traits (Burrow, 2001), although they are affected by the adaptability of the animal to the production environment (Gaughan et al., 1999; Burrow, 2001). The traits form the basis of selection in many of the genetic improvement programmes due to their early expression and ease of measurement.

2.1.2. Reproductive traits

Reproductive traits describe the animal's ability to conceive, calve down and successfully suckle the calf to weaning (Davis, 1993). These traits are important because they affect the herd size and off take. They also influence overall calf crop from the herd and are good indicators of the animals that will be availed for market. However, they are influenced by both productive and survival traits. Reproductive performance is commonly evaluated by analysing female reproductive traits; the traits regularly considered include age at first

calving, calving interval and calving date. McGregory and Casey (1999) established that calving date was a better measure of reproductive performance in beef cattle under strict seasonal breeding scheme than calving interval. This was because the former was positively influenced by previous calving date than calving interval. However, calving interval remains the principle measure of reproduction efficiency in continuous breeding schemes (MacGregory and Casey, 2000). Male fertility traits are rarely included in genetic evaluations despite their influence on the female reproductive performance. These traits include semen quality and quantity traits, and scrotal size.

2.1.3. Survival traits

Survival traits describe the potential of the animal to grow, reproduce and remain productive under given production conditions. They are measures of the animals' adaptability to the production environment and are herd traits described as survival rates at various developmental stages measured in terms of tolerance to pathogenic parasites (Mackinnon et al., 1991) and mortality (Burrow, 2001; Hearnshaw et al., 2002). The information on animal mortality and survival is useful when modelling the herd-age structures in a production system (Hearnshaw et al., 2002). Genetic prediction of stayability of females is important for cost reduction and increased profits through selection for persistent reproduction and productivity. However, in most of the tropics, survival traits are selected for indirectly during direct selection of production traits in restrictive production environments. Survival traits tend to have widely varied parameter estimates due to high environmental influences (Davis, 1993; Hearnshaw et al., 2002).

2.1.4. Carcass traits

Carcass traits describe the characteristics of beef. Broadly they are divided into carcass quality (composition) and carcass quantity traits. The carcass quality traits include, marbling score, fat thickness, kidney, pelvic and the heart fat percentages, rib eye area and yield grade. On the other hand, carcass quantity traits comprise pre-slaughter live weight, hot carcass weight and dressing percentage (Pariacote et al., 1998). Carcass characteristics differ between breeds and are influenced by the plane of nutrition and production system (Keane and More O'Ferrall, 1992). Selection for these traits is greatly influenced by the market demand. For instance, in Japan carcass value is primarily determined by the degree of marbling. Consequently only carcass quality trait (i.e. marbling score) has been strongly emphasised in selecting beef bulls (Hirooka and Groen, 1999). In Kenya, there is no specific criterion of

carcass valuation. Majority of slaughterhouses and butcheries value carcass quantitatively (Kilung'o and Mghenyi, 2001). A few high-class butcheries consider carcass quality traits as valuation criteria, and sell beef in specified cuts emphasising marbling score and tenderness of the cuts.

Heritability estimates for carcass traits are generally medium implying ability for improvement by selection. The correlations between the traits are varied. However, breeding strategies to increase dry carcass weight (the greatest determinant of carcass value) would lead to improvement of other carcass traits apart from marbling score (Keane and More O'Ferrall, 1992; Pariacote et al., 1998).

2.2. Performance of the *Bos indicus* breeds and their crosses

Tropical environments, under which the indigenous beef cattle are produced, are nutritionally restrictive and have high ambient temperatures as well as parasite load to the animals (Gaughan et al., 1999). These environmental conditions not withstanding, the *B. indicus* breeds have shown superiority, especially in their survival ability (Mpofu, 2002). A number of studies have evaluated the performance of tropical African beef breeds (Trail and Gregory, 1981; Gregory et al., 1984; Haile-Mariam and Kassa-Mersha, 1994,1995; Gaughan et al., 1999; Lunstra and Cundiff, 2003). Table 1 shows the growth and reproductive performance of *B. indicus* cattle and their crosses under tropical production environments. The variation in animal performance could be attributed to the variation in the environmental conditions and the history of the populations considered.

2.2.1. Productive performance

Several studies under temperate conditions have rated the Kenya Boran cattle breed as an intermediate performer among the tropical breeds for weaning weight (WW), marbling and tenderness (Mpofu, 2002). Under tropical environments, breed comparison studies have concentrated more on the growth and fertility traits than on carcass traits (Trail and Gregory, 1981; Gregory et al., 1984; Trail et al., 1984). The Kenya Boran cattle reportedly mature early and have high fertility under conditions of nutritional and thermal stress (Mpofu, 2002; Lunstra and Cundiff, 2003). This is due to the adaptation developed during evolution of the breed in the stressful semi-arid conditions (Indetie et al., 2000b). In a cattle germplasm evaluation programme in the USA, Boran-sired progeny were heavier at birth than those of Angus and Tuli although lighter than Hereford and Brahman (Cundiff et al., 1998). The Boran progeny had faster pre-weaning growth rate than Tuli-, Belgium Blue-, Hereford- and Angus-

sired crosses (Lunstra and Cundiff, 2003). Boran sired bulls had heavier 12-month weight (12W) than Tuli sired bulls. This was due the faster average daily gain in Boran cattle than the Tuli (Lunstra and Cundiff, 2003). Boran crosses with *B. taurus* beef breeds have heavier WW than its crosses with *B. indicus* breeds as shown in Table 1. This is due to the superior additive genetic effects of the *B. taurus* breeds and heterosis. More heterosis is expressed in *B. indicus* x *B. taurus* breed crosses as a result of heterozygosity. Therefore, the differences in gene frequencies are much wider between *B. taurus* and *B. indicus* breeds, and this leads to high levels of heterosis in crosses between them.

Table 1. Growth and reproductive performance of *B. indicus* cattle and their crosses

Genotype[a]	Trait[b]							Country	Sources
	AFC (days)	CI (days)	BW (kg)	AWn (days)	WW (kg)	12W (kg)	18W (kg)		
Boran	1271	442	24	253	169	192		Ethiopia	Haile-Mariam and Kassa-Mersha (1994, 1995)
,,			25	180	98	138		,,	Demeke et al. (2003)
,,	1223	413		240	170			Kenya	Trail and Gregory (1981)
,,			30	180	155			Kenya	Indetie et al. (2000b)
,,	1093	421			173			,,	Trail et al. (1984)
,,	1049	412			194			,,	Gregory et al. (1984)
,,					142		190	,,	Mwandotto et al. (1988)
Sahiwal	1195	390		240	170			,,	Trail and Gregory (1981)
Brahman			30	205	162		269	Venezuela	Plasse et al. (2002)
Boran x SEAZ					122		170	,,	,,
Boran x Redpoll		401			177			,,	Trail et al. (1984)
Boran x Charolais	1021	398			211			,,	Gregory et al. (1984)
Boran x Santa Getrudis	1037	411			203			,,	,,
Boran-sired progeny			46	186	254	424		USA	Lunstra and Cundiff (2003)
Tuli-sired progeny			39	185	242	408		USA	,,
Brahman-sired progeny			50	184	260	443		USA	,,

[a]SEAZ, Small East African Zebu.
[b]AFC, age at first calving; CI, calving interval; BW, birth weight; AWn, age at weaning; WW, weaning weight; 12W, 12-month weight; 18W, 18-month weight.

Compared to temperate breeds, there is scarcity of information on the performance of *B. indicus* cattle in tropical environments. Boran crosses with Red Poll, Charolais and Santa Getrudis tended to be heavier at weaning than the purebred Boran (Table 1). This is due to heterotic effects in the crossbred genotypes. However, purebred Brahman cattle raised in flooded savannah of Venezuela have better growth performance than Kenya Boran cattle raised in the ASALs (Table 1). This shows the influence of the production environment on the growth performance of beef cattle. The flooded savannah have a comparatively better

nutritional environment than the ASALs and therefore facilitate the better performance of the Brahman cattle in addition to the breed's high growth potential (Plasse et al., 2002; Lunstra and Cundiff, 2003).

Trail and Gregory (1981) evaluated the performance of Kenya Boran and Sahiwal cattle in Kenya. Both breeds weaned calves of equal weight (170kg) although the Kenya Boran cattle weighed heavier at 660 days of age (292kg) against 266kg of Sahiwal. This demonstrates the higher individual additive genetic influence on the growth of Kenya Boran cattle than Sahiwal. The WW of the Boran observed in the study is higher than estimates obtained by Haile-Mariam and Kassa-Mersha (1995) and Demeke et al. (2003) in Ethiopia (Table 1). This could however, be attributed to the calf rearing systems and environmental conditions of the production areas where the data used in the studies were obtained. For instance, calves in the study by Demeke et al. (2003) had the lowest WW (Table 1) due to bucket feeding compared to calves in other studies, which were allowed to suckle their dams. The 12W observed by Demeke et al. (2003) was lower than that estimated by Haile-Mariam and Kassa-Mersha (1995). Due to artificial rearing of the calves in the former study, maternal effects on calf growth tended to die out earlier than in naturally reared cases. As a result, the 12W in the latter study is under both the animal's individual growth potential and the carry over effects of the dam, leading to the higher 12W, unlike in the study by Demeke et al. (2003).

2.2.2 Reproductive performance

Reproductive performance of the Kenya Boran cattle, like other *B. indicus* beef breeds is influenced by productive performance, survival ability and environmental conditions. Most of the studies considered female fertility traits with only a few evaluating male fertility of the Boran cattle and their (Haile-Mariam and Kassa-Mersha, 1994). The Kenya Boran cattle have a mean age at first calving (AFC), calving interval (CI) and calving rate of about 1,093 days, 421 days and 89.4%, respectively (Gregory et al., 1984; Trail et al., 1984).

Generally, Boran crosses attain AFC earlier and have shorter CI than the purebred Boran. This could be attributable to the effect of heterosis in the crossbred genotypes. On the other hand, Kenya Boran cattle in Kenya had shorter CI and AFC than those in Ethiopia (Table 1). The Kenya Boran cattle were exposed to the bull at the age of 660 days while the Ethiopia Boran cattle were introduced to the breeding herd at the age of between 720-1080 days, consequently accounting for the later AFC in the Ethiopian Boran cattle (Table 1). The low reproductive efficiency in the Ethiopian Boran was also attributed to the low fertility in

the bulls and the high cow to bull ratios in the herds (Haile-Mariam and Kassa-Mersha, 1994). From Table 1, the Sahiwal had higher reproduction efficiency than the Kenya Boran cattle under similar production conditions. The younger AFC in the Sahiwal than in the Boran indicates early sexual maturity in the former. The shorter CI in the Sahiwal cattle can be attributed to shorter postpartum period than in the Boran (Trail and Gregory, 1981).

2.2.3. Non genetic factors influencing productive and reproductive performance

Knowledge of non-genetic factors and their influence on performance of beef cattle is important in the formulation of management and selection decisions (Goyache et al., 2003). In various studies, a number of factors have been included in analyses as main factors or their two- and/ or three-way interactions either as fixed effects or as continuous effects to account for environmental sources of variation in animals' performance (van Bebber et al., 1997). Fixed effects are sources of variation with defined classes comprising of all the possible levels of interest (Mrode, 2005). Examples of fixed effects include herd, year, season, sex, breed and parity. Continuous effects are sources of variation usually not defined into class levels and have a continuous influence on the observation. Such effects include age related effects like age of the calf at weaning and age of the dam at birth or weaning of the calf. They are usually fitted as covariates to account for their non-constant influence on the response variable (Duchateau et al., 1998). Table 2 presents some of the factors and their effect on production and reproduction traits.

Herd effect is fitted to account for anticipated differences in management between herds when an analysis involves animals from various herds (van Bebber et al., 1997). A significant effect of the herd (Table 2) is an indicator of difference in management levels between the herds, and therefore a source of variation in animal performance. Sex of the animal is another effect that significantly affects growth traits in beef cattle. This is due to the differences in growth physiology between the sexes resulting in sexual dimorphism in growth performance (Trail and Gregory, 1981; Indetie et al., 2000a). Male cattle tend to be heavier than their female counterparts at all ages due to higher influence of testosterone hormone. Parity of the dam shows varying levels of influence on both production and reproduction traits (Table 2). Significant effect of parity on growth performance could be attributed to the better nursing ability in later parities than the earlier parities as a result of fully developed udders of older cows that confer high milk production (Indetie et al., 2000a; Plasse et al., 2002; Goyache et al., 2003).

The interactions between main effects also influence productive and reproductive performance of beef cattle (Table 2). Significant effect of year-season of birth effect implies dependence of cattle performance on the climatic conditions at the time of birth of the animal in which unfavourable conditions would result in deprived performance. Fitting year-season effect accounts for variation in animal performance due to variation in climatic conditions (van Bebber et al., 1997). Also, the significant effect of interaction between the herd and year of birth implies changes in both management and climatic conditions would result in changes in reproductive performance. For instance, animals born in herds under good management and favourable climatic conditions would calve down earlier and their calving interval would be shorter and vice-versa.

Table 2. Non-genetic factors influencing productive and reproductive performance in beef cattle

Factor	Traits[ab]						Source
	BW (kg)	WW (kg)	12W (kg)	18W (kg)	AFC (Days)	CI (Days)	
Fixed effects							
Herd		***					Goyache et al. (2003)
				**			Mwandotto et al. (1988)
Sex		**		**			"
	*	*					Indetie et al. (2000b)
		**					Trail and Gregory (1981)
		***					Goyache et al. (2003)
					NS	NS	Haile-Mariam and Kassa-Mersha (1994)
Parity					NS	NS	"
		***					Goyache et al. (2003)
		NS				**	Trail and Gregory (1981)
	*	*					Indetie et al. (2000b)
Year-Season of birth		**		**			Mwandotto et al. (1988)
		**			**	*	Trail and Gregory (1981)
						**	McGregory and Casey (1999)
					*	*	Haile-Mariam and Kassa-Mersha, (1994)
Herd-year of birth					***	***	van der Westhuizen et al. (2001)
Continous effects							
AWn		***					van der Westhuizen et al. (2001)
		***					Goyache et al. (2003)
		**					Mwandotto et al. (1988)
Age of dam at weighing		**					"
	*	*					Indetie et al. (2000b)

[a]***P<0.001; **P< 0.01; *P<0.05; NS= Not Significant

[b] BW, birth weight; WW, weaning weight; 12W, 12-month weight; 18W, 18-month weight; AFC, age at first calving; CI, calving interval.

Age of the dam significantly affected BW and WW (Table 2). The significant effect on BW could be attributed to nutrient competition between the maintenance functions of the dam (always given higher priority) and foetal development, which is high in younger than

older dams (Indetie et al., 2000a). On the other hand, heavier WW are expected in calves from older dams due to their well developed mammary tissue relative to younger dams, and subsequently confer better maternal environment in terms of milk for the suckling calf (Mwandotto et al., 1988). This effect is not significant in post weaning traits due to the withdrawal of maternal environment at weaning.

Variability in results on significance of environmental effects has also been reported (Table 2). This variation comes as a result of differences in classification of factors into class levels, data and population structure, which influence the distribution of the observations among the fixed effect classes. In cases where there is poor distribution of observations, there are likelihoods of reporting of non-significance when in essence the effect was significant (Duchateau et al., 1998). This is due to the high prediction error variances obtained in fixed effects when groups having limited number of records per subclass are used (Maniatis and Pollott, 2003).

2.3. Variance components

Biological variation is an important aspect of genetic progress because the aim of selective breeding is reliable identification of animals with superior genes to form parents of the next generation (Falconer and Mackay, 1996). Since the actions of the individual genes are largely unknown, quantitative methods based on the infinitesimal model have been designed to analyse the effects of genes and partition phenotypic variance into its components (Lynch and Walsh, 1998; Mrode, 2005).

Classically, variance components are partitioned into genetic and environmental components. However, their inefficiency to explain the variance structure have spurred the use of more complex models, which attribute variance to both direct and indirect sources (Falconer and Mackay, 1996). This has resulted in genetic and environmental variances being partitioned into direct additive, maternal additive genetic variance and direct permanent, maternal permanent and random environmental variances, respectively. In multi-parous species the environmental variance is further partitioned into common environmental variance (Lynch and Walsh, 1998; Mrode, 2005). These components and their interactions are important in estimation of animal breeding values for each trait (Falconer and Mackay, 1996). Variance components have been estimated for various tropical beef cattle, especially in Australia and Brazil (Mackinnon et al., 1991; Meyer, 1992; Davis, 1993; Burrow, 2001; Nobre et al., 2003b). However, these estimates remain scarce in the tropical Africa indigenous beef breeds, a situation that has led to selection of cattle based largely on their conformation

and phenotypic performance (Haile-Mariam and Kassa-Mersha, 1994,1995; Demeke et al., 2003).

2.3.1. Genetic variance

Genetic variance is a component of phenotypic variance attributable to the genetic composition of the animal. It is a source of variation due to the sample of the genes that an animal receives from its parents (1/2 from either parents) and how they interact (Bourdon, 2000). This component of variation can be partitioned into additive and maternal genetic variances due to individual animal genetic and maternal genetic effects, respectively.

Additive direct genetic effects

Additive direct genetic effects are effects on performance of the animal that can be attributed to its own genes. They are effects due to the average parental genes and constitute the breeding value of the animal. Since these effects are heritable, they form the core component of genetic improvement due to their ability to be selected for. In growth traits, these effects are large, leading to high variances that are suggestive of higher genetic gains compared to reproductive traits. The effects are subject to a number of influences, including Bulmer effect, which comes after several generations of selection and tends to enhance genetic relatedness (Lynch and Walsh, 1998).

