GENETICS OF GROWTH AND FERTILITY OF CHAROLAIS AND POLLED-HEREFORD BEEF CATTLE BREEDS IN KENYA

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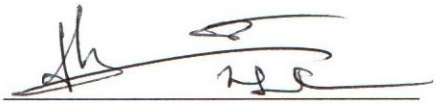
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This thesis is my original work and has not, wholly or in part, been presented for an award of a degree or diploma in any other University.

Juvinalis S. Kenaly Orenge

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Date: 13·10·08

RECOMMENDATION

This thesis has been approved for final submission with our approval as the official University Supervisors.

1. Prof. Dr. A. K. Kahi

Signed: 

Date: 15/10/2008

2. Dr. I. S. Kosgey

Signed: 

Date: 15/10/2008

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ACKNOWLEDGEMENTS

My sincere appreciation goes to several institutions and persons who, in one way or another, opened doors and answered my ceaseless questions in the quest for knowledge that culminated in the successful completion of this study. I, therefore, wish to express my heartfelt gratitudes to individuals in the organisations who made this study a success. Many thanks to my Employer, the Ministry of Livestock and Fisheries Development for granting me study leave. I thank Egerton University's Graduate School and the Department of Animal Sciences for the opportunity to pursue postgraduate studies. I am deeply indebted to the Management of the Agricultural Development Corporation (ADC) of Kenya and Solio Ranch Ltd. for allowing me to use their data and facilities, and for providing an excellent working environment in the course of this work.

I had the privilege of working with an experienced team on the material content of this thesis, Prof. Dr. A.K. Kahi and Dr. I.S. Kosgey, my official supervisors who immensely shaped this thesis through a thorough conceptualisation of the scientific content and critique. They effectively coped with my numerous daft scripts, sized and simplified my complex paragraphs, and with continuous red marks, they ensured that I remained focused to the end. My special tribute goes to Mr E.D. Ilatsia for his unswerving guidance throughout this work; he was always by my side even when there seemed no light at the end of the tunnel. My sincere gratitude also goes to my fellow graduate students at the Department of Animal Sciences, especially Mr. W. Bwire and Ms. S.A. Migose for their constant encouragement.

I am grateful to the staff of both ADC and Solio Ranch Ltd. farms (Mr W. Rogo, the Complex Manager, Chepchoina Farm, Dr. D. Tanui and Mr. S. Bundotich of ADC Kitale and Mr C.E. Perfet (Director of Solio Ranch Ltd.), Mr. J. Muune and Mr. N.G. Duncun of Solio Ranch Ltd. for their continued assistance during data collection.

While everything has been falling so well into place up to this point, it is not just a coincidence. I thank the Almighty God for this.

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DEDICATION

This work is dedicated to

my parents, Mr. Orenge Mogire (late) and Mrs. Robina Orenge (late), for their never ending support for my education,

my loving wife, Mrs. Elder Kenaly, for her great sacrifice, ceaseless prayers, support and encouragement

and

my sons; Brian, Bramwel and Brandon who endured with patience my constant absence while I was out of home for long periods in search of knowledge.

ABSTRACT

The Charolais and Polled-Hereford constitute some of the *Bos taurus* beef cattle breeds in Kenya. They are used in different production systems, i.e., as pure breeds in the medium to high potential areas and for crossbreeding with the *B. indicus* breeds in the arid and semi-arid lands. In this study, records on growth and fertility performances were used to estimate genetic and phenotypic parameters using various univariate and multivariate models, and to examine genetic and environmental trends in performances of the two traits. Sex, age of the animal, parity of dam and year-season effects were the main environmental effects that influenced birth weight (BW), pre-weaning average daily gain (ADG) and weaning weight (WW). Fertility performance; age at first calving (AFC) and calving interval (CI) were affected by herd-year-season of birth and calving, respectively. Direct heritability estimates from univariate analyses of growth traits were 0.36 and 0.21; 0.25 and 0.10, and 0.23 and 0.13, for BW, ADG and WW in the Charolais and Polled-Hereford, respectively. Maternal heritability estimates were, correspondingly, 0.11 and 0.01; 0.18 and 0.00; 0.17 and 0.17 for BW, ADG and WW for the Charolais and Polled-Hereford. Direct-maternal genetic correlations ranged from -0.45 and 0.1.00; -0.51 and -0.10; -0.47 and -0.39 for BW, ADG and WW in the Charolais and Polled-Hereford, respectively. The heritability estimates for fertility traits were, correspondingly, 0.06 and 0.16; 0.00 and 0.05 for AFC and CI for the Charolais and Polled-Hereford. The genetic correlations between growth traits ranged from -0.99 to unity, and between growth and fertility traits from -1.00 to unity. The genetic correlations between AFC and CI were high and negative (-0.99) for both breeds. Phenotypic correlations between growth traits ranged from 0.0 to 0.28, and between growth and fertility traits from -0.16 to 0.12. There seemed to be no phenotypic correlation between AFC and CI. However, the high and negative genetic correlation between AFC and CI implies that selection for short AFC could not result into improved reproductive efficiency. The high and positive (1.00) genetic correlation between BW and ADG in the Charolais suggests that selection for BW would result into faster growing animals. Based on the heritability estimates for growth traits, there are opportunities for genetic improvement of these *B. taurus* breeds by selection for early growth traits. This means that growth and fertility traits could be used in genetic evaluation in *B. taurus* cattle breeding programmes in Kenya.

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LIST OF ABBREVIATIONS

ADC	Agricultural Development Corporation of Kenya
ADG	Pre-weaning average daily gain
$ADGP^{a}$	Post-weaning average daily gain
$ADGP^{m}$	Post-weaning average daily gain in males
AEZ	Agro-ecological zone
AFC	Age at first calving
AM	Simple animal model
AMM	Maternal animal model
AP	Age at puberty
ASAL(s)	Arid and semi-arid lands
BW	Birth weight
CD	Calving date
CF(s)	Covariance function(s)
CI	Calving interval(s)
CR	Calving rate
DC	Days to calving
EBV	Estimated breeding value
FW	Final weight
KMC	Kenya Meat Commission
MALDM	Ministry of Agriculture, Livestock Development and Marketing
MoA	Ministry of Agriculture
MoARD	Ministry of Agriculture and Rural Development
NDP	National Development Plan
NR	Non-return rate
NSC	Number of services per conception
REML	Restricted Maximum Likelihood
RRM	Random regression model
SEAZ	Small East African Zebu
WW	Weaning weight
YW	Yearling weight

CHAPTER ONE

INTRODUCTION

In Kenya, beef production forms a vital component of the livestock sub-sector with a significant contribution to the national food security (MALDM, 2000; Kahi et al., 2006). It accounts for about 70% of the domestic meat consumed (NDP, 1997). The supply of beef is mainly from the *Bos indicus* cattle found in the ASALs, *B. taurus* beef cattle found in medium- to high-potential areas and a few culls from the dairy industry (Trail et al., 1984; Mwandotto et al., 1988; Indetie et al., 2000; MALDM, 2000; Irungu and Ouda, 2001; Rewe et al., 2006a and b; Wasike, 2006). Some of the *B. taurus* beef breeds found in Kenya include the Charolais, Polled-Hereford, Angus, Simmental and Red Poll, which in the medium to high potential areas, are used as purebreeds. In the ASALs, they are used for crossbreeding with the *B. indicus* breeds, especially the Boran, to improve on the overall production efficiency (Gregory et al., 1984; Trail et al., 1984).