Additive maternal genetic effects

Maternal effects refer to the dam's influence to her offsprings. These are in form of maternal environment (prenatal and post natal) and the sample of genes passed to the offspring. Therefore, these effects are partly environmental and partly genetic. Knowledge of the maternal contribution to performance is necessary in planning a sound-breeding programme (Meyer, 1992; Arthur et al., 1994). Evidence for maternal effects in cattle can be seen in crossbreeding experiments due to the differences in performance among the reciprocal crosses. However, these do not help in quantifying the relative variation due to maternal effects (Koch, 1972).

Various studies have shown the importance of maternal effects on the efficiency of selection for growth in beef cattle (Arthur et al., 1994). Maternal genetic effects have been demonstrated to be significant for growth up to weaning after which it declines. However, the upper age limit at which this effect disappear varies among the reported results (Meyer, 1992; Khombe et al., 1995; Rumph et al., 2002). Therefore, fitting of models that account for

maternal additive genetic effects for traits up to weaning and covariance between direct and maternal additive effects is important (Vaez et al., 1996). Rumph et al. (2002) and Maniatis and Pollott (2003) demonstrated the extent of overestimation of direct heritability if maternal effects were ignored in genetic parameter estimation of growth traits in Hereford cattle and sheep, respectively. Not accounting for maternal effects inflated direct heritability estimates for mature cow weight of Hereford cattle (Rumph et al., 2002). Therefore, selection based on estimated breeding values from models accounting for maternal effects result in increased efficiency of selection.

A negative correlation exists between additive and maternal genetic effects (Baker, 1980; Maniatis, 2000). This has a strong implication on the genetic progress made in selection for beef traits in which maternal effect is paramount. Genetic progress is achieved faster when this correlation tends to zero (Baker, 1980). This can only be met when multi-trait models are used for genetic analysis because they reduce the correlation due to adjustments through the residual covariance matrix when accounting for more than one trait at a time (Rumph et al., 2002). The correlation could also be reduced by use of data that has a detailed pedigree in which high proportions of the dams and maternal grand dams have their own records (Maniatis and Pollott, 2003). This remains a limiting factor in genetic evaluation in tropical Africa where performance and pedigree recording is not consistent. This limitation also hinders the partitioning of maternal effects into genetic and permanent environmental maternal effects, which require repeated records on individual dams and the presence of these dams in the data.

2.3.2. Environmental variance

This is a component of phenotypic variance that is due to the effects of the environment where the animals live. The effects range from physical factors like climate to nutrition and general management. Environmental variance can be partitioned into permanent, common and residual (measurement error) variances, each resulting from different effects. Common environmental variance is prominent in multi-parous animals and will therefore not be discussed here.

In successively recorded traits, several records/ observations are made on an individual. For instance, weight records from an animal at different times in beef cattle and milk yield records in different lactations or same lactation in dairy cattle are observations taken repeatedly on the same individual at different times (Jamrozik et al., 1997; Meyer, 2000b). The variations that arise from such observations are partly related and therefore

constitute a permanent variance that is due to the environment (Mrode, 2005). In analyses of growth and reproduction characteristics, the environmental variance is partitioned in order to accurately estimate the residual variance, which estimates the effect of the environment on the measurement. The permanent environmental effects are modelled as random effects because they are peculiar to the animals. The sum of these effects and the breeding value of the animal represent an estimated future performance of the animal in the same herd (Mrode, 2005).

Residual variance is the component of phenotypic variation due to all other factors that cannot be accounted for in the analysis. These consist of all modes of gene interactions such as dominance and epistasis, and the random environmental effects (Mrode, 2005). This component of variance is an important indicator of the accuracy of the estimates and consequently has a great influence on the reliability of the results. In genetic evaluation, the residual variance is mostly assumed to be homoscedastic; but this assumption is only viable in measurements taken at the same time (Mackinnon et al., 1991). In records made at different times, this assumption introduces bias in the estimated variance components and should therefore be modelled as a heterogeneous component (Burrow, 2001). Residual variance is influenced by the structure of the data. Its value is inflated when the data has missing records and several outliers (Aziz et al., 2002; Maniatis and Pollott, 2003). All these components of variance are important in the estimation of genetic parameters for use in genetic improvement programmes. As a result, their accuracy is indispensable for high genetic progress.

2.4. Genetic parameters and their importance in beef production

Effective breeding programmes depend on the accuracy of genetic and phenotypic parameter estimates, which include heritability, repeatability and correlations between traits (Burrow, 2001). These parameters are ratios of (co) variance components described above and are important in performance evaluation and selection of beef animals. As mentioned earlier, parameters for productive, reproductive and adaptive traits for tropical beef cattle have been estimated. However, breed and environmental specific estimates for tropical Africa beef breeds are scarce (Davis, 1993; Albuquerque and Meyer, 2001). The review of Lôbo (2000) indicates that genetic and phenotypic parameter estimates are variable. This variability has been attributed to various factors such as population history, data size and structure, the model of analysis used, breed and environmental effects (Meyer, 1992; Davis, 1993; Meyer, 1993c; Burrow, 2001; Aziz et al., 2002; Hearnshaw et al., 2002; Rumph et al., 2002; Maniatis and Pollott, 2003). Table 3 presents the estimates of genetic and phenotypic parameters for growth and reproductive traits for beef cattle.

Table 3. Estimates of genetic and phenotypic parameters for growth and reproductive traits for beef cattle

Trait 1[a]	Trait 2[a]	Breed[c]	Model[b]	Parameter estimates[d]					Country	Source
				$h^2_{trait\ 2}$	$m^2_{trait\ 2}$	$r_{AM\ trait\ 2}$	$r_{a\ (1,\ 2)}$	$r_{p\ (1,\ 2)}$		
BW	BW	Boran	AM	0.26					Ethiopia	Haile-Miriam and Kassa- Mersha (1995)
"	"		AMM		0.09	-0.45				
"	"		"	0.14	0.07	0.47			Ethiopia	Demeke et al. (2003)
"	"	Angus	AM	0.52					Australia	Meyer (1993)
"	"		ARM	0.48					"	
"			AMM	0.41	0.12	0.33			"	
"	WW		AM	0.40			0.70	0.51	"	
"			AMM	0.20	0.19	0.27	0.81	0.51	"	
"		Boran	"	0.07	0.03	0.07			Ethiopia	Demeke et al. (2003)
"	12W	Hereford and Angus	AM	0.20					Australia	Meyer (1992, 1993)
"			ARMM	0.12	0.09	0.08	0.70	0.45	"	
	18W	AX and AXBX	AMM	0.26	0.09				"	Mackinnon et al. (1991)
			AM	0.42			0.54	0.36	"	
WW	WW		AMM	0.17	0.34	-0.19			"	Burrow (2001)
	12W		AM	0.41			0.90	0.73	"	
		Boran	AMM	0.12	0.01				Ethiopia	Demeke et al. (2003)
	18W	Angus	"	0.21	0.12	0.27	0.86	0.71	Australia	Meyer (1993)
		Zebu- x	"	0.43	0.28	-0.69	0.69	0.65	"	
12W	12W		AM	0.28					"	
	18W		AMM	0.23	0.18	-0.35	0.92	0.77		
AFC	AFC	Crossbred beef cattle	ARM	0.40					S.Africa	van der Westhuizen et al. (2001)
	CI			0.01			0.03			
	AFC	Boran	"	0.06					Ethiopia	Haile-Miriam and Kassa- Mersha (1994)
	CI			0.04						

[a] BW, birth weight; WW, weaning weight; 12W, 12-month weight; 18W, 18-months weight; AFC, age at first calving; CI, calving interval.

[b] AM, simple animal model; ARM, repeatability animal model; AMM, maternal animal model; ARMM, maternal repeatability animal model.

[c] AX, Africander cross with 50% Africander, 25% Shorthorn and 25% Hereford; AXBX, Africander-Brahman cross with equal contributions from Africander, Brahman, Shorthorn and Hereford; Zebu- x, various zebu crosses.

[d] $h^2_{trait\ 2}$, direct heritability of trait 2; $m^2_{trait\ 2}$, maternal heritability of trait 2; $r_{AM\ trait\ 2}$, direct- maternal genetic correlation for trait 2; $r_{a\ (1,\ 2)}$, additive genetic correlation between traits 1 and 2; $r_{p\ (1,\ 2)}$, phenotypic correlation between traits 1 and 2.

2.4.1. Heritability

Heritability is defined as the proportion of phenotypic variance that is due to heredity. For tropical beef cattle, heritability estimates show a high level of variability (Table 3). This variation is as a result of the differences in the population structure of the herds that provided the data, the model fitted for the analysis, the breed and the environment where the data was obtained. Consequently, it is important that estimates from one population are treated with caution when used in other populations. These estimates are partitioned into maternal and direct heritabilities attributed to maternal and individual animal genetic effects, respectively. Generally, the maternal genetic variance is smaller than the direct genetic variance resulting in higher estimates of direct heritability than maternal heritability (Table 3).

Heritability estimates varied between the models of analysis (Table 3). Estimates obtained using simple animal models (AM) were larger that those obtained using models that consider maternal effects (AMM). This was due to fitting of only one random effect (additive genetic effect) to account for all the genetic sources of variation. The effect of the dam on the growth of its offspring was therefore not accounted for independently as in the latter model but lumped together with the individual genetic effect as genetic variance. When maternal effect model was fitted, the estimate of direct heritability is drastically reduced due to partitioning of the genetic variance into direct and maternal genetic variances (Meyer, 1992). There was a difference in the heritability estimates between breeds (Table 3). This was expected since the genetic potential of various breeds differ for the various traits of interest. In addition, breeds have been subjected to varying levels of selection, which has an effect on the additive genetic variation (van Dyk et al., 2001).

Comparison of heritability estimates for productive and reproductive traits depict lower estimates for female reproductive than productive traits (Table 3). This was because female reproductive traits were highly influenced by the environment and the reproductive performance of the cattle could therefore be improved more through manipulation of production environment than selection (van der Westhuizen et al., 2001). The high heritability estimates for productive traits were due to the high genetic variances attributed to these traits implying a possibility of improvement through selection. There was an increase in maternal heritability up to weaning after which the estimates decreased. Maternal heritability is a function of maternal variance that arises from the environment the dam provides to the calf. However, at weaning when the calf is separated from the dam, the maternal environment is

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withdrawn and the effects of this environment on variance declines as the calf grows and becomes independent (Meyer, 1992).

2.4.2. Repeatability

In many cases, several measurements are taken on an individual for a particular trait. For instance, daily milk recorded in a lactation of dairy cattle and weekly weight gain measured in beef cattle. These measurements are related and therefore constitute a covariance between them due to permanent environmental factors (Mrode, 2005). To account for this covariance in measurements as a component of phenotypic variance, a parameter, repeatability is estimated (Lynch and Walsh, 1998). It is treated as within individual variance and computed as correlation between the repeated measurements (Falconer and Mackay, 1996). If the repeatability estimate is large, it implies the variability in measurements is genetically influenced while small estimates indicate high environmental influence on the measurements.

2.4.2. Correlation

Correlations are measures of the strength of relationship between two variables. High correlation values imply strong relationships between variables and vice-versa (Bourdon, 2000). Correlations can also be positive or negative, implying positive and negative relationship, respectively. A positive correlation between WW and 18W presented in Table 3 implies selection for high WW will result in increased 18W. Correlations are important as they aid in prediction of response to selection in one trait due to selection in another and are partitioned into phenotypic, genetic and environmental correlations.

Phenotypic, genetic and environmental correlations are measures of the strength of the relationships between animal performances among traits, breeding values and environmental effects between traits, respectively. As shown in Table 3, correlations between weight traits were favourable. For example, the correlation between WW and 12W (0.90) indicates that selection for heavier WW would also increase 12W. Estimates of correlations between weight and fertility traits in beef cattle in the tropics are scarce. There is therefore the need to design experiments to estimate them. The genetic correlation between AFC and CI was low. Other important correlations are those between different values of the same trait (e.g., the correlation between maternal and additive effects). A negative additive-maternal correlation explains why selection in traits subject to maternal influence could be ineffective (Baker,

1980). Generally, within trait category correlations are higher than between category correlations (Meyer, 1992; Davis, 1993).

2.5. Models for the analysis of growth and reproductive traits

In most of the tropics, conventional finite animal models have been used in the analysis of growth and reproduction traits. These models include univariate and multivariate models (Haile-Mariam and Kassa-Mersha, 1994,1995; Khombe et al., 1995; Demeke et al., 2003). These models are useful in the analysis of traits that exhibit constant variance such as reproduction traits (Mrode, 2005). However, evaluations of growth performance by these models give estimates with lower accuracies due to the assumption of constant variance. Growth traits are influenced by time variance and therefore this assumption does not hold (Meyer, 2000b; Lewis and Brotherstone, 2002). As a result, models that account for time variance are more appropriate.

2.5.1. Univariate models

Univariate models are those models that analyse one trait at a time (Mrode, 2005). The main limitations of these models relate to their inability to account for relationships between traits, leading to biases in estimates due to selection and their inefficiency in data utilisation (Lynch and Walsh, 1998). Meyer (1993c) observed lower estimates of variance components for final and 12-month weights in Angus cattle that were later increased by bivariate analysis. This was attributed to the removal of selection bias in the univariate estimates when bivariate animal model was invoked. Rumph et al. (2002) obtained higher heritability estimates for growth traits in Hereford cattle using univariate models than bivariate models. Univariate models are however preferred due to their ease of manipulation and reduced computational demands (Meyer, 1992). This explains why most of the growth and reproductive trait analyses revolve around these models.

2.5.2. Multivariate models

These are models in which parameters of several traits can be estimated at once. Multivariate models have the highest level of accuracy of estimates although their use is limited by their high computational demands and the need for accurate estimates of genetic and environmental covariances among traits (Lynch and Walsh, 1998; Albuquerque and Meyer, 2001; Nobre et al., 2003b). The accuracy of estimates resulting from these models are however comparatively higher than univariate analysis. This enhanced accuracy is due to the

ability of the model to account for relationship between the traits and better connections in the data due to residual covariance between traits (Mrode, 2005). An overestimation of the correlation between direct and maternal genetic effects was evident in univariate analysis of growth traits compared to bivariate analysis (Rumph et al., 2002). The difference in the estimates of this correlation was linked to adjustments through the residual covariance matrix when accounting for more than one trait at a time. Strabel et al. (2001) found multivariate models to give better reliabilities than univariate models for purposes of prediction of genetic merit. This was as a result of the model's ability to use extra information from correlated traits.

2.5.3. Covariance functions and random regression models

Evaluation of performance using conventional finite models give estimates with a lower accuracy due to the assumption of constant variance between measurements for traits that change along a trajectory. Biological variables such as growth, feed intake, lactation, and average daily gain change with age following a prescribed trajectory (Huisman et al., 2002). Growth in animals described by weight, increases with time as the animal matures. However, this increase reaches a final or asymptotic value at an intermediate age, meaning that the relative growth rate decreases monotonically as the animal ages (Lewis and Brotherstone, 2002). These changes can be described by genetic parameters, which reflect the extent and direction of genetic change in performance patterns over time due to selection (Albuquerque and Meyer, 2001; Huisman et al., 2002).

Weight in beef cattle is taken on the same individual at various times. These constitute records often referred to as longitudinal data (Meyer and Hill, 1997). In practice, weighing of animals at the same age is not done, and hence weights measured are corrected to certain landmark ages such as age at weaning, 12-month weights, among others (Meyer, 2000b; Nobre et al., 2003b; Fischer et al., 2004b). In some instances, these weights are treated as repeated records of the same trait and analysed by univariate models, assuming a correlation of unity among measurements, which does not always hold (Meyer and Hill, 1997). However, more generally, they are treated as distinct traits in which measurements are taken at these landmark ages (defined by arbitrary age ranges) and analysed by multivariate analysis, assuming constant variance. This results in highly over-parameterised analysis, which increases the sampling errors and makes comparison of animals for the same trait difficult, especially when the spread over age ranges for some traits overlap (Meyer and Hill, 1997; Fischer et al., 2004b). Due to these limitations, a more flexible and accurate method namely,

random regression models (RR), based on covariance functions (CFs) that are described by orthogonal polynomials, has been advocated for estimation of parameters for traits that change continuously with time (Jamrozik et al., 2000; Meyer, 2000b; Fischer et al., 2004b; Meyer, 2004; Schaeffer, 2004).

Covariance functions

A covariance function (CF) is a continuous function that represents the variance and covariance of traits measured at different times along a trajectory. It gives covariance between records taken at different times as a function of time (Meyer, 1998). Covariance functions are an infinite dimensional equivalent of a covariance matrix for a given number of records taken at different ages (Meyer and Hill, 1997; Huisman et al., 2002). Orthogonal polynomials are the most suitable functions to describe CFs because they enable modelling of data with least number of parameters, hence limiting problems associated with over-parameterisation without affecting the accuracy of the estimates (Meyer and Hill, 1997; Albuquerque and Meyer, 2001). van der Werf et al. (1998), Meyer (2000b) and Nobre et al. (2003a) showed how CFs for observations could be estimated by RR using fewer parameters than conventional multivariate models. In these studies, they proposed the use of eigenfunctions and eigenvalues corresponding to the observations, which were significantly different from zero to estimate the covariance between the observations. This reduced computational demands without compromising the accuracy of the estimates. Orthogonal polynomials however, suffer from bending problems especially at the bounds of parameter space when the principle of linearity does not hold, leading to overestimation of genetic parameters (Lewis and Brotherstone, 2002). Schnyder et al. (2001) and Albuquerque and Meyer (2002) suggested the use of Hierarchical models and parametric correlation, respectively; while Lewis and Brotherstone (2002) suggested the transformation of non-linear functions into their linear analogues to circumvent this problem.