Despite the importance of *B. taurus* beef breeds in different production systems, their numbers remain low, which limits the exploitation of their beef production potential. However, general permanent improvement in performance can be realised through the design of appropriate breeding programmes (Smith, 1984). To effectively design breeding programmes and predict selection responses in traits of economic importance, genetic evaluation of economically important traits becomes important (Demeke et al., 2003). Growth and fertility traits are important in beef production because they directly influence the rate of off-take. Other traits include survival and carcass traits. Survival traits are of importance within the strenuous tropical production conditions where the environment greatly influences performance (Burrow, 2001; Hearnshaw et al., 2002). Carcass traits include carcass quality and quantity traits, e.g., pre-slaughter live weight, hot carcass weight and dressing percentage (Pariacote et al., 1998). Selection for carcass quality traits is greatly influenced by the market demand. In most cases in the tropics, survival and carcass traits 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 annual trends (Albuquerque and Meyer, 2001; Plasse et al., 2002; de Mattos et al., 2000; Abdel-Aziz et al., 2003). Performance is influenced by both the genetic constitution of an animal and the environmental circumstances under which it is performing (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). The efficiency of beef cattle genetic improvement programmes based on exotic breeds will, therefore, depend on the accuracy of identifying and selecting genetically superior animals using precise and accurate estimates of performance parameters (Sharma et al., 1982; Davis, 1993; Meyer, 1993b; Arthur et al., 1994; Mrode, 2000; Burrow, 2001). Genetic and phenotypic parameters have been estimated for most *B. indicus* cattle breeds in the tropics (e.g., Rege and Wakhungu, 1992b; Davis, 1993; Meyer, 1993b; Haile-Mariam and Kassa-Mersha, 1994 and 1995; Lôbo et al., 2000; Demeke et al., 2003 and 2004; Wasike, 2006). Similarly, direct and maternal effects have been estimated in beef cattle under temperate environments (Dodenhoff et al., 1998; Ferreira et al., 1999; de Mattos et al., 2000; Duangjinda et al., 2001; Quintanilla et al., 2002; Phocas and Laloe, 2004; Meyer et al., 2004). However, these estimates are scarce for *B. taurus* beef breeds reared under tropical environments.

The recent re-opening of the KMC processing plant at Athi River, with an anticipated slaughter capacity of 1,000 head of cattle daily, is bound to exert demand for beef cattle for use in the facility, in addition to other slaughter houses. This calls for more efficient beef cattle breeds that can be genetically and environmentally manipulated for sustainable beef production. However, no organised improvement programme exists for the *B. taurus* beef breeds in Kenya, mainly because there are no accurate parameter estimates in place, yet the records are available. The *B. taurus* beef breeds have high growth rates and attain mature weight earlier than the *B. indicus* beef breeds. Since the introduction of *B. taurus* beef breeds into Kenya in the 1960's, the performances and suitabilities of the Charolais and the Polled-Hereford beef breeds under the local conditions is relatively unknown. Genetic and phenotypic parameters for growth and reproductive traits of these breeds under local production circumstances are lacking.

1.1. Statement of the problem

The population of the Charolais and Polled-Hereford breeds has remained low, and their performances and suitabilities under the local conditions is relatively unknown. Despite their low numbers, these breeds are important in the beef industry as they are used as pure breeds and/ or in crossbreeding with the local breeds, especially the Boran. Genetic parameters for growth and fertility traits of these beef breeds under local production circumstances are lacking. These parameters are needed to facilitate development of effective breeding programmes.

1.2. Objectives of the study

The overall objective of this study was to determine the genetics of growth and fertility traits in the Charolais and the Polled-Hereford beef cattle breeds in Kenya. The growth traits studied were: birth weight (BW), pre-weaning average daily gain (ADG) and weaning weight (WW). Fertility traits included: age at first calving (AFC) and calving interval (CI). The specific objectives addressed were to:

(i) Determine factors affecting performance and obtain mean estimates for growth and fertility traits of the Charolais and the Polled-Hereford beef cattle breeds.

(ii) Estimate genetic and phenotypic parameters for growth and fertility traits of the Charolais and the Polled-Hereford beef cattle breeds.

(iii) Estimate the genetic and environmental trends in the growth and fertility traits of the Charolais and the Polled-Hereford cattle over the years.

1.3. Hypotheses of the study

H_0: Environmental factors are not the cause of observed variation in growth and fertility traits in the Charolais and the Polled-Hereford cattle.

H_0: Genetic and phenotypic parameters for growth and fertility traits in the Charolais and the Polled-Hereford cattle are comparable.

H_0: No genetic and environmental improvements have occurred in the Charolais and the Polled-Hereford cattle in Kenya over the years.

CHAPTER TWO

LITERATURE REVIEW

2.1. Beef cattle production in Kenya

In Kenya, beef is produced under pastoral systems and commercial beef ranching, which are pasture-based (Peeler and Omore, 1997; Kahi et al., 2006). These systems complement each other in that the ranches sell breeding animals to pastoral producers and *vice versa*. Crossbreeding between indigenous (*B. indicus*) cattle and the exotic (*B. taurus*) beef breeds such as the Shorthorn and the Polled-Hereford started in the early 1930's (Gregory et al., 1984; Trail et al., 1984). Beef production was initially practiced on large-scale ranches of 405 hectares (1,000 acres) and above as well as by pastoralists in the ASALs. However, the sub-division of land in the late 1960's contributed to a depression in beef output because a producer required at least 100 breeding cows in an optimum stocking area of 405 hectares (1,000 acres) for sustainable production (Berry, 1993; Prettejohn and Retief, 2001).

2.1.1. Beef cattle production systems in Kenya

Beef production in Kenya is carried out in different production systems in high and medium potential lands and in the ASALs (Irungu and Ouda, 2001; Rewe et al., 2006a and b). A large proportion of the beef is produced in the ASALs and relies on extensive grazing (NDP, 1997; Kahi et al., 2006). According to Irungu and Ouda (2001) specialised beef production is done by the commercial large-scale ranches found in the Rift Valley, Eastern and Coast provinces. Commercial large-scale beef ranching is characterised by good management practices such as maintaining pastures by stocking within the carrying capacity, controlling breeding and providing veterinary care. The ranchers also record performance of their cattle, which are used for selecting for improved growth, fertility and partly survival performance. Generally, cattle are finished on pasture under extensive grazing. Under ranching systems, the most important factors are adaptability, fertility, and genetic potential for growth and mature weight. As a result, most ranches realize high growth rates and have their stock ready for market within 3 years, when the animals weigh over 300 kg live weight.

Feedlot finishing of beef cattle was practised in Kenya in the late 1960's up to mid 1970's. Cattle were acquired from the pastoralists by ranchers and intensively fed for about three months then sold for beef (Irungu and Ouda, 2001). This practice increased the live weight gain and market value of the meat (Creek, 2003). As reported by Peeler and Omore

(1997), the other systems are pastoralism, dairy-meat and dairy. Pastoralism involves movement of animals in search of pasture. Pastoralists keep cattle primarily for milk and beef, but other products are secondary compared to dairy values. The milk is used for subsistence, while non-breeding stock are sold directly for slaughter or for growing and finishing in higher potential areas.

2.1.2. Marketing structures

Beef cattle marketing is one of the controversial issues in the livestock sub-sector in Kenya (Kilungo and Mghenyi, 2001). It is constrained by a number of factors; ranging from lack of proper market channels for beef cattle and beef products, inaccessibility to the export market, to static prices of beef products (Kahi et al., 2006). Until 1987, the KMC was the main marketer of beef and beef products in the country, and it determined prices of both live animals and beef (MoARD, 1998). This ensured an extra step in the marketing of beef. After the collapse of the KMC (currently revived) beef marketing became an individual producer's effort whereby those producers who were less efficient have been forced out of the market (Prettejohn and Retief, 2001). The restructuring of the beef industry during this time coupled with the collapse of the KMC resulted in livestock producers seeking alternative markets (Kilungo and Mghenyi, 2001). This saw some of its functions taken over by local government (municipal/ county) council abattoirs, and a rise in the number of middlemen. An illustration of various beef marketing channels before and after the revival of the KMC is presented in Figure 1.