Random regression models

Random regression models despite the shortcomings mentioned above, provide a more useful alternative of analysing repeated records than the conventional multivariate models. They provide a means of estimating genetic parameters for all ages without correcting the observations to certain landmark ages (Lewis and Brotherstone, 2002; Nobre et al., 2003a). The models use fixed regression coefficients to account for overall and within fixed class trends while fitting the random regression coefficients for each individual to allow for

individual variations in the trajectory and thereby assuming a particular covariance structure (Meyer, 1998; van der Werf et al., 1998; Schaeffer, 2004). Random regression models are a special case of CFs by which covariance function coefficients are estimated directly by Restricted Maximum Likelihood (REML) (Meyer and Hill, 1997; Albuquerque and Meyer, 2001).

The RR models are advantageous over conventional analytical methods in that they allow for easy interpolation between ages at which recording took place, accurate prediction of selection response and make more efficient use of the data (Meyer and Hill, 1997; Lewis and Brotherstone, 2002; Grzesiak et al., 2003). Besides, a comparison of model performance between RR methodology and Gompertz approach in genetic evaluation of sheep growth was in favour of RR model (Lewis and Brotherstone, 2002; Lewis et al., 2002). Gompertz approach uses an equation with three mathematical parameters to explain growth assuming that relative growth rate declines linearly with the weight of an animal on a logarithmic scale (Lewis and Brotherstone, 2002; Lewis et al., 2002). The RR model provided solutions for genetic and environmental effects simultaneously for all animals, allowing the use of family information in the estimation, which was not the case in the Gompertz approach (Lewis and Brotherstone, 2002). Analysis of weight gain in station-based bulls using two-step procedure (in which fixed linear regressions were first fitted on weight records of bulls to determine weight gain on test that was then subjected to mixed model analysis) and RR methodologies favoured the latter (Schenkel et al., 2002). The results were suggestive of higher genetic progress in animals evaluated by RR than those by two-step procedure. With RR models, it is possible to select animals based on their growth curve. This is important because selection can be done to achieve certain growth patterns for efficient production (Fischer et al., 2004b).

Random regression models have been used in evaluation of lactation performance of dairy cattle (Jamrozik et al., 1997; van der Werf et al., 1998) and growth and feed intake in sheep and pigs (Huisman, 2002; Lewis and Brotherstone, 2002). In beef cattle, RR models have been used mostly in the description of adult and early growth traits with a few considering the evaluation of growth trajectory from birth to mature age (Meyer, 1999; Albuquerque and Meyer, 2001; Meyer, 2001a; Schenkel et al., 2002). Meyer (2000b) showed the ability of RR models to describe the complex variability in growth pattern due to seasonal environmental changes when RR on orthogonal polynomials of age was used. That study showed lack of susceptibility of these models to convergence problems even when over 200 parameters were analysed therefore solving over-parameterisation problems observed in the conventional multivariate analyses. The study also emphasised the flexibility of the RR

models to accommodate data with missing records and additional random effects. Meyer and Hill (1997) and Albuquerque and Meyer (2001) in their studies concluded that CFs and RR models would more accurately estimate genetic parameters and breeding values than the multivariate models due to minimisation of problems resulting from over-parameterised analyses.

With the inconsistent recording and variability of growth patterns of beef cattle in developing countries, the use of RR offers a better means for estimation of performance parameters for genetic evaluation of livestock. Schaeffer (2004) suggested the use of RR models in analysis of various economically important traits in livestock such as survival, fertility and genotype x environment interaction with minor modification of the models to allow for a trajectory.

A number of estimates of genetic parameters for traits in beef cattle using RR models have been published (Table 4). Most of these parameters were obtained from data collected on cattle in station based experimental settings (Meyer, 2000b; Lewis and Brotherstone, 2002; Schenkel et al., 2002) with a few estimates based on field data (Meyer, 1999; Albuquerque and Meyer, 2001; Meyer, 2002; Nobre et al., 2003a; Nobre et al., 2003b).

Table 4. Estimates of direct and maternal heritabilities by random regression models with different orders of fit[a]

Trait[b]	h^2_d	h^2_m	Sources
BW	0.1 (0.14)	0.11	Nobre et al. (2003a)
60d	0.19 (0.12)	0.08 (0.1)	"
152d	0.20 (0.14)	0.09 (0.12)	"
243d	0.20 (0.15)	0.09 (0.12)	"
333d	0.21 (0.17)	0.07 (0.11)	"
601d	0.35 (0.25)	0.03 (0.07)	"
BW	0.32	0.02	Albuquerque and Meyer (2001)
110- 120d		0.25	"
120- 180d	0.14		"
240d		0.20	"
270d	0.17		"
Weight gain to: 28d	0.14		Schenkel et al. (2002)
56d	0.24		"
84d	0.31		"
140d	0.38		"

[a]Estimates in parentheses are from data with no missing records; h^2_d, direct heritability; h^2_m, maternal heritability.
[b]BW, birth weight; 60d, weight at day 60; 110- 120d, weight between day 110 and 120; 120- 180d, weight between day 120 and 180; 152d, weight at day 152; 240d, weight at day 240; 243d, weight at day 243; 270d, weight at day 270; 333d, weight at day 333 and 601d, weight at day 601.

A feature of random regression models prominent in this table is its ability to estimate parameters at any point of the growth curve. These estimates however, vary between authors due to differences in the variables included in the models, the orders of fit and data structure, which influenced the standard errors (Maniatis and Pollott, 2003; Nobre et al., 2003a).

Besides, the influence of genotype x environment interaction and breed differences limit the universal application of the estimates obtained in these studies (Maniatis and Pollott, 2002). It is therefore important that environmental and breed specific estimates are availed for increased accuracy of selection.

2.6. Genetic and environmental trends

Genetic and environmental trends are measures of changes that take place in herds (Falconer and Mackay, 1996). They are indicators of genetic and management progresses made and therefore are important in evaluation of the effectiveness of breeding programmes and determining the success of a selection programme (Musani and Mayer, 1997; Hofgren and Schinckel, 1998; Ebangi et al., 2000). They provide information about herd improvement over time and are a reflection of the herd's progress compared to the breed as a whole (Hofgren and Schinckel, 1998). Positive genetic and environmental trends are indicators of favourable selection methods and good management, respectively. Plasse et al. (2002) observed fluctuating phenotypic trends for 548- day weight, which was attributed to the deterioration in pastures during the study period.

Estimation of annual genetic trends in growth and reproductive traits is achieved by regression of average breeding value in that trait on the year while the annual environmental trend are estimated by regression of year-season effects for each season on the year to obtain coefficients whose average gives the annual environmental trends (Musani and Mayer, 1997). In the evaluation of growth performance of swine between herds, Hofgren and Schinckel (1998) calculated genetic trends by regressing the maternal line index on the year of birth. They observed an increase in the index annually, a phenomena they attributed to extensive use of expected progeny difference in selection decisions. Herds selected on the basis of estimated breeding values have higher genetic trends than those selected based on physical appraisal. This was also the scenario in herds where proven bulls are used against herds where untested bulls are used (Plasse et al., 2002).

There is scarcity of information on genetic and environmental trends in beef herds in developing countries, which clearly indicates lack of evaluation of breeding programmes of these herds (Plasse et al., 2002). Therefore, examination of trends in Kenya Boran cattle will provide information for re-evaluation of management practices and earlier selection programmes for efficient growth and reproductive performance of these cattle.

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CHAPTER THREE

ENVIRONMENTAL SOURCES OF VARIATION IN GROWTH AND REPRODUCTIVE PERFORMANCE

3.1. Introduction

In a beef production enterprise, growth and reproduction efficiency are of economic importance. The expression of these characters in an animal is influenced by the production environment and the animal's genetic constitution (Falconer and Mackay, 1996; Lynch and Walsh, 1998; Bourdon, 2000). Production environments vary as a result of different management practices and constantly changing climatic conditions, leading to variability in animal performance. An animal of high genetic value may perform dismally when the production environment is not right due to the negative interaction between the animal's genes and its environment. Therefore, the magnitude of environmental influence on animal performance should be quantified by evaluating the various environmental sources of variation. This is important in facilitating unbiased performance comparison, better management practice and successful design of efficient breeding strategies for genetic improvement (van Bebber et al., 1997).

Due to the dynamism of production systems, constant evaluation of environmental variables ought to be an integral part of any animal performance evaluation scheme. This ensures close monitoring of the systematic sources of variation in performance for effective animal management. The objective of this chapter was to determine environmental factors affecting growth and reproductive traits in the Kenya Boran cattle for subsequent inclusion in the animal model evaluation and obtain mean estimates for these traits.

3.2. Material and methods

3.2.1. 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 north-west of Nairobi, Kenya, respectively. These farms were considered because they maintain stud herds registered with the Kenya Studbook and are members of the Kenya Boran cattle Breeders' Society (KBCBS). In addition, they had consistent records that could facilitate the use of the analytical methods

proposed for the study. 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 800mm. 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 with long and short rains falling between March and June, and September and October, respectively. The two rainy seasons are separated by dry seasons. The hottest and driest months in both farms are January and February.

3.2.2. 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 were grazed during the day and "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 and weaning weights taken at 7 and 9 months of age on the research station and ranch, respectively. 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 dispatched 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. 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 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 ratios on the ranch and research station were 1:50 and 1:60, respectively. 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 pasteurelosis.

3.2.3. Data and traits

Data on growth and reproduction performances 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 AFC below 640 and over 1827 days and 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 high number of growth records was due to consistent recording of weights on both farms, unlike recording of reproductive performance that was more consistently done on the commercial ranch than the research station. 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 since these weights were not recorded on the ranch. Among the growth traits, only records on WW were analysed from the commercial ranch. The reproductive traits consisted of AFC and CI. In addition, calving in the first three parities (CI1, CI2 and CI3) were also considered as separate traits.

3.2.4. Statistical analysis

Analyses of variance were conducted for different traits in order to assess the environmental effects on performance using the GLM procedures of GENSTAT (GENSTAT, 2003). Preliminary analyses examined the relative proportions of variation that were accounted for by various fixed effects in order to establish the most suitable model to describe the data. The effects included in the model for the analysis of growth traits were sex (2 classes), parity of the dam (five classes), year (15 classes) and season (2 classes) of birth and their first order interaction, and their second order interaction with herd (2 classes), year (11 classes) and season (2 classes) of weaning and their first order interactions, and age at weighing as a covariable.

For BW and WW, year and season of weaning and their first order interactions, and age at weighing were omitted in the model. For 12W, 18W and 24W, year and season of birth and their first order interactions were omitted in the model. Among the growth traits, herd effects and their interactions with season and year effects were fitted only for WW since data from both farms were used.

For the analyses of reproductive traits, the fixed effects included in the model were herd (2 classes), year (11 classes) and season (2 classes) of birth and calving and their second order interactions. For AFC, herd, year and season of birth and their second order interaction were the only fixed effects while for CI in each parity, herd, year and season of calving, their second order interactions and age at calving as a covariable were the only effects fitted because preliminary analysis fitting herd, year and season of birth and calving together resulted in low R^2, with the former accounting for a relatively low proportion of variance.

From the preliminary analysis, fitting main effects and their interactions in the model resulted in over-parameterisation of the models. In such cases, the interactions which accounted for the larger proportions of variation than the main effects were fitted in preference to the main effects.

The year of birth and weaning were from 1989 to 2003 and 1993 to 2003, respectively, 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 - June and September-October and the dry season comprising of January- February, July- August and November - December. 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.

3.3. Results

The results of analyses of variance of various factors influencing growth are presented in Table 5. Sex significantly ($P<0.01$) influenced all growth traits. Parity of the dam significantly ($P<0.05$) influenced all growth traits apart from 24W. The year-season of birth influenced BW and WW significantly ($P<0.001$). Similarly, year-season of weaning significantly ($P<0.001$) influenced 12W, 18W and 24W. The herd effect was significant ($P<0.001$) for WW. Age of the animal at weighing significantly ($P<0.01$) affected 24W.

Results of analyses of variance of various factors influencing reproductive performance are presented in Table 6. All calving intervals were significantly ($P<0.001$) affected by the effect of the herd-year-season of calving. The influence of herd-year-season of

birth on AFC was significant (P<0.001). The effect of age at calving as a covariate was significant for all calving intervals except CI3. Age at first calving as a covariate was significant for CI.

Table 5. Analysis of variance for factors affecting growth performance

Trait[a]	Source of variation	df	Mean squares	F value
BW				
	Sex	1	223.12	10.23**
	Parity	4	63.86	2.93*
	Year-season of birth	21	109.33	5.01***
WW				
	Sex	1	390973.20	533.94***
	Parity	4	578529.7	790.08***
	Herd	1	38158.0	52.11***
	Year-season of birth	30	39591.4	54.07***
12W				
	Sex	1	22005.7	34.32***
	Parity	4	1562.3	2.44*
	Year-season of weaning	21	10653.7	16.61***
	Age (covariate)	1	1946.0	3.03ns
18W				
	Sex	1	38363.0	34.69***
	Parity	4	2903.0	2.62*
	Year-season of weaning	22	13653.0	12.34***
	Age (covariate)	1	968	0.87ns
24W				
	Sex	1	65412.0	45.39***
	Parity	4	2130.0	1.48ns
	Year-season of weaning	20	14423.0	10.01***
	Age (covariate)	1	19748.0	13.70***

[a]BW, birth weight; WW, weaning weight; 12W, 12-month weight; 18W, 18-month weight; 24W, 24-month weight.
*P < 0.05, **P < 0.01, ***P < 0.001, ns = not significant.

Table 6. Analysis of variance for factors affecting reproductive performance

Trait[a]	Source of variation	df	Mean squares	F value
AFC				
	Herd-year-season of birth	41	394012.0	12.67***
CI1				
	Herd-year-season of calving	41	144164.0	9.12***
	Age (covariate)	1	869497.0	54.99***
CI2				
	Herd-year-season of calving	39	100446.0	6.4***
	Age (covariate)	1	62025.0	4.0*
CI3				
	Herd-year-season of calving	33	88964.0	7.23***
	Age (covariate)	1	2396.0	0.2ns
CI				
	Herd-year-season of calving	41	61765.0	0.99***
	Age (covariate)	1	220647.0	24.27***

[a]AFC, age at first calving; CI1, first calving interval; CI2, second calving interval; CI3, third calving interval; CI, pooled calving interval.
*P < 0.05; **P < 0.01; ***P < 0.001; ns, not significant.

Estimates of least square means for growth and reproductive traits by sex, herd and parity are presented in Table 7. Figures 1 and 2 show trends in the least square means for growth and reproductive traits grouped by the effect of the year, respectively. The overall mean for BW was 27.99 kg. There was a significant difference in BW between sexes in which male calves weighed heavier at birth than females (Table 7). The trend of BW remained fairly constant throughout the years considered in the study (Figure 1).

The mean WW was 184.55 kg. Weights between sexes were significantly different where male calves tended to weigh heavier at weaning than female calves. This trend was also evident in post- weaning growth traits (12W, 18W and 24W). Male calves were about 0.88 times heavier than female calves at weaning. Herd 1 produced calves which were 1.14 times heavier at weaning than herd 2. Trends in WW depict a fluctuation in performance across the years with peak performances observed in 1996 and 2000 and low performances in 1991, 1993 and 1998 (Figure 1).

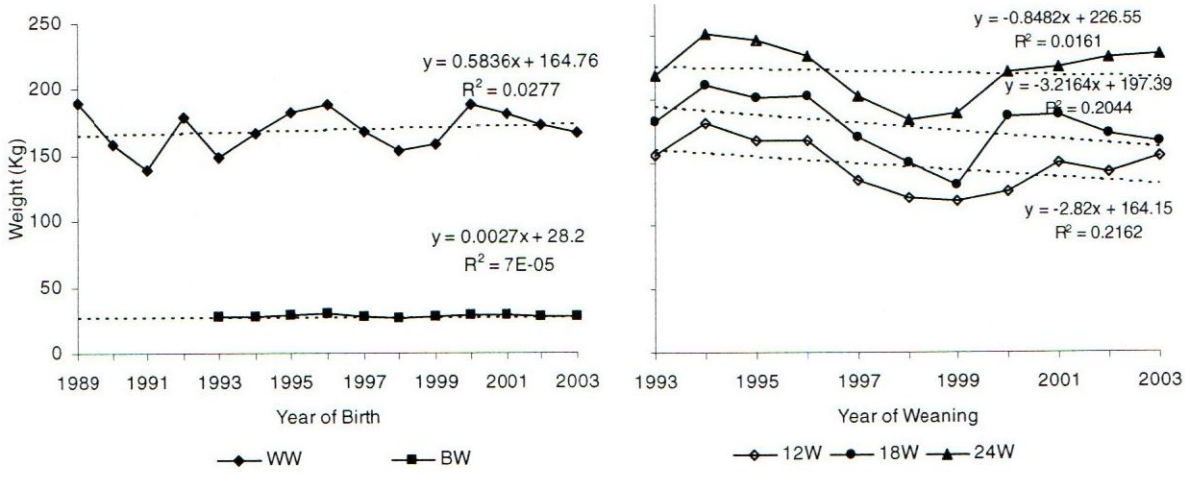


Figure 1. Trends in least square means for growth traits

The mean 12W was 145.39 kg. This trait and other post-weaning traits were recorded in only herd 2; therefore between herds comparison was not feasible. Male animals were 1.07 times heavier than females. 12W showed a declining trend across the years (Figure 1). Performance improved from 155.8 kg in 1993 to peak at 180.2 kg in 1994, after which it continuously dropped to 119.2 kg in 1999 and improved thereafter.

Table 7. Least square means (±s.e.) of growth and reproductive traits by sex, herd and parity

Effect[a]	Trait[b]									
	BW (kg)	WW (kg)	12W (kg)	18W (kg)	24W (kg)	AFC (days)	CI1 (days)	CI2 (days)	CI3 (days)	CI (days)
Overall	27.9	184.6	145.4	178.8	220.9	1187.7	496.6	460.1	442.6	476.9
% CV	17.4	22.5	20.7	21.9	19.6	16.1	27.1	28.6	27.1	20.9
Sex										
1	27.8[a]	158.5[a]	141.9±1.6[a]	171.1±2.9[a]	210.1±4.3[a]					
2	28.7[b]	180.4[b]	151.6±1.6[b]	185.1±2.9[b]	232.8±4.3[b]					
Herd										
1		208.5[a]				1148.6±8.6[a]	483.4±6.2[a]	465.8±8.6[a]		470.4±5.5[a]
2		130.4[b]				1392.2±14.8[b]	586.2±11.4[b]	492.6±14.5[b]		538.1±8.2[b]
Parity										
1	27.6[a]	168.6[a]	143.3[a]	173.5±3.3[a]	211.5±4.7[a]					
2	28.3[b]	172.0[b]	145.7[b]	182.4±3.4[b]	224.5±4.8[b]					
3	27.8[ac]	164.4[c]	144.6[ac]	171.9±3.8[ac]	214.6±4.9[ac]					
4	28.7[bd]	170.4[ab]	148.4[d]	180.1±4.1[ab]	224.7±5.7[bd]					
5	28.2[bd]	163.4[c]	146.2[bcd]	182.6±4.6[b]	232.1±6.4[bcd]					

[a]Within effects, means with the same superscript are not significantly different ($P < 0.05$).
[b]BW, birth weight; WW, weaning weight; 12W, 12-month weight; 18W, 18-month weight; 24W, 24-month weight; AFC, age at first calving; CI1, first calving interval; CI2, second calving interval CI3, third calving interval; CI, pooled calving interval.

The mean 18W was 178.82 kg. The weights among animals varied significantly between sexes and parities at this age. Males were 1.08 times heavier than females. Animals born in second, fourth and fifth parities were significantly heavier than those born in first and third parities. A downward trend was evident in 18W across the years (Figure 1). Peak performance was in 1994 (211.3 kg) followed by a continuous decline until 1999 (132.4 kg). Thereafter, an improvement was observed.

The mean 24W was 220.98 kg. Sexual dimorphism was evident whereby male animals were 1.11 times heavier than females. Animals born in first and third parities weighed lighter than those born in second, fourth and fifth parities. Like 12W and 18W, 24W performance depicted a declining trend. Performance was highest in 1994 (251 kg), dropped through to 1998 (183 kg) then increased thereafter.

The mean AFC, CI1, CI2, CI3 and CI were 1187.74 days, 496.62 days, 460.14 days, 442.57 days and 476.91 days, respectively. Animals in herd 1 tended to have shorter AFC and CI than herd 2. Generally, there was a negative trend in AFC across the years. However, AFC increased from 1989 to 1992 followed by a decline thereafter. The trends in CI were negative throughout (Figure 2). However, there were observable fluctuations with an increase in CI1 in 1992 from 1991, followed by a declining CI, which increased between 1996 and 1999. A similar pattern was observed in other CIs.

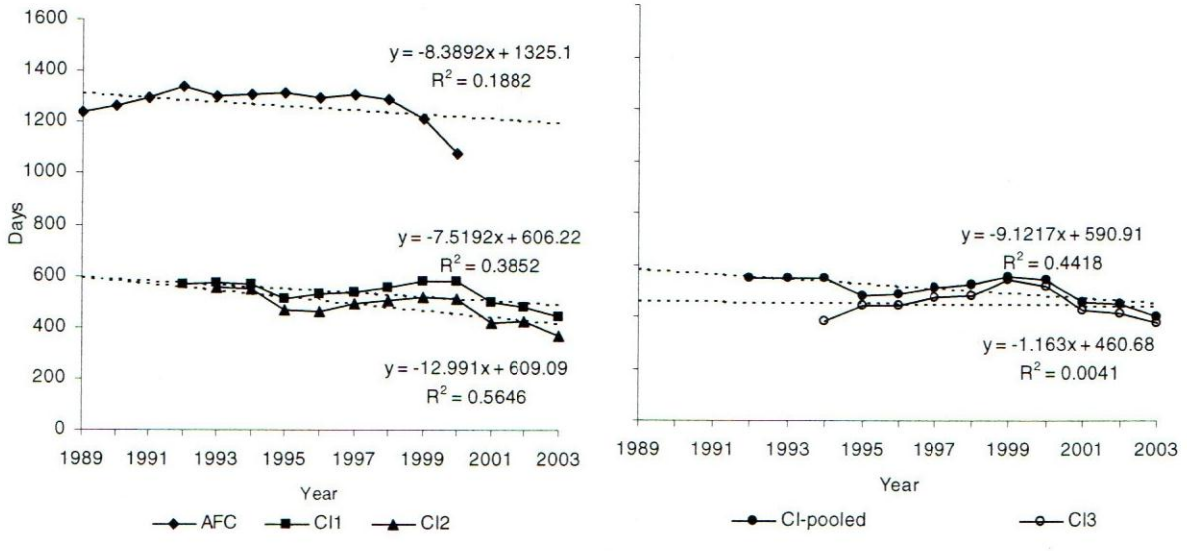


Figure 2. Trends in least square means for reproductive traits

3.4. Discussion

Environmental effects influencing performance of tropical beef cattle have been reported under various production conditions. This is important in formulating management

policies and production decisions on the farms. From this study, sexual dimorphism was evident in growth performance of Kenya Boran cattle in which male animals weighed heavier than females. This is a physiological phenomena arising from higher levels of testosterone hormone in males, which accelerate muscle deposition and therefore faster growth rate compared to females. Characterisation studies reported sexual dimorphism in growth performances of Boran and Sahiwal cattle in the ASAL (Trail and Gregory, 1981; Mwandotto et al., 1988).

The significant effect of year-season on growth depicts the effect of climatic conditions on performance. Years which experienced rainfall scarcity recorded a decline in growth performance relative to years that had adequate rainfall. Fairly constant trends in BW across years indicate the ability of the Boran dams to provide a neutral prenatal environment for calf growth irrespective of the fluctuations in environmental conditions. Fluctuations in WW performance across the years depict the sensitivity of calves to postnatal stress. Exposure of nursing dams to prolonged nutritional stress due to long drought led to reduced milk production and consequent nutrient deprivation in the calves.

Calves born in early parities had low BW than those born in later parities due to nutrient competition between reproduction and maintenance needs of the animals, which is high in younger dams than older dams. In separate studies, (Okeyo et al., 1998; Indetie et al., 2000a) reported significant influences of parity and age of the dam on BW of calves. The significant effect of parity in later weights (WW, 12W and 18W) was occasioned by low milk production of the young dams. Lower 18W in the third parity could be explained by the relatively shorter CI2 implying minimal post-natal rest, which did not adequately allow for regeneration of mammary tissues and therefore reduced maternal ability in the third parity. Significant effects of parity were also observed in the characterisation study of the Boran and Sahiwal cattle (Trail and Gregory, 1981).

Weaning weight performance was significantly different between the herds in which animals from herd 1 weighed heavier at weaning, implying better management than animals from herd 2. The significant effect of age at weighing for 24W shows the potential bias in decisions to select or cull animals based on performance parameter estimates from analyses where their ages were not accounted for. If age at weighing is not accounted for, selection would tend to favour older animals.

Reproductive performance is usually a critical censure of the efficiency of the production system. In less efficient systems, performance of animals is usually lower than in more efficient systems. Effect of the herd-year-season was a significant source of variation for

reproductive performance. The significant effects of the year of calving and AFC on CI have been reported in populations of Boran and Boran-Friesian crosses in Ethiopia (Demeke et al., 2004). The significant effect of the herd on reproduction performance implies differences in reproductive management of the animals between the herds. Management in herd 1 was vigilant on reproductive performance that the animals in the herd had shorter AFC and CIs compared to herd 2.

Age at first calving and CIs declined across the years. This depicts continuous improvement in reproductive performance through reduction of CI and early maturity of the Boran females. This was after a management decision on both herds to reduce age of introduction of heifers into the breeding herds from 24 months to 18- 20 months and culling of animals that did not calve down within two year after the introduction. However, observed fluctuations were a response of the animals to nutritional stresses, given that the animals were not supplemented during dry periods. (Haile-Mariam and Kassa-Mersha, 1994) observed late AFC and long CIs in Boran cattle in Ethiopia, which were attributed to late sexual maturity of females due to nutrition related stressors that depressed growth leading to late attainment of weight at sexual maturity and low male to female ratio.

The significant influence of sex, parity of the dam, year of birth, weaning and calving, and their interactions on growth and reproductive traits is an indicator of the role played by non-genetic factors on their expression. This has implications on accuracy of genetic evaluation such that in analyses where environmental effects are well accounted for, accuracy of parameter estimates is enhanced. Therefore, significant effects influencing performance as found in this chapter would constitute models for subsequent genetic evaluation of growth and reproductive traits by univariate, multivariate and random regression analyses under a mixed animal model framework in the subsequent chapters.

3.5. Conclusions

There is evidence of environmental influence on both growth and reproductive performance of the Kenya Boran cattle. From this study, climatic conditions had a great influence on performance levels arising from feeding systems in the ASAL that were dependent on rain fed natural pastures. Supplementary feeding of animals with high feed requirements such as in-calf and suckling females (in-calf heifers and young dams) would greatly ease the nutritional stress during dearth periods. There is need to examine management practices to check the negative trends in growth performance and fluctuations in

reproductive traits. For fair ranking of animals between environments, it is important to adjust for environmental effects on their performance.

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CHAPTER FOUR

DIRECT AND MATERNAL (CO)VARIANCE COMPONENTS, GENETIC PARAMETERS AND ANNUAL TRENDS FOR GROWTH AND REPRODUCTIVE TRAITS

4.1. Introduction

Growth and reproductive performances are influenced by direct additive genetic effects. Growth performance is influenced by additional effects attributed to the dam (maternal effects) (Dodenhoff et al., 1998). In temperate beef breeds, direct and maternal (co)variance components for growth traits have been estimated (van Vleck et al., 1996; Dodenhoff et al., 1998; Dodenhoff et al., 1999a; Ferreira et al., 1999). In tropical breeds, maternal effects are often omitted during genetic evaluation. Where maternal genetic effects are of importance, but omitted, genetic parameters are biased upwards (Baker, 1980; Meyer, 1992) and realised selection-efficiency reduced (Hazel et al., 1994). In few studies where maternal effects have been accounted for, they have been considered as either a genetic component only or a permanent environmental effect separately from birth to final weight (Haile-Mariam and Kassa-Mersha, 1995; Demeke et al., 2003). There is the need to examine maternal effects holistically to accurately account for the various sources of variation in growth performance.

The need to incorporate growth and reproductive traits in the selection programme for the Kenya Boran cattle breed cannot be over-emphasised. Knowledge of the magnitude of the (co)variance components for growth and reproductive traits is critical. Therefore, the complete covariance structure of these traits needs to be estimated. This chapter estimates direct and maternal additive genetic (co)variance components, genetic parameters and annual trends for growth and reproductive traits in the Kenya Boran cattle breed in Kenya.

4.2. Material and methods

4.2.1. Data and traits

Data on growth traits (BW, WW, 12W, 18W and 24W) and reproduction traits (AFC, CI, CI1, CI2 and CI3) of Kenya Boran cattle were collected from 1989 to 2004 on a large-scale commercial ranch and a national beef research station. The description of the farms and herd management practices has been presented in Chapter 3. After editing the data for

consistency of pedigree information and correct dates of birth, calving and weighing, a final data set comprised of 4502 records for analyses of growth traits and 2681 records for analyses of reproduction traits. The data structure and summary statistics for each trait are presented in Table 8.

4.2.2. Statistical analyses and modelling

Estimates of (co)variance components and genetic parameters were obtained using the ASREML programme (Gilmour et al., 2001) fitting both univariate and multivariate animal models. The fixed part of the model consisted of effects that significantly influenced growth and reproductive performance in Chapter 3. They were sex (2 classes), parity of the dam (5 classes), year-season of birth (22 classes), year-season of weaning (22 classes) and age at weighing as a covariable for the analysis of growth traits and herd-year-season of birth (40 classes), herd-year-season of calving (40 classes) and age at calving as a covariable for analysis of reproductive traits. The following six models were fitted on the data:

Model 1 $\mathbf{y} = \mathbf{Xb} + \mathbf{Z_1a} + \mathbf{e}$ (1)

Model 2 $\mathbf{y} = \mathbf{Xb} + \mathbf{Z_1a} + \mathbf{Z_3c} + \mathbf{e}$ (2)

Model 3 $\mathbf{y} = \mathbf{Xb} + \mathbf{Z_1a} + \mathbf{Z_2m} + \mathbf{e}$ (3)

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

Model 4 $\mathbf{y} = \mathbf{Xb} + \mathbf{Z_1a} + \mathbf{Z_2m} + \mathbf{e}$ (4)

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

Model 5 $\mathbf{y} = \mathbf{Xb} + \mathbf{Z_1a} + \mathbf{Z_2m} + \mathbf{Z_3c} + \mathbf{e}$ (5)

with $\text{cov}(\mathbf{a}, \mathbf{m}) = 0$, $\text{var}(\mathbf{c}) = \mathbf{I}_{NC}\sigma^2_c$ and $\text{var}(\mathbf{e}) = \mathbf{I}_n\sigma^2_e$

Model 6 $\mathbf{y} = \mathbf{Xb} + \mathbf{Z_1a} + \mathbf{Z_2m} + \mathbf{Z_3c} + \mathbf{e}$ (6)

with $\text{cov}(\mathbf{a}, \mathbf{m}) = \mathbf{A}\sigma_{am}$, $\text{var}(\mathbf{c}) = \mathbf{I}_{NC}\sigma^2_c$ and $\text{var}(\mathbf{e}) = \mathbf{I}_n\sigma^2_e$

where **y** is a vector of observations on the specific trait of the animal; **b, a, m** and **c** the vectors of fixed effects including covariables, direct additive genetic effects, maternal additive effects and maternal permanent environmental effects, respectively; **X, Z_1, Z_2** and **Z_3** the corresponding incidence matrices relating the effects to **y; e** the vector of residual error. **A** the numerator relationship matrix; **I** the identity matrix. NC the number of dams, n the number of animals in the analysis including parents without records, σ_{am} the direct additive genetic by maternal genetic covariance and σ^2_c and σ^2_e the maternal permanent environmental and residual error variances, respectively.

Table 8. Data structure and summary statistics for 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
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
Summary statistics										
Mean	27.99	184.6	145.39	178.8	221.0	1187.7	476.91	496.6	460.1	442.5
SD	4.88	41.57	30.15	39.11	43.30	191.47	99.842	134.3	131.4	120.0
CV (%)	17.42	22.53	20.74	21.87	19.60	16.12	20.94	27.05	28.56	27.11

[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.

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. Phenotypic variance (σ^2_p) was calculated as the sum of direct additive genetic variance (σ^2_a), maternal genetic variance (σ^2_m), σ_{am}, σ^2_c and σ^2_e. Total heritability (h^2_T) was calculated as total additive genetic variance as a proportion of phenotypic variance ($\sigma^2_{\text{total-additive}}/ \sigma^2_p$). The total genetic variance is the sum of all the genetic effects in the model, i.e., $\sigma^2_{\text{total-additive}} = (\sigma^2_a + 0.5\sigma^2_m + 1.5\sigma_{am})$. Likelihood ratio tests were conducted to determine the most suitable model for each growth trait in a univariate analysis. For reproductive traits, it was not possible to perform likelihood ratio tests due to limitations of the data. 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.

Due to constraints arising from the data structure, the use of the most suitable model in multivariate analysis was not permissible. As a result, a simple animal model (Model 1) was used to carry out a series of multivariate analyses to estimate the full range of covariances amongst the traits considered. The resulting (co)variance components and ratios were pooled, weighting each estimate by the inverse of its sampling variance ($S.E^2$). Analyses between trait categories consisted of female animals that had at least one growth and one reproductive trait.

4.2.3. Estimation of annual trends

Genetic trends were estimated by regression of the average predicted breeding values in the particular trait on the year of birth. The environmental trends were estimated using the

solutions for the year-season effects. The predicted breeding values were from univariate analyses. Due to the interaction between year and season, differences between the years are not estimable functions. Therefore, for each season the solutions for the year-season were regressed on the year (Musani and Mayer, 1997). This gave two sets of regression coefficients for the two seasons (dry and wet) across the years.

4.3. Results

4.3.1. Univariate analyses

From the likelihood ratio tests, the 'best' model for BW did not include maternal effects (Model 1). The appropriate models for WW, 12W, 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 9. 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 proportion of total variance than maternal genetic effects. Maternal genetic effects were lowest at 18W.

Table 9. Estimates of variance components and genetic parameters[a] from univariate analyses using the "best" models for growth traits and model 1 for reproductive traits

Trait[b]	σ^2_a	σ^2_m	σ^2_c	σ^2_e	σ^2_p	h^2	m^2	r_{am}	c^2	h^2_T
BW	7.70			15.19	22.88	0.34				0.34
WW	64.25	73.60	83.46	324.91	528.60	0.12	0.14	-0.25	0.16	0.14
12W	129.18	224.55	29.35	379.41	664.40	0.19	0.34	-0.58	0.04	0.14
18W	81.98	38.28	104.82	872.71	1090.00	0.08	0.04	-0.14	0.10	0.08
24W	207.31	158.70		1162.91	1434.00	0.14	0.11	-0.52		0.10
AFC	1264.29			29847.20	31110.00	0.04				0.04
CI	26.08			8930.28	8956.00	0.00				0.00
CI1	0.00			15538.50	15540.00	0.00				0.00
CI2	2391.84			13066.70	15460.00	0.15				0.15
CI3	0.00			12213.90	12210.00	0.00				0.00

[a] σ^2_a, additive genetic variance; σ^2_m, maternal genetic variance; σ^2_c, maternal permanent environmental variance; σ^2_e, residual error variance; σ^2_P, 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^2_T, total heritability. Standard errors for direct heritability, maternal heritability and maternal environmental variance as a proportion of phenotypic variance ranged from 0.04 to 0.10, 0.09 to 0.15 and was 0.09, respectively.
[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.