The beef market in Kenya lacks stratification (MoARD, 1998). Kilungo and Mghenyi (2001) defined three main beef marketing categories in operation as primary, secondary and terminal markets. Primary markets comprise local herders as the main sellers with local butcheries and itinerant traders as the main buyers. Secondary markets consist of local herders as the main sellers, and larger and more established traders and butcheries as the main buyers. Terminal markets comprise of traders as main salers while traders and butchers are the main buyers. In both primary and secondary markets, animals are traded for both resale to middlemen and slaughter. Animals in terminal markets are mainly sold for slaughter. The recent reopening of the KMC is expected to shift the scenario and, consequently, improve the average revenues to the producers who will in turn be encouraged to propel the enterprise further.

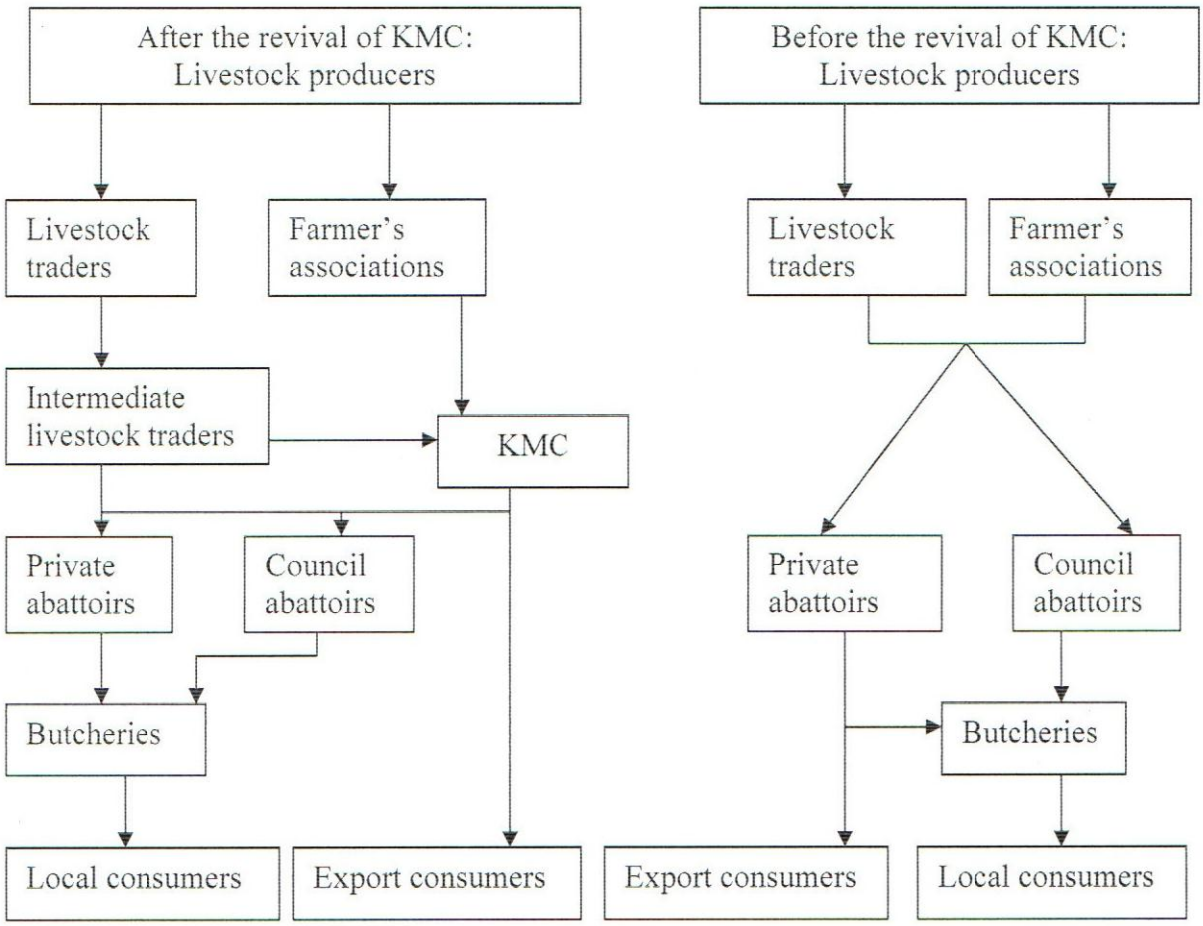


Figure 1. Beef marketing channels before and after the revival of the Kenya Meat Commission (Source: Kilungo and Mghenyi, 2001)

2.1.3. Breeding of beef cattle

Breeders utilize strategies that are designed to integrate new technologies and to improve on the old ones, for the purposes of maximising performance of existing stock (Gibson and Dekkers, 2003). Beef cattle breeding schemes follow a series of logical steps; specifying the planned breeding, production and marketing systems and, consequently, defining the breeding objective, evaluating available breeding stocks (nucleus or stud units), developing testing and selection systems for further improvement of economic merit (multiplier) and, lastly, dissemination of the improved stock to industry (commercial) so as to enjoy the benefits of improved work (Harris et al., 1984; Smith, 1988; Ponzoni and Newman, 1989; Blair and Garrick, 1994; Rewe et al., 2006a and b). Such a scheme is already being practiced in Kenya, although unconsciously (Rewe et al., 2006a and b). It resembles a pyramid, with the stud unit at the peak and commercial unit at the base. Breeding structures

may, therefore, consist of either simple isolated sub-populations or complex populations with flow of genes from the nucleus to the field populations and *vice-versa*. Through appropriate breeding structures, there is transfer of improved genes from the nucleus to the entire population (Cunningham, 1980).