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^2_T) 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 (i.e., CI1, CI2 and CI3), which arose from the highly variable data sizes in the constituent traits.

4.3.2. Multivariate analyses

Estimates of variance components and genetic parameters for growth and reproductive traits obtained from multivariate analyses using model 1 are presented in Table 10. Due to limitations in the size and structure of the data, other combinations within reproductive trait category, and between reproductive trait and growth trait categories were not estimable. Estimates of genetic variances from multivariate analyses of growth and reproductive traits were higher than those from univariate analyses (Table 9). Among the growth traits, 12W had a lower estimate of phenotypic variance from multivariate analyses than from univariate analyses. For reproductive traits, only AFC had a phenotypic variance that was higher from multivariate analyses than from univariate analyses.

The heritability estimates for BW and reproductive traits estimated from multivariate analyse were generally comparable to those obtained from univariate analyses. The estimates for all other growth traits studied (WW, 12W, 18W and 24W) were higher in multivariate analysis than in the univariate analysis. The change in magnitude of heritability estimates was most pronounced for WW, 12W and 18W, which increased from 0.12 to 0.40, 0.19 to 0.38 and 0.08 to 0.21, respectively. Under univariate analyses, these traits were analysed using a model that also accounted for maternal genetic effect, maternal permanent environment and covariance between genetic effects (model 6).

Table 10. Estimates of variance components and genetic parameters[a], from multivariate analyses using model 1

Trait[b]	σ^2_a	σ^2_e	σ^2_p	h^2	Correlations[c]							
					BW	WW	12W	18W	24W	AFC	CI1	CI2
BW	8.32	14.77	23.01	0.36		0.13	0.13	0.17	0.20			
WW	232.21	338.61	576.93	0.40	0.49		0.80	0.62	0.54	-0.05		
12W	215.80	375.76	600.17	0.38	0.36	0.94		0.82	0.71			
18W	231.66	858.64	1096.07	0.21	0.49	0.88			0.86			
24W	252.87	1215.98	1469.15	0.17	0.52	0.64	0.73	0.79				
AFC	2317.38	26534.56	29316.37	0.08		0.72					-0.42	
CI1	644.31	16816.36	17128.13	0.04						-0.18		0.03
CI2	2420.30	13045.20	15470.00	0.16							-0.30	

[a] σ^2_a, additive genetic variance; σ^2_e, residual error variance; σ^2_p, phenotypic variance; h^2, direct heritability. Standard errors for direct heritability, genetic and phenotypic correlations ranged from 0.04 to 0.10, 0.01 to 0.04 and 0.02 to 1.23, respectively.

[b] BW, birth weight; WW, weaning weight; 12W, 12-month weight; 18W, 18-month weight; 24W, 24-month weight; AFC, age at first calving; CI1, first calving interval; CI2, second calving interval.

[c] Genetic correlations below the diagonal, phenotypic correlations above the diagonal.

The correlations between the various growth traits were positive but variable in magnitude. The phenotypic correlation between BW and other growth traits (WW, 12W, 18W and 24W) were low ranging from 0.13 to 0.20. Phenotypic correlations between WW and other growth traits declined as the age of the animals increased from 0.80 for 12W to 0.54 for 24W. Phenotypic correlation between 12W and 18W and 24W, and between 18W and 24W were all high (>0.70). Genetic correlations between the traits were higher than the corresponding phenotypic correlations. The most notable differences were between BW and the other growth traits, which ranged from 0.36 to 0.52.

The phenotypic correlation between WW and AFC was low and negative (-0.05) but the corresponding genetic correlation was high and positive (0.72). The phenotypic correlation between AFC and CI1 was strong but negative (-0.42) while the genetic correlation between the two traits was weak (-0.18). The phenotypic correlation between CI1 and CI2 was low but positive. The genetic correlation between these traits was moderately strong and negative (-0.30).

4.3.3. Genetic and environmental trends

Genetic trends for growth traits are presented in Figure 3. A fluctuating performance pattern was observed across years for all traits up to 1997 after which there was a positive trend in post-weaning growth traits over the years. The coefficients of genetic progress for BW, WW, 12W, 18W and 24W were 0.05, -0.02, 0.67, 0.21 and 0.37 kg/yr, respectively.

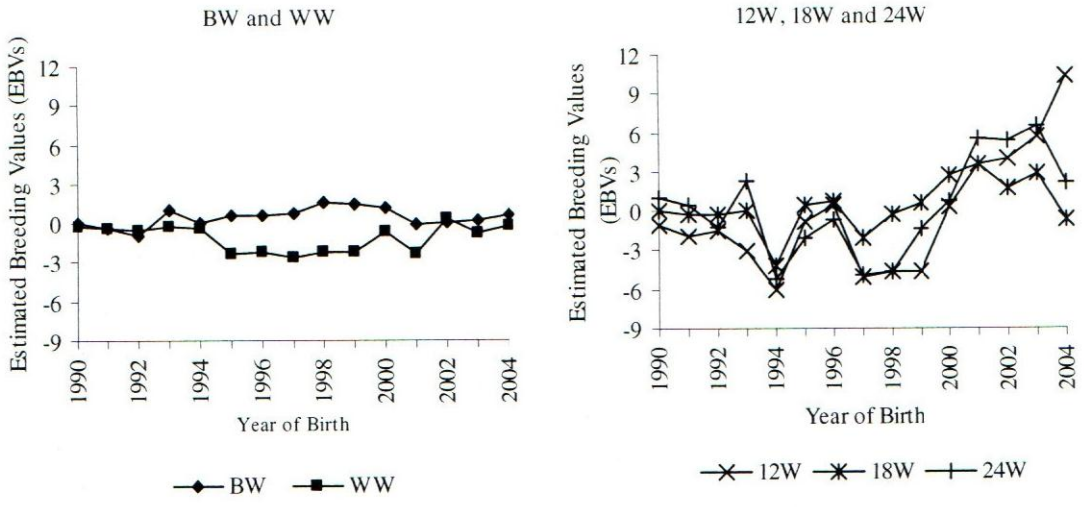


Figure 3. Genetic trends for growth traits

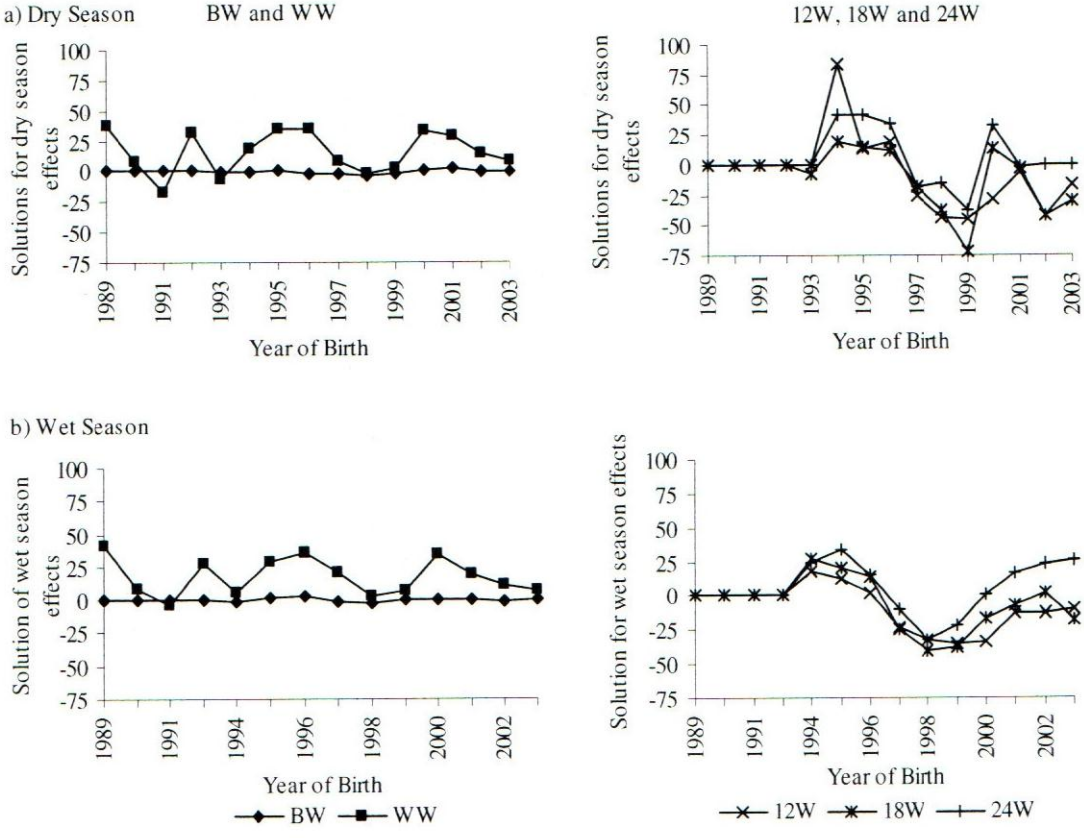


Figure 4. Environmental trends for growth traits during the dry and wet seasons

Environmental trends for growth traits for animals born within the two different seasons are presented in Figure 4. Birth weight tended to remain the same over the years irrespective of the season of birth. Weaning weight fluctuated over the years. However,

seasonal differences were not significant. For post-weaning traits (12W, 18W and 24W), seasonal differences in growth were evident with a more consistently positive change in the traits evident during the wet season from 1998- 2003. The coefficient of change in environmental trends for BW, WW, 12W, 18W and 24W were 0.05, 0.10, -3.41, -2.71 and –0.60 kg/yr during the dry season, respectively. In the wet season, the corresponding coefficients of change in environmental trends were –0.07, -0.53, -2.32, -2.03 and 0.6 kg/yr.

Genetic and environmental trends for reproductive traits are presented in Figures 5 and 6, respectively. No significant genetic trend was evident. The coefficients of change in genetic trends were –0.03, 0.00, 0.52 and 0.00 days/yr for AFC, CI1, CI2 and CI3, respectively. Environmental trend lines were negatively sloped in both dry and wet seasons for AFC, CI1 and CI2. The trend for calving interval in the third parity was slightly positive in both seasons. The coefficients of change in environmental trends for AFC, CI1, CI2 and CI3 were –10.82, -12.07, -7.54 and 45.45 days/yr, respectively during the dry season and –9.31, -7.62, -8.50 and 16.68 days/yr during the wet season.

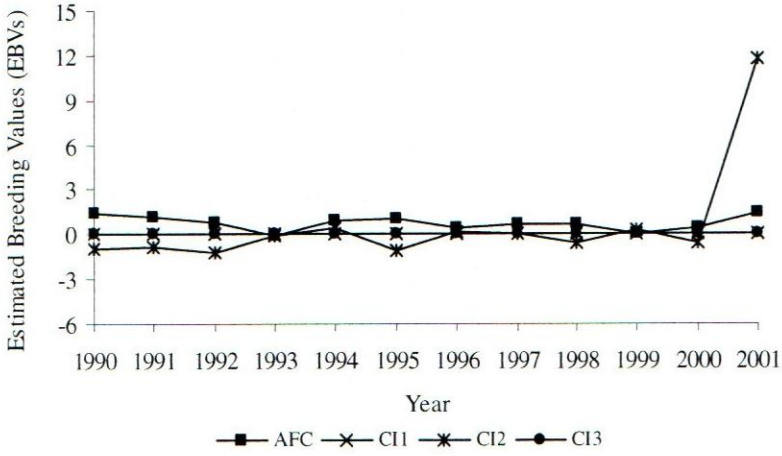


Figure 5. Genetic trends for reproductive traits

4.4. Discussion

4.4.1. Univariate analyses

The estimate of heritability for BW (Table 9) was higher than that reported for the Boran cattle in Ethiopia (Haile-Mariam and Kassa-Mersha, 1995; Demeke et al., 2003). The Kenya Boran has been shown to have a higher proportion of taurine blood than the Boran cattle in Ethiopia (Rege et al., 2001). Maternal effects did not account for any variation in

BW. This is contrary to other results on tropical beef cattle in which maternal influence was observed (Meyer, 1992,1993b; Haile-Mariam and Kassa-Mersha, 1995; Burrow, 2001; Demeke et al., 2003; Norris et al., 2004). Maternal effects at birth are generally as a result of the prenatal maternal environment and cytoplasmic effect (Maniatis, 2000). 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.

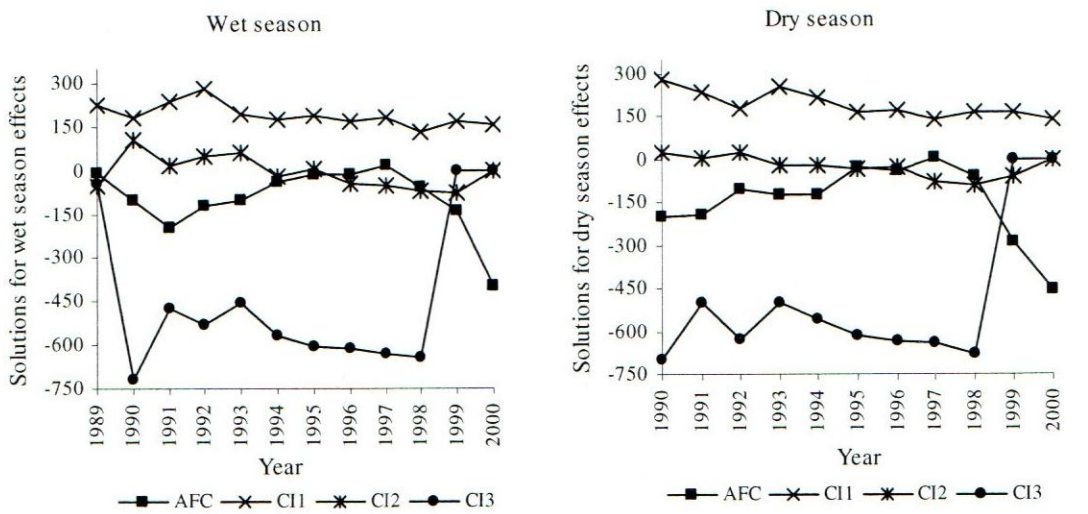


Figure 6. Environmental trends for reproductive traits during the wet and dry seasons

The estimate of direct heritability for WW (0.12) from model 6 (Table 9), was lower than estimates of 0.40, 0.24 and 0.25 reported by Meyer (1993a), Haile-Mariam and Kassa-Mersha (1995), Maiwashe et al. (2002), for Angus, Boran and South African Bonsmara cattle, respectively. Maternal effects were more pronounced at weaning. Maternal permanent environmental effects were 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 (Trail and Gregory, 1981).

The negative direct-maternal genetic correlation (-0.25) estimated for WW was similar to average genetic correlation (-0.25) reported by Koots et al. (1994) from nine studies on beef cattle. Different estimates have been reported for this parameter in various studies. These include highly negative estimates (-0.54) reported by Maiwashe et al. (2002) and positive estimates of 0.22 reported by Meyer (1992) for Angus. The differences between estimates may be attributed to the differing levels of genetic variation between populations. A negative

estimate of direct-maternal genetic correlation indicates an antagonistic relationship between these components. Omitting the direct-maternal genetic covariance in analyses where maternal effects are important would therefore result in an upward bias in estimates of direct and maternal heritabilities (Meyer, 1997).

Direct heritability for 12W (0.19) was lower than reported by Haile-Mariam and Kassa-Mersha (1995) on suckled Boran calves in Ethiopia. The low direct heritability for 12W could be due to the stressful post-weaning environment under which the animals were kept. Environmental stress highly affects the magnitude of additive genetic variances for different traits (Demeke et al., 2003).

Maternal genetic effects were more evident at 12W than any other age. This 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 (Mortimer and Atkins, 1994; Swan and Hickson, 1994). However, other studies on maternal effects have reported a tendency of maternal effects to peak before or at weaning and dropped thereafter due to the withdrawal of maternal environment (Meyer, 1992; Haile-Mariam and Kassa-Mersha, 1995; Norris et al., 2004).

The negative direct-maternal genetic correlation (-0.58) for 12W could indicate that daughters of the Kenya Boran dams with high maternal ability tended to provide an inferior maternal environment to their offsprings. Lower estimates were reported by Meyer (1992), Haile-Mariam and Kassa-Mersha (1995) and Norris et al. (2004) in the Australian beef cattle, Boran cattle in Ethiopia, and Nguni cattle in South Africa, respectively.

The estimate of direct heritability for 18W (0.08) was lower than reported in the literature (Mackinnon et al., 1991; Meyer, 1993a). The data available for this trait was limited (Table 8), 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 they 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 studies on beef cattle in the tropics have reported negligible maternal effects at 18W (Meyer, 1992; Haile-Mariam and Kassa-Mersha, 1995; Khombe et al., 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. The estimate of maternal heritability (0.11) was higher than estimates reported for final weight by Burrow (2001) and Meyer et al. (2004) in a composite beef breed and Australian Hereford cattle, respectively.

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 correlations. Either due to existence of true genetic antagonism between the components or overestimation of the parameters arising from small datasets and of poor structure (Meyer, 1997). Given the data size considered in this study, highly negative estimates 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 correlations 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. This could be attributable to the high phenotypic variance arising from high environmental variations. 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 (Haile-Mariam and Kassa-Mersha, 1994; van der Westhuizen et al., 2001). Low h^2 estimates for reproductive traits have been reported in tropical beef cattle (Haile-Mariam and Kassa-Mersha, 1994; Rust and Groeneveld, 2001; Olori et al., 2002; Demeke et al., 2004). 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).

4.4.2. Multivariate analyses

Estimates of variance components and heritability for BW and some reproductive traits from univariate and multivariate analyses were generally comparable. These findings were consistent with those of Meyer (1993a) for BW on Australian Polled Hereford cattle. However, for the other growth traits (WW, 12W, 18W and 24W), the estimates of direct additive genetic variances were higher from the multivariate analyses than obtained in the univariate analyses. Several studies have attributed the increase in the magnitude of the estimates of genetic variances and heritabilities from multivariate analyses to elimination of

selection bias that leads to underestimation of parameters in univariate analyses (van Dyk et al., 2001; Mrode, 2005). This could be the basis of higher heritability estimates for WW, 12W and 18W in the present study when multivariate models were used. However, it should be noted that under univariate analyses, these traits were analysed using a model that accounted for maternal genetic effects, maternal permanent environment and covariance between genetic effects, while a simple animal model (model 1) was used in the multivariate analyses. Heritability estimates for the growth traits suggest that these traits would respond to selection. Higher estimates from multivariate analyses depict a relatively higher response to selection when multiple trait selection is practised (Hazel et al., 1994; Mrode, 2005).

The low heritability estimates of reproductive traits indicate slow response to selection. Therefore, producers should opt for a long-term strategy of achieving change in these traits, which incorporates improvement of the production environment and a higher selection intensity of the breeding females.

The genetic correlations between BW and other growth traits were positive and moderate ranging from 0.36 to 0.52. This implies that improvement of BW is achievable when selection is done on the basis of other growth traits, as a result of genetic linkage between loci of these traits (Bourdon, 2000). This may not be desirable because selection for instance, on the basis of WW could result in calving difficulties due to increased BW. Studies on beef cattle in the tropics reported estimates within this range (Meyer, 1993c; Burrow, 2001; Meyer et al., 2004).

Estimates of genetic correlations between post weaning growth traits were high (>0.7), implying strong relationships among these traits. The genetic basis of these high estimates is the high number of similar loci influencing the expression of these traits. Due to the strong genetic relationship between these traits, selection at any point of the growth curve in the post-weaning period is bound to improve the growth performance of the animals (Meyer, 1993c; Haile-Mariam and Kassa-Mersha, 1995; Burrow, 2001; Meyer et al., 2004).

Most of the correlations between reproductive traits were negative. The negative genetic correlation between AFC and CI1 (-0.18) implies that selection for early AFC could result in prolonged CI1. The negative genetic correlation between CI1 and CI2 (0.30) suggests that selection for shorter CI1 leads to a prolonged subsequent CI, possibly as a result of protracted post partum return to oestrus. The estimate of phenotypic correlation between AFC and CI1 was similar to that reported for the Boran cattle in Ethiopia (Haile-Mariam and Kassa-Mersha, 1994).

A strong positive genetic relationship was observed between WW and AFC, indicating that younger heifers weaned lighter calves. Given the strong positive correlation between WW and other growth traits, selection for early AFC would result in diminished growth performance. As an improvement strategy, producers should put their heifers in the bullying herds on the basis of weight rather than age. A point to note is that correlations between other growth traits and reproductive traits were not estimable due to data limitations.

4.4.3. Genetic and environmental trends

The genetic trends for growth traits indicated a slow but positive rate of progress in growth performance in the Kenya Boran cattle in the area studied (Figure 3). The results of stringent selection of animals on the basis of their 18 and 24 months weight initiated in the herds in 1994 are evident from the steady positive genetic trend in growth traits from 1997 to 2004.

As shown in Figure 4, the insignificant change in trends of BW and fluctuations in WW imply that calf BW was independent of environmental influences while WW fluctuated due to the fluctuation in milk production ability of the dam. The negative trends in post-weaning growth traits up to 1997 were due to a lapse in management on the farms, which improved in the later years. This shows that management of cattle in the rangelands have a great impact on their growth performance. The environment provided determines the ultimate growth achieved. The rate of change in growth performance was higher in the wet than in the dry season. Pastures in the rangelands tend to be more abundant and succulent during the wet season than in the dry season, and therefore animals tend to gain weight and are in better condition than during the dry season. A similar performance pattern was observed in Brahman cattle in flooded savannah (Plasse et al., 2002). The marginal rate of change in growth traits in this study was however small in post weaning traits, just enough to compensate for the lost weight during dry periods and confer a minimal extra growth resulting in the virtually flat environmental trend. However, their ability to compensate for the lost weight could be attributed to their high feed intake during the wet seasons when pasture became available.

Changes in reproductive performance over time were negligible (Figure 5). The flat genetic trend presuposes inefficiency in selection for reproductive performance. As shown in Figure 6, the negative slope in environmental trends for AFC, CI1 and CI2 from 1997 arose from changes in reproductive management practices in the herds. There was change in age of introduction of heifers to the breeding herd from 24 months to 18-20 months and stringent culling of heifers and cows that did not calve down within 2 years after introduction, and

within two years from the previous calving. The consistently high environmental trend for CI1 could be attributed to prolonged period to post-partum oestrus due to nursing stress in relatively young dams than their older counterparts (CI3) that are considerably mature physiologically. Progress in reproductive performance in Kenya Boran cattle herds was quite slow compared to dairy herds in the country (Musani and Mayer, 1997; Ojango and Pollott, 2001).

4.5. Conclusions

This chapter has shown the possibility of genetic progress for all growth traits. Weaning weight as a basis of selection would result in overall improvement of growth performance. Apart from BW, maternal effects influenced the performance of the other growth traits. Maternal effects should be accounted for in genetic analyses of growth traits, by fitting it as either a genetic or a permanent environmental effect or both, to eliminate the upward biasness in estimates of direct heritability, which leads to sub-optimal selection decisions. 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.

Selection for improvement of both reproductive and growth traits should be practised with caution given the strong positive correlation between WW and AFC. A compromise age of introduction of heifers to the breeding herd should be sought for effective breeding. It has also been shown that use of multivariate models would result in improved accuracy of estimates due to additional information as a result of covariances between the traits. The results indicate slow genetic progress in improvement of Kenya Boran cattle under the current selection and management conditions. Consequently, there is the need to review the selection programme for the Kenya Boran cattle and develop breeding programmes that effectively account for changes in environmental factors and genetic trends. The estimates of variance components and genetic parameters presented in this chapter are important in this regard.

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CHAPTER FIVE

GENETIC EVALUATION OF GROWTH USING RANDOM REGRESSION MODELS

5.1. Introduction

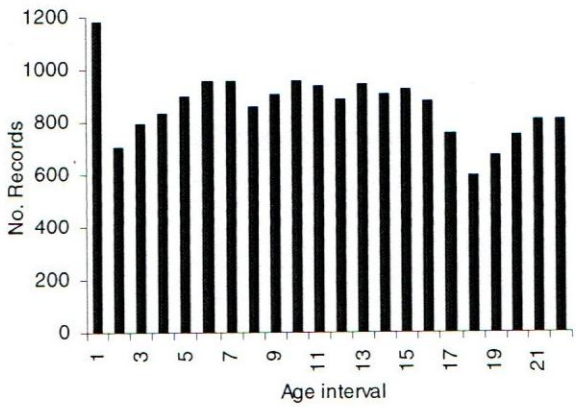
Growth in Boran cattle has been described using univariate and multivariate models, in which each individual weight measured at a particular age was considered a different trait, assuming constant variances between ages (Haile-Mariam and Kassa-Mersha, 1995; Demeke et al., 2003; Wasike et al., 2006b). 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 are made to the closest landmarks and weights that fall way 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 functions methodology are used in evaluation of longitudinal data (Albuquerque and Meyer, 2001; Meyer, 2001a; Fischer et al., 2004b). This is because the models provide an efficient method of evaluating traits that change with time due to their ability to account for the temporal variation in addition to allowing for data interpolation and efficient data utilisation (Kirkpatrick and Heckman, 1989). The models present a flexible means of estimating (co)variances between the ages without adjustment of the ages, thereby minimising the errors due to approximations and provide estimates for the particular ages when the measurements were taken (Fischer et al., 2004a; Fischer et al., 2004b; Meyer, 2004). The objective of this chapter was to estimate covariance functions and genetic parameters for growth in Kenya Boran cattle using RR models and to examine the applicability of the estimates obtained in determining the optimal ages for recording and selection of animals for growth on large-scale commercial ranches.

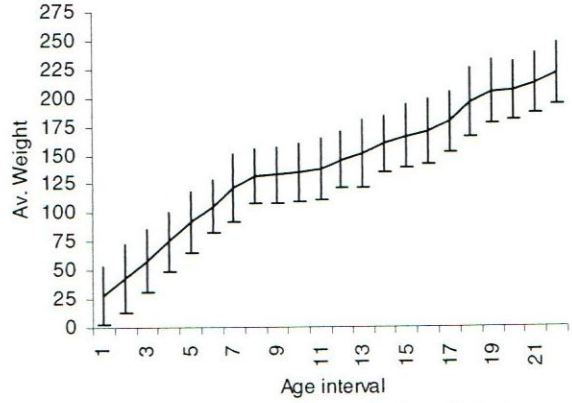
5.2. Material and methods

5.2.1. Data

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 in the National Beef Research Station. Chapter 3 gives a detailed account of the production environment and herd management practices on the station. Dates of weighing within a month were highly variable, resulting in very high variability in ages 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-month 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 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 7.



Distribution of weight records among age intervals from birth to 735 days



Average weight at age intervals from Birth to 735 days

Figure 7. Distribution of weight records among age intervals and average weights at various age points from birth to 735 days

5.2.2. Analyses

Effects that significantly influenced growth performance in Chapter 3 (sex, parity of the dam, the year-month of weighing and age at weighing) constituted the fixed part of the

animal model in the analysis. Step down procedures using a fixed effect model were used to determine the best order of polynomial fit for fixed regression to model the mean population curve. 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 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. 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 programme (Meyer, 2000a). The general model used was as follows:

$$y_{ijk} = f_{ijk} + \sum_{m=0}^{k} \beta_m \Phi_m(a^*_{ijk}) + \sum_{m=0}^{k_{a-1}} \alpha_{im} \Phi_m(a^*_{ijk}) + \sum_{m=0}^{k_{c-1}} \gamma_{im} \Phi_m(a^*_{ijk}) + \varepsilon_{ijk} \qquad (7)$$

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

$$\Phi_m(a^*_{ijk}) = \frac{1}{2^m} \sqrt{\frac{2m+1}{2}} \sum_{r=0}^{m/2} (-1)^r \binom{m}{r} \binom{2m-2r}{m} (a^*_{ijk})^{m-2r} \qquad (8)$$

where *r* is an index number needed to determine the m^{th} polynomial.

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 the direct additive genetic effect, the matrix notation of the equation to estimate variance components was:

$$G_0 = \Phi K \Phi' \quad (9)$$

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:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Za} + \mathbf{Wpe} + \mathbf{e} \quad (10)$$

where **y** a vector of observations, **b, a** and **pe** vectors of fixed, additive genetic and permanent environmental effects, respectively, **e** a vector of temporary environmental effects and **X, Z** and **W** incidence matrices relating observations to fixed, additive genetic and permanent environmental effects, respectively.

5.3. Results

5.3.1. Variance component estimates

Estimates of additive genetic, permanent environmental, temporary environmental and phenotypic variance obtained using RR model are presented in Figure 8. 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 low at initial ages but 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 at interval 9 (280 days) and remained low to the end of the trajectory. Phenotypic variance increased throughout the trajectory. There was however, a drop in variance estimates at age interval 9 after which it increased again.

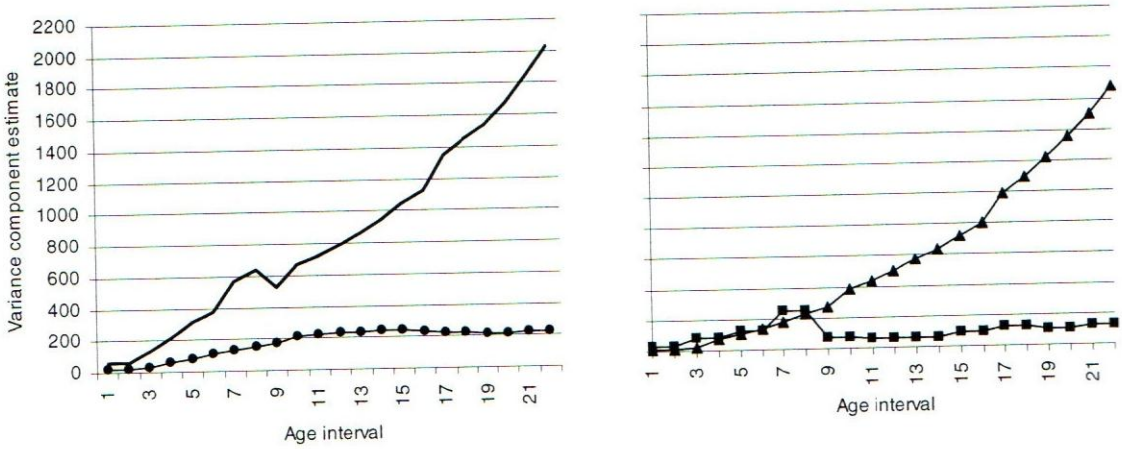


Figure 8. Estimates of direct additive genetic (•), phenotypic (—), permanent environmental (▲) and temporary environmental (■) variances

Estimates of variance components from the SRM are presented in Table 11. Unlike in RR analysis where variance components varied with age, a constant variance between weights at all points was assumed in the SRM. As a result, single estimates of variance components for the whole growth curve were obtained.

Table 11. Estimates of variance components and genetic parameters for growth from a simple repeatability model

Trait	Parameter[a]					
	σ^2_a	σ^2_{pe}	σ^2_e	σ^2_p	h^2±S.E	c^2±S.E
Body weight	240.46	240.42	369.64	850.52	0.28±0.037	0.28±0.30

[a] σ^2_a= additive genetic variance, σ^2_{pe}= permanent environmental variance, σ^2_e= temporary environmental variance, σ^2_p= phenotypic variance, h^2= heritability and c^2= permanent environmental variance as a proportion of phenotypic variance.

5.3.2. Proportions of phenotypic variance

Estimates of direct heritability and permanent environmental variance as a proportion of phenotypic variance from RR analysis are presented in Figure 9. Direct heritability estimate was 0.30 at birth, fluctuated but on a declining trend until 0.23 at age interval 7 (210 days) after which it increased slightly to 0.33 at interval 9 (280 days) then deceased monotonically to 0.11 at age interval 22 (735 days). Permanent environmental effect as a proportion of phenotypic variance was low (<0.2) from birth to age interval 3 (70 days), 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 (735days).

The estimates of heritability and permanent environmental variance as a proportion of phenotypic variance from SRM are presented in Table 11. These estimates though equal (0.28) had different standard errors.

5.3.3. Covariance functions

Estimates of CF for additive genetic and permanent environmental effects and their corresponding correlations and eigenvalues are presented in Table 12. The variances of RR coefficients were highest at k=0 and lowest at k=2. Estimates of permanent environmental variance were higher than those of the 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 91and 94.5% of the total additive genetic and permanent environmental variances,

respectively. The second eigenvalues accounted for 7.8and 5.3% of the total variation in the two random effects while the third eigenvalues explained 1.2and 0.20% of the variation, respectively.

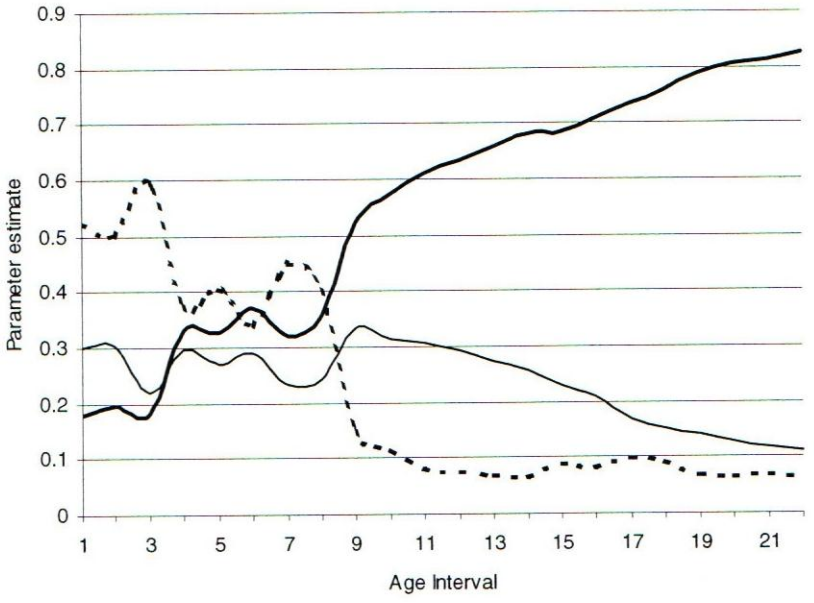


Figure 9. Estimates of direct heritability (—) and permanent environmental variance as a proportion of phenotypic variance (▬) and temporary environmental variance as a proportion of phenotypic variance (– – –)

Table 12. Estimates of variances (diagonal), covariances (below diagonal), and correlations (above diagonal) between RR coefficients and eigenvalues (λ) of coefficient matrix when order of fit (k) = 3

Effects	0	1	2	λ
Additive genetic				
	277.44	0.70	-0.71	309.18
	70.63	36.46	-0.15	26.62
	-60.50	-4.66	25.96	4.06
Permanent environmental				
	797.93	0.92	-0.16	1049.16
	437.60	286.48	0.22	58.75
	-22.82	18.92	25.90	2.40

5.3.4 Additive genetic, permanent environmental and phenotypic correlations

Estimates of additive genetic correlations between the ages are presented below the diagonal in Table 13. 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.

Table 13. Additive genetic correlations (below diagonal) and permanent environmental correlations (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
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

Estimates of permanent environmental correlations between the ages are presented above the diagonal in Table 13. The correlations between weight at age interval 1 (birth weight) and other ages were peculiar such 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 correlations between weights at other ages followed a similar pattern as the additive genetic correlations. The correlations ranged from –0.13 between age interval 1 (birth) and intervals 16 to 22, to unity (1.00) between several adjacent intermediate and older ages.