A nucleus is either open or closed. The former implies that replacement stock for the nucleus population is being selected from both the nucleus and commercial populations, leading to a two-way flow of genes. A closed nucleus means that replacement stock for the nucleus herds are selected only within the nucleus and no importation is done from the commercial population, resulting in a one-way flow of genes. The open or closed nucleus herds can either be dispersed or centralised. The open nucleus schemes are beneficial when offspring in the commercial tiers are superior to the average of their parents and when selecting for lowly heritable traits (Garrick, 1993). The movement from the commercial to the nucleus herds ensures continuous screening of the commercial females transferred into the nucleus. However, closing the nucleus has the advantage of blocking unimproved genetic material from commercial populations (Garrick, 1993).

Breeding strategies for beef cattle should be aimed at improvement of productivity without loss in adaptation to the environment. Basic principles of genetics for livestock improvement can be applied for beef cattle. These include: (a) selection within breeds, (b) selection among breeds (breed substitution) and (c) crossing between breeds (Taneja, 1982). Within breed selection is a strategy of genetic improvement usually carried out in individual populations and is intended to increase the average level of genetic merit of the population (Kosgey et al., 2005). Successful selection within breeds relies on genetic variation and the ability to detect the variation, in addition to the proportion of parents needed to produce the next generation (Bett, 2005). Larger proportions result in lesser genetic progress and *vice-versa.* Significant genetic variation exists between and within breeds for most important traits in beef production (Koch et al., 1989). For example, breeds with the greatest retail product growth potential produce carcasses with less fat trim, meat with lower levels of marbling, but very acceptable meat palatability. However, they also sire progeny with heavier birth weights and increased calving difficulty. The rate of progress also depends on the speed with which successive generations (not only successive offspring) can be produced (Taneja, 1982). For example, progress by selection must be expected to be moderately high for a trait like growth rate, which is moderately heritable. Replacing one pure breed with another might be contemplated if the difference in performance is large. However, the performance of the new breed should be assessed along with the old breed under the conditions in which the breed

will be kept (Taneja, 1982). This strategy can achieve rapid genetic change when there are large genetic differences between breeds (populations) in traits of importance (Simm et al., 1996). On the national scale involving a very large number of animals, breed replacement by importation is impracticable, even impossible, to achieve over reasonable periods of years.