Phenotypic correlations between weights at different ages (Figure 10) followed a similar pattern as permanent environmental correlations. The 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 intervals 21 (666 days) and 22 (735 days), respectively. Correlation estimates between weights at younger ages were lower than estimates between weights at older ages. Eminent among the phenotypic correlations were the spikes along the diagonal of the correlation graph that were more prominent at early than later ages (Figure 10).

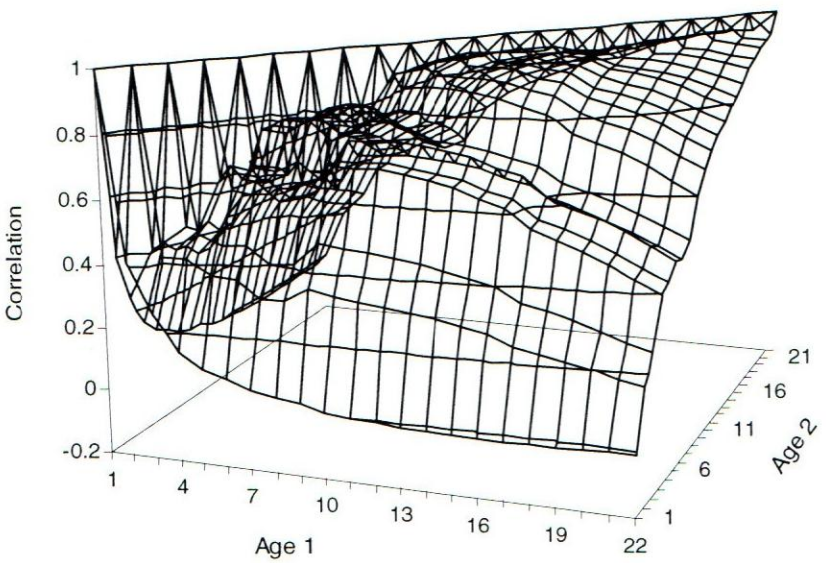


Figure 10. Phenotypic correlations between weights at various age points along the trajectory

5.3.5. Estimates of breeding values

Breeding value estimates for fifteen sires with more than 20 progeny each are presented in Figure 11. 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 two years.

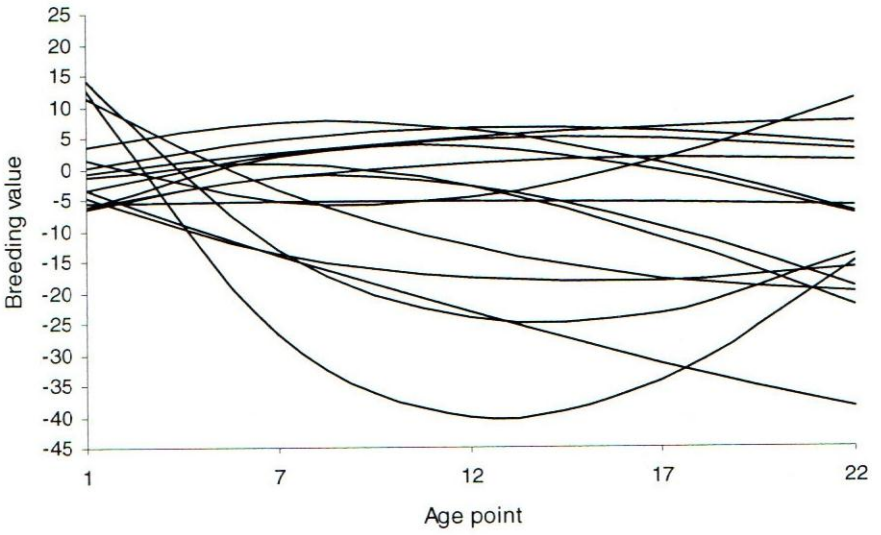


Figure 11. Estimated breeding values for fifteen sires with more than 20 progeny each

5.4. Discussion

5.4.1. Variance components

The estimates of variance components for the range of ages presented in Figure 8 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 was 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). Kenya Boran cattle are raised in the ASAL environment with no feed supplementation. Low permanent environmental variances during early stages of growth were as a result of the good mothering ability of the Boran dams, which buffered the calves against the harsh environmental conditions, resulting in 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

due to the dependence of later weights on early weights, implying that nutritional interventions at these two months post-weaning would greatly reduce permanent environmental variances 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 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 varied with age. This indicates that the assumption of homogenous variance adopted in the traditional 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 depict enhanced accuracy of estimation when RR models are used. Nobre et al. (2003a) in evaluation of growth of Nelore cattle reported higher estimates while (Albuquerque and Meyer, 2001) observed a similar pattern of variation to that observed in the current study.

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 which animals have to endure as earlier mentioned. A similar pattern was observed in the analysis of phenotypic variation of monthly weights of Australian beef cattle (Meyer, 2000b).

5.4.2. Variance proportions

The relatively lower estimates of heritability and permanent environmental variance as proportions of phenotypic variance (Figure 9) 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. Consequently, a more uniform growth was achieved and much of the phenotypic variation was due to the measurement error variances. The higher heritability estimates than permanent environmental variance as proportions of phenotypic variance from birth to age interval 3 (70 days) indicate 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. Withdrawal of maternal environment at weaning

implies the animal has to depend on its inherent growth potential (direct additive genetic effect). However, due 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.

High heritability between age interval 8 (211 days) and 11 (350 days) 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 in later ages. Heritability estimates reported here are within the range of estimates reported in Chapter 4 using multivariate model on a larger dataset. 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 relationship between genetic and permanent environmental variances was evident as these effects tended to balance out each other. This was due to the persistently increasing permanent environmental variance, emanating from high environmental influence on performance of the Kenya Boran cattle. In evaluation of growth performance of the U.S.A beef cattle, a positive and complementary relationship was reported (Arango et al., 2004). This was due to greater environmental control that facilitated better expression of the animals' genetic potential.

In this study, there were fluctuations in estimates of heritability and permanent environmental variance as a proportion of phenotypic variance during the early stages of growth. In this analysis, orthogonal polynomials were used. However, they tend to have poor mathematical properties to model growth at extreme data points on the trajectory (Arango et al., (2004) and hence the fluctuations. 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. In evaluation of growth in pigs and Australian Angus cattle, cubic splines were shown to improve estimates at extreme ages relative to orthogonal polynomials (Huisman et al., 2002; Meyer, 2005b).

Estimates of heritability from SRM and RR models depicted growth as a low to moderately heritable trait. The estimate of repeatability from SRM on the other hand indicated low reliability between weight records. This was similar to estimates from RR model at early ages as predictors of weight at older ages. However, weights from intermediate ages upward could reliably predict one another. As a result, positive responses to selection in later ages would be achieved if selection was based on intermediate ages.

5.4.3. Covariance functions

Covariance and correlation structure between RR coefficients observed in this study indicate strong relationship between the intercept and the linear and quadratic coefficients. The present study reported higher covariance and correlation between the RR coefficients for the permanent environmental effects than additive genetic effects. This was due to the high environmental influence on growth performance of the animals in the ASAL. Under fairly favourable production environments RR coefficients for the additive genetic effects would tend to be higher than permanent environmental RR coefficients (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 leading eigenvalue of the additive genetic coefficient matrix in this study (Table 12) 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 account for very little amount of additive genetic variation. This was also observed in studies evaluating growth of beef cattle in the tropics (Albuquerque and Meyer, 2001; Meyer, 2001a,2005a). Eigenvalues and functions associated with the permanent environmental effects showed a similar pattern as genetic covariance functions. These imply that changes in the environmental conditions would tend have a greater influence on absolute and linear growth than non-linear growth.

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 the current study indicates that selected animals would reach mature weight relatively late, which is a hint of little progress that would be achieved when selecting to improve growth rate. Selection to alter the growth pattern of Kenya Boran cattle would yield little given the proportion of variation explained by the quadratic eigenvalue.

5.4.4. Correlations

Genetic correlations between birth weight and other weights were low. 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 (Fischer et al., 2004b). Selection for increased weight at

older ages would not cause much change in birth weight. On the other hand correlations between intermediate and later ages were high, implying pleiotropy and therefore selection for heavier animals at two years could be done based on weight at earlier ages. The pattern of genetic correlations between ages was similar to those 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 correlations between later weights increase because they are more dependent on the previous weights (Huisman, 2002; Fischer et al., 2004b). Estimates reported in this chapter were lower than those reported in Chapter 4 using a simple animal model in multivariate analysis.

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 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 positively at later ages as depicted by the moderate to high positive correlations 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 or less the same. Therefore, it would be important to control the strenuous post-weaning conditions which Boran weaners are subjected to avoid depressed performance later in life. Arango et al. (2004) observed environmental correlations between older weight measures that were close to unity in evaluation of beef cattle growth performance.

Phenotypic correlation patterns though somewhat erratic between early ages and negatively low between weights at birth and 24 months were moderately to highly positive between intermediate and later ages (Figure 10). 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. In a study to evaluate growth of Bonsmara cattle, low phenotypic correlations were observed between extreme ages while high correlations were reported between intermediate and later ages (Nephawe, 2004). The observed spikes along the diagonal of the plot of phenotypic correlations depict inflation of phenotypic variance caused by measurement error variance (Figure 10). Earlier studies on growth in beef cattle reported similar results (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 (Chapter 4).

5.4.5. Estimated breeding values

Estimated breeding values for sires varied across age points and between sires (Figure 11). The variability in the breeding values between sires depict differences in the growth patterns of offsprings 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. The advantage of 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 as at its point of recording.

5.5. Conclusions

Results from the present study show the potential of RR models to model growth of Kenya Boran cattle even when recorded herds are small and recording inconsistent. Results from the study show a large scope for selection to alter growth patterns of the Kenya Boran cattle in the ASAL. This is of interest to the beef industry where selection for varied objectives could be achieved given the varied production environments. The estimates from the current study could be used to effectively select for growth in Kenya 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 by RR models given the economic implications of performance recording.

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CHAPTER SIX

GENERAL DISCUSSION AND CONCLUSIONS

6.1. Aim of the study

A genetic improvement programme comprises of five main components, namely definition of breeding objectives, choice of selection criteria, performance recording and evaluation, selection and design mating systems. Efficiency and effectiveness of a breeding programme is dependent on choice of breeding objective traits for improvement and accuracy in performance evaluation. This therefore implies that records on animal performance for traits of economic importance are needed for genetic evaluation.

Animal genetic evaluation process has evolved systematically from use of simple least square methods to maximum likelihood procedures of partitioning variation into its component sources. With advent and increase in computation power, more sophisticated models and procedures to explain various sources of variation (both genetic and environmental) influencing economic traits have been used. Unlike genetic evaluation of *Bos taurus* cattle where these models have been extensively used, genetic evaluation is hardly done among the *Bos indicus* cattle particularly in tropical countries. As a result, selection of animals is based on phenotypic appraisal of individual animal performance. This exercise is common due to absence of genetic parameters arising from scarcity of records on animal performance in traits of economic importance. This study aimed at genetically evaluating growth and reproductive performance of the Kenya Boran cattle raised in the ASAL to provide quantified estimates for initiation of a genetic improvement programme for beef cattle. The study was based on three hypotheses: (i) there is no difference between direct and maternal (co)variance components of growth and reproductive traits estimated using different genetic models, (ii) there are no differences in the genetic and phenotypic parameters estimated for growth traits at certain age points along the growth trajectory using random regression models and (iii) prior breeding programmes and management practices did not confer improvement in performance of the cattle populations over the years.

6.2. Study methodology

Evaluation of environmental sources of variation in growth and reproductive performance was done by subjecting the whole dataset to fixed effect analyses using (GENSTAT, 2003). The effects included in the analyses were sex of the animal, parity of the

dam, year-season/month effects and age of the animal as a covariate. Effects that were significant constituted the fixed part of the models in genetic evaluation of performance.

Estimation of genetic and phenotypic parameters and evaluation of trends in this study was done using univariate, multivariate and random regression (RR) models based on two datasets. The first dataset consisted of growth traits, comprising of weights taken at birth (BW), weaning (WW), 12 months (12W), 18 months (18W) and 24 months (24W), and reproductive traits which included age at first calving (AFC), calving interval in parity one (CI1), two (CI2), three (CI3) and pooled calving interval (CI). The second dataset comprised of weights taken at monthly intervals from birth to 24 months. The first dataset was subjected to univariate and multivariate analyses to estimate variance components for direct additive genetic effects in growth and reproductive traits. In addition, variance components were estimated for maternal genetic and maternal permanent environmental effects in growth traits. In these analyses, ASREML programme (Gilmour et al., 2001) based on average information algorithm was used. Evaluation of genetic and environmental trends was done by regression of breeding values and solutions for year-season effects on the year of birth and calving for growth and reproductive traits, respectively. Multivariate analyses involved various bi- and trivariate estimation of variance components considering traits within growth and reproductive trait categories and traits between the two categories. The second dataset was subjected to RR analysis to estimate covariance functions and genetic parameters for growth when herd size is small and recording inconsistent. Derivative free restricted maximum likelihood procedure (Meyer, 2000a) was used to obtain covariance functions, (co)variance components and genetic parameter estimates.

6.3. Limitation of the study

Livestock performance and pedigree recording within the tropics is highly variable and inconsistent. Farms considered in this study were not an exception. There was high variability in the performance records between the farms. Recording of growth performance was more in the research station whereas only WW records were available on the ranch, which instead emphasised more on reproductive records. Pedigree recording was also done partially because in most instances only the dam line was known as a result of multiple bulls in the breeding herds, making it difficult to identify the sires of the animals. These data limitations hindered complete evaluation of animals between herds. In addition, coupled with the small data size, multivariate and RR analyses of growth had to be done ignoring maternal effects, which were seen to be important from the univariate analyses. The study was limited

to growth and reproductive performance, not considering conformation index and survival traits that could equally be important in a breeding programme, due to the unavailability of the records on these traits. Parameter estimates from this study are based on a relatively small database and therefore should be revised with accumulation of data. The study was based on data from the mild stress regions of the ASAL; consequently, use of results from this study on evaluation of animals in high stress areas of the ASAL should be done with caution.

6.4. Genetic basis of the study

In beef production within ASAL, growth performance, reproductive efficiency and adaptability to production environment are critical. Therefore, for efficient utilisation of an animal genetic resource, a comprehensive understanding of the genetics of inheritance of traits that influence its competitiveness among other animal species is required. It is by understanding these principles that effective breeding programmes for sustainable utilisation of the resource can be designed.

This study focused on growth and reproductive performance because Kenya Boran cattle are selected within the production environments and therefore the assumption is that adaptability is indirectly selected for. Inheritance of growth traits is bilateral. Growth of an animal is influenced by its genes acquired from both parents, which constitute the direct additive genetic effect and the ability of the dam to provide good maternal environment that is partly genetic and partly environmental and constitute the maternal genetic and permanent environmental effects, respectively (Lynch and Walsh, 1998; Bourdon, 2000; Mrode, 2005). Given the cow-calf rearing system practiced in the ranches, maternal effects would be anticipated. Kenya Boran cattle selection is based on physical appraisal. This means that only direct additive genetic effects are considered and maternal effects are ignored. In chapter 4 of this study high influence of maternal effects on growth is shown. When maternal effects are ignored, the selection index based on direct additive genetic effects (such as in physical appraisal) is biased upwards, leading to low intensities of selection and sub-optimal genetic progress (Meyer, 1992,1993b). It is therefore important that selection programme for genetic improvement of growth consider both direct additive and maternal effects.

Inheritance of reproductive traits is mainly influenced by direct additive genetic effects. The expression of these traits is greatly influenced by environmental effects expressed by the high estimates of residual error variance (Chapter 4). Kenya Boran cattle in the ASAL are constantly under nutrition and disease stress. These environmental influences limit the expression of genetic potential of these animals. Therefore, desirable genetic gain in

reproductive performance would be achieved through direct selection for reproductive efficiency and enhancing uniformity in the production environment. Genetic parameter estimates for reproductive traits are usually low, requiring a wide scope of information source (increased data sizes and good pedigree structure) to enhance accuracy and reliability of the estimates.

6.5. Status of beef cattle performance and pedigree recording in Kenya

Genetic evaluation depends on availability of records on the animals' pedigree and performance. Performance records provide information on the potential of the animal for a particular trait of interest. They are therefore important for evaluation of the environmental and genetic potential of the animal. Pedigree records provide information on biological relationships between animals in a genetic evaluation scheme. The records are important in building the relationship matrix during evaluation (Mrode, 2005). Consistent performance and pedigree records are important for accurate estimation of genetic parameters and prediction of breeding values. A sparse structure in records results in estimates with large prediction error variances (PEV), which in turn reduce accuracy of estimation.

Performance and pedigree recording of Kenya Boran cattle, in Kenya is done by large-scale producers but the quality and quantity of records vary between farms. Records on animal performance collected on farms are sent to the Livestock Recording Centre (LRC) for within-farm performance evaluation. The performance records emphasised by the recording scheme include WW, AFC and CI. Other information provided, depending on the recording ability of the producers include BW, 12W, 18W and 24W. In the 1970's when the recording scheme was initiated, producers had high enthusiasm to record and sent animal performance records to LRC consistently. However, this enthusiasm waned away following the inconsistency and lateness of LRC to release the evaluation results back to them, considering the expenses associated with recording. Most of the producers pulled out of the recording scheme. However, due to the desire to evaluate their animals, some have gone to the extent of purchasing various computer programmes to enable them do simple on-farm evaluation for management purposes. This has resulted into re-orientation of performance recording on the farms to suit management purposes.

Pedigree recording is done by the Kenya Studbook (KSB) in collaboration with the breed societies. Recording of Kenya Boran cattle is done after inspection and subsequent classification of the animals by the inspectors from the KBCBS. It is upon their recommendation that the animal's pedigree information is recorded and a certificate of

registration given. However, notable at the KSB is the lack of validation mechanisms of the information that is sent from the farms, making it difficult to detect any anomalies in pedigree information. This implies that erroneous information from the farms is archived which makes genetic evaluation difficult.

A more efficient way of undertaking performance and pedigree recording would be achieved through harmonisation of the recording process right from the identification of the animals on the farms to the evaluation. Operating performance and pedigree recording as separate entities (LRC and KSB) lead to multiplication of errors. A single animal information entry form would go a long way in reducing errors. Recording is a cost component in a production system and therefore its sustainability depends on the returns from it. Efficient recording of performance involves collection of information at points in animal's life when there are changes in their physiological status and/or when management practices change. For Kenya Boran cattle production under ranching conditions, recording growth performance at weaning, 18 or 24 months and at sale would be adequate while considering AFC and the first two CI for reproductive performance. Unbiased evaluation of animals under an animal model framework requires consistent pedigree information. This should include the animal's sire and dam since other relationship linkages are implicitly created during development of the numerator relationship matrix. Based on this, a single animal record would contain its date of birth and calving, and when weights were recorded, their dam and sire and ultimately their performance measures.

The desire of beef producers, particularly Boran breeders, is to have a home-grown joint evaluation programme. If LRC could provide this service and give consistent output to the producers, the recording process will be back on track. This however, calls for institutional changes and a more all-inclusive framework of operation to encourage more participation by producers. It is evident that there is need for a beef cattle breeding programme. Rewe (2004) defined breeding objectives for the Kenya Boran cattle considering various production systems. The current study has provided the basic genetic parameter estimates to jumpstart the evaluation process. It is now imperative that stakeholders in the beef industry are involved to chart the way forward for strategising on development and implementation of the breeding programme. Among the main issues of concern that need to be addressed is a uniform animal identification system, definition of breeding objective and selection criteria traits, validation mechanisms of records from the farms and logistics of sustainability of the evaluation programme.

6.6. Univariate and multivariate animal model genetic evaluation

Various animal models have been suggested and used in genetic evaluation of beef cattle and range from a simple univariate animal model to more complicated maternal and grand maternal multivariate animal models (Meyer, 1993c; Dodenhoff et al., 1999b; Quintanilla et al., 1999). A univariate animal model evaluates a single trait of an animal at a time. It may be in the form of a repeatability model assuming equal variance between observations on the same trait on the same animal (simple repeatability model in Chapter 5) or split analysis in which observations are treated as separate traits and analysed independently, assuming constant but different variances for each trait (Chapter 4). Univariate analyses are handy in situations where computation resources are limiting and recording not consistent.

In a situation where observations considered as separate traits are simultaneously evaluated in a model, this constitutes a multivariate model analysis (Tempelman, 1998). Multivariate models assume a covariance between the traits in the analysis based on the pretext of interdependence in the expression of the traits. Selection of Kenya Boran cattle is stepwise, i.e., in selection for growth performance only, animals selected at weaning will be available for evaluation at yearling age and only those selected at yearling age will be available for 24 month evaluation. With this kind of selection, evaluation of post-weaning growth based on univariate models would be affected by culling bias that results in underestimation of genetic parameters. This bias is offset by use of multivariate models and. explains the higher estimates of genetic parameter estimates from multivariate analyses in Chapter 4 than from univariate analyses. In addition, multivariate models enhance the accuracy of evaluation that result from better connections in the data due to genetic and residual covariances between the traits. The gain in accuracy is such that the larger the difference in absolute covariance between the traits the greater the gain in accuracy (Mrode, 2005). Multivariate evaluation considering both growth and reproductive traits would therefore result in more accurate estimates than multivariate evaluation of growth traits alone.

The main disadvantages of multivariate models that limit their application and favour univariate models are their high computational demands and unavailability of reliable estimates of genetic and phenotypic correlations among traits. Computational costs of multivariate analysis of n traits is more than the cost of n univariate analyses (Mrode, 2005). However, lack of an evaluation scheme for the Kenya Boran cattle in Kenya is as a result of unavailability of proper records due to poor recording infrastructure.

Heritability estimates from multivariate analysis for growth traits in this study indicate that these traits are fairly heritable. This means that phenotypic expression of the traits is a

fairly good indicator of the breeding value. On the other hand heritability estimates for reproductive traits were low, depicting the inadequacy of phenotypic values as indicators of the underlying breeding values (Bourdon, 2000). Despite the low heritability estimates, there was substantial amount of genetic variability to effect genetic change in the population. Therefore, low heritability estimates should not be interpreted to mean that genetic selection for improvement is not worthwhile. The high estimates of environmental variances in the traits indicate high variability in the production environments under which these animals are raised (Bourdon, 2000).

Other than individual genetic effects (direct additive genetic effects), there are other genetic and non-genetic sources of variation in performance, which have been explored in genetic evaluation programmes as a result of increase in computing power. These include grand maternal effects, sire by herd effects, regression of offspring performance on maternal phenotype, and maternal genetic and permanent environmental effects. Effective evaluation of these effects requires substantial amounts of performance data and well-linked pedigree to enable accurate partitioning of the variance components. The current study considered maternal genetic and permanent environmental effects in evaluation of growth traits.

Parameter estimates for traits under influence of effects other than the direct additive genetic effects would be biased upwards when the factors of influence are not accounted for. This was evident in the results of genetic evaluation using model 1 where maternal effects were omitted (Chapter 4). Unlike reproductive traits that are influenced largely by direct additive genetic effects, the study revealed high maternal influence on growth traits. The effects were prominent on WW, 12W, 18W and 24W. This indicated that Boran dams exerted much influence on the performance of their offsprings such that in the event where a selection programme considered direct additive effects alone, slow genetic progress would be eminent. This could be the explanation for the observed genetic trends in Chapter 4. Selection of Kenya Boran cattle is based on individual phenotypic performance and therefore the slow progress is due to ignored maternal effects. Effective improvement of growth performance calls for inclusion of both direct additive genetic and maternal effects in the evaluation.

Associated with maternal effects model is the negative correlation between direct additive and maternal genetic effects. This genetic antagonism has implication on the design and implementation of a selection programme. Maternal additive genetic effects are expressed when their female offsprings have progeny of their own. As a result of this negative correlation, female animals born of good dams will themselves confer poor maternal environments to their offsprings (Baker, 1980; Dodenhoff et al., 1999a). High negative

estimates of direct-maternal genetic correlations obtained in this study confirm the existence of antagonistic relationship between the direct additive and maternal genetic effects. This indicates the potential bias in estimates of direct additive genetic effects and an eminent reduction in genetic progress for the traits where these effects were prominent. To overcome this problem, Baker (1980) suggested selection of males for growth based on direct effects alone and females to be selected considering both direct and maternal effects. The question that remains unanswered by the present study is whether the highly negative relationship between the two effects is due to true negative biological correlation or a result of other effects. Following observations made by Meyer (1997), Maniatis (2000) and Wasike et al. (2006a) about high estimates of these correlations, these estimates are a subject of debate and therefore a further evaluation of maternal effects is warranted. The data size in the current study was relatively small for conclusive analysis of maternal effects. However, the estimates provide good indication of the genetics of inheritance of growth traits and thus form a good starting point for genetic evaluations and selection programmes for beef production.

Additional outputs of a multivariate model are estimates of correlations between traits in the analysis. These measure the strength (reliability and consistency) of the relationship between, for instance trait A and trait B. Estimates of genetic correlations between post-weaning growth traits were high, implying that genes that increase WW are bound to have similar pleiotropic effects on 12W, 18W and 24W. Therefore, selection for improvement of any of the growth traits other than BW would result in overall improvement of growth. Effective selection could therefore be done during weaning, given that WW is expressed relatively early in the life of the animal, has high heritability, and high positive correlations with other traits. The phenotypic correlations were also high except with BW, indicating that high performance for instance, in 12W would result in higher 24W. The low and negative genetic correlations between reproductive traits indicate a lower level of pleiotropic effects for these traits. The negative relationship shows that the genes that influence these traits act antagonistically, and therefore caution should be taken when selecting for either of these traits.

6.7. Genetic evaluation based on conventional finite versus random regression animal models

Genetic evaluation of performance has conventionally been done using univariate and multivariate animal models (finite models). These models assume constant variances between traits. However, growth is a continuous biological process and the assumption of constancy in

the variance component estimates is not valid (Kirkpatrick and Heckman, 1989; Kirkpatrick et al., 1994). Based on this biological principle, a random regression model, which is more flexible and employs covariance functions between observations on the trait, was developed for application in genetic evaluation of traits that vary continuously along a trajectory (Kirkpatrick and Heckman, 1989). In this study (Chapter 5), three parameters were used to estimate the variance components for the entire growth curve from birth to 24 months, which could have required 22 parameters if a multivariate model was used. Though the estimates of genetic parameters were generally similar between the models (Chapters 4 and 5), the gain in accuracy was greater in RR models than multivariate and univariate models as suggested by the estimates of the residual error variances in both models. This was due to increased residual covariance between observations and more precise apportioning of variances to their components sources.

Estimates of breeding values for 15 sires with at least 20 progeny were similar between the models for corresponding weight measures as indicated by the moderate to high positive correlations between breeding values from both models (Figure 12). The correlation between breeding values of animals for WW from multivariate model and 210-240 day weight from RR model, 12W from multivariate model and 365 day weight from RR model and 24W from multivariate model and 735 day weight from RR model were 0.45, 0.61 and 0.55, respectively. The estimates were lower than unity depicting re-ranking of animals when either model is used. Similar observations were made by Fischer et al. (2004b) in evaluation of a breeding programme for sheep. The question that needs to be tackled relates to the model that should be adopted for selection purposes. This is well answered by use of prediction error variance (PEV). This is a measure of the accuracy of the estimated/ predicted breeding value as a predictor of the true breeding value. The lower the PEV, the higher the accuracy. Therefore, the model that estimates breeding values with lower PEV would provide better estimates and therefore recommended for use in genetic evaluation. Prediction error variance was not estimable in RR analysis in the current study, which hindered comparison of accuracies in the breeding value estimates between the models.

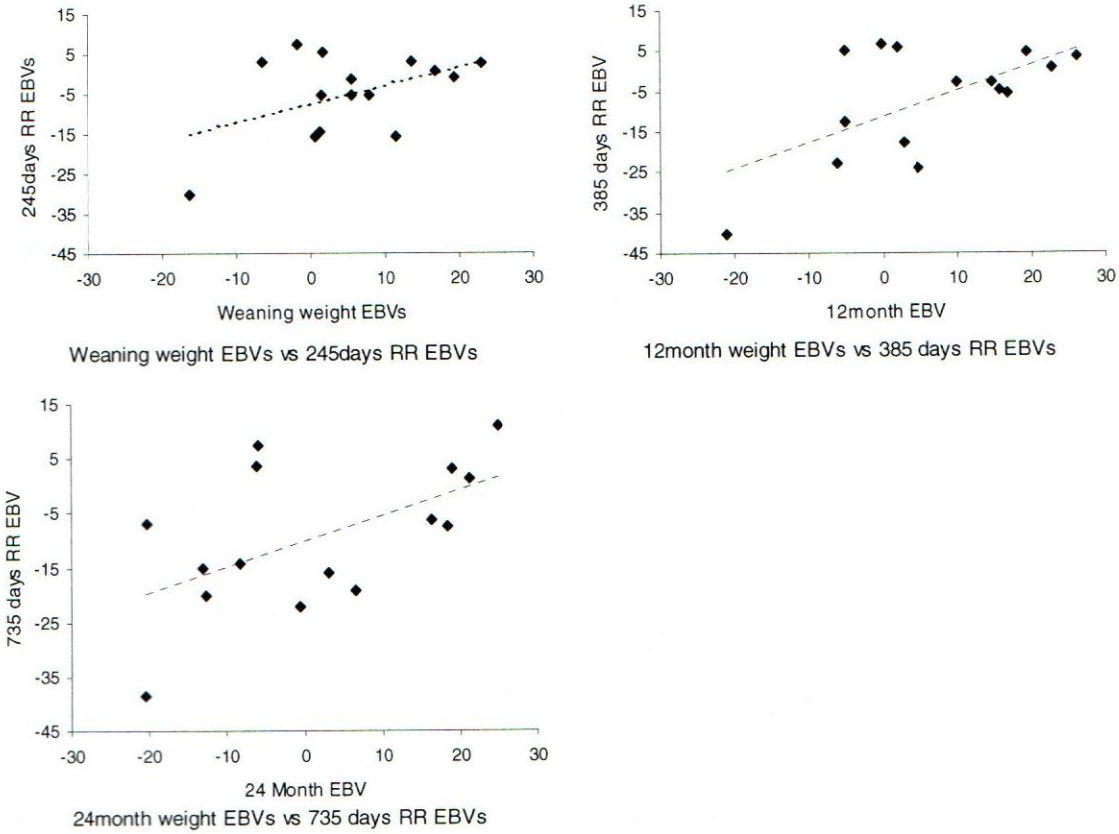


Figure 12. The relationship between EBVs from multivariate and random regression model analyses

6.8. Using random regression models in genetic evaluation of Kenya Boran cattle

A large-scale genetic evaluation scheme for the Kenya Boran cattle based on any of the conventional finite models is lacking and no attempts have been made to initiate one. However, RR models have successfully been used in large-scale genetic evaluation in the Canadian dairy cattle genetic improvement programmes (Jamrozik et al., 1997) and evaluation of growth performance in Australian and Brazilian beef cattle (Meyer, 1999; Albuquerque and Meyer, 2001). So far, use of random regression models in genetic evaluation of growth traits in tropical beef cattle in Africa has been reported in South African Bonsmara cattle (Nephawe, 2004). Potential use of RR models in genetic evaluation of functional traits have been demonstrated but not yet exploited (Schaeffer, 2004). Results from this study (Chapter 5) indicate the potential of these models to evaluate growth performance. The limitations to multivariate analysis arising from the data size and structure were not important to the estimation of genetic parameters for the full growth trajectory from birth to 735 days using RR models. The main requirement of RR models is availability of records,

particularly at data points on both extreme ends of the trajectory. Huisman et al. (2001) analysed growth performance of pigs using data with only three data points with interpolations in between the points to make the curve smoother.

The extensive production system practiced by the beef cattle ranchers hinders consistent recording of performance, especially at birth. Because of the restrictions of finite models, animals whose ages fall far off the described age range for a particular trait are normally not included in the evaluation. However RR models enable evaluation of animals at the ages when the weights were taken. It should be noted that consistency of recording remains important for precise and accurate parameter estimates. So far, the achievements of RR models from the present study warrant its use in genetic evaluation of growth performance given the general similarity in parameter estimates from this model and the conventional finite models. However, monthly weight records were used in this study, which is not a practical recording situation in ranching conditions. It is therefore important that before conclusively endorsing utilisation of RR models in genetic evaluation, an analysis is done to examine the most optimal number of records that would guarantee accuracy and reliability of estimated genetic parameters and breeding values. If a recording scheme was set up, age interval 1 (BW) would be considered as the first weight record. Because of the high correlations between weights at age intervals 2 (3 days) to 5 (140 days) any record at this point could be a better descriptor of this range while age intervals 6 (141 days) to 16 (526 days) could be represented by one weight and another weight to represent the remaining part of the trajectory. On this basis, four records at any of the above age points would yield satisfactory results with interpolation of data points between measurements to make the trajectory smoother.

Genetic gain is a function of accuracy of selection, selection intensity, genetic variation and generation interval. The rate of genetic change would be highest if selection of replacement animals was done between age interval 9 (246 days) and 15 (490 days), assuming other factors influencing genetic change remained constant. This is because this was the age bracket when genetic variance was highest. Selection of Kenya Boran cattle was done during weaning at 7 months (210- 245 days) of age. Selection at this point from a conventional finite model (multivariate analysis) stand point, could be justified since this was the point shown to have the highest genetic variance expressed early in the life of the animal. However, on the basis of RR evaluation, the highest genetic variance was recorded between 351 and 455 days and would therefore be the most appropriate age for selection for genetic improvement of growth performance. Economic efficiency of selecting animals between these two ages should

be evaluated because selection at the latter age translates to more costs to keep animals in the herd that could otherwise be culled if selection was done at weaning.

6.9. Conclusions

From the present study environmental sources of variation (sex, parity, herd and year-season effects) play a major role in the expression of growth and reproductive traits. These should be adjusted for if effective performance evaluation is expected. Variance components and genetic parameter estimates will vary, depending on the model of analysis chosen. Growth traits in Kenya Boran cattle are highly influenced by both maternal and direct additive genetic effects. As a result, maternal effect animal models should be adopted in evaluation of growth performance. Reproductive performance on the other hand would adequately be described by a simple animal model.

There is a large scope for selective breeding for improvement of growth traits as depicted by the additive genetic variances for these traits. However, for higher response to selection, there is need to enhance uniformity in the production environment. Improvement of reproductive performance would be achieved if emphasis were put on improving the production environment and high intensity of selection among the breeding females.

Animals tended to lose weight in the first two months post-weaning as they became independent. Therefore, selection done two months post-weaning rather than at weaning would be most effective because heavier animals at this time would be those with better direct additive genetic potential for growth and faster ability to acclimatise to the ASAL conditions.

As earlier mentioned, based on results from the present study, weight records taken at birth, 140 days, 351 days and 720 days could adequately describe growth while calving intervals in the first three parities would satisfactorily describe reproductive performance. The study was conducted using data from a research station where recording of performance and pedigree was well done compared to the ranching situation. Therefore further evaluation should be done into the optimal number of records needed for accurate parameter estimation.

Genetic and environmental trends depicted slow progress implying ineffectiveness of the prior breeding programmes and management practices. Consequently there is need to revise selection and management strategies such that selection for growth is done at the age when genetic variance is at peak alongside improved reproduction management. If this is done, higher rates of genetic gain and general animal performance should be expected.

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