Crossbreeding is a means of producing animals that are expected to be on average halfway of their parental breeds in their performance. Crossing may be between *B. indicus* breeds or *B. indicus* and *B. taurus* breeds. Crossbred animals provide an opportunity for upgrading to the better parental breed by back-crossing with males of that breed. However, crossbreeding depends on a number of circumstances which include: (i) the genetic combination best suited to the conditions under which the animals must live and (ii) the extent to which the filial generation one (F1) is actually better than the average of the parents, i.e., the extent to which it manifests the hybrid vigour (Taneja, 1982). The two circumstances may change with time as a result of changes in the environment. In the past, it was often assumed that *B. taurus* breeds from temperate areas, with high production in their homelands, would automatically raise productivity when crossed with local breeds in tropical areas. Beef cattle breeds for harsh environments must be able to survive prolonged droughts, by having the ability to walk over long distances in search of water and pasture, and utilise coarse forages for growth, fertility and lactation (Mucuthi and Munei., 1996). Beef cattle breeding programmes in the ASALs are largely lacking because only in a few areas do farmers practice better breeding by upgrading (Kilungo and Mghenyi, 2001). Genetic improvement takes time and, therefore, likely changes in production conditions or in the market should be taken into account.

2.1.4. Constraints to beef production in Kenya

The beef industry in Kenya has lagged behind other agricultural enterprises mainly due to policies that did not favour the ASALs (Kahi et al., 2006). The ASALs support over 50% of the livestock population, and more than 25% of the human population in the country, consequently forming an important avenue for rural development. Beef production is negatively influenced by production and market constraints. Production constraints refer to factors that influence beef production and include; policies governing land ownership, production and marketing, research (genetic improvement), disease surveillance, drought (disaster preparedness), feeding and insecurity (cattle rustling) (Kahi et al., 2006). Most of the beef is produced under rain fed pasture-based systems in the ASALs. These areas are characterised by high solar radiation and ambient temperatures, high incidences of livestock

diseases, and inadequate and low quality pastures due to low rainfall and unreliable water supply, especially during droughts, which often lead to losses of body condition and to deaths (Kahi et al., 2006). Continued sub-division of land due to human population pressure and persistent droughts poses a big challenge to beef production mainly during dry seasons. This sub-division has led to shrinkage in the grazing resource base that, consequently, affects the productivity of the animals (Kilungo and Mghenyi, 2001; Kinyamario and Ekeya, 2001).

Low growth rates of *B. indicus* cattle owing to their low genetic potential coupled with environmental limitations result to low off-take. Low destocking rates among the pastoralists often lead to overgrazing of pasture fields, causing environmental degradation and livestock losses during droughts. Major shifts from beef to dairy and cropping enterprises in medium to high potential areas constrain expansion in the sub-sector (Kilungo and Mghenyi, 2001). Poor disease control as a result of animal movements within rangelands and across national borders, and interaction of animals with wildlife (leading to wildlife-livestock and wildlife-human conflicts) often enhances the spread of zoonotic diseases. This negatively impact on the sub-sector, particularly in relation to the external markets. Slaughter facilities are generally located far from the production points. This, coupled, with poor infrastructure, lead to long distance walking of animals destined for slaughter that often results to loss of weight and, therefore, income to the producer. Small-scale producers lack information on price and price shifts in forward markets and, as a result, are often exploited by middlemen (traders) (Kilungo and Mghenyi, 2001). Generally, the potential for beef production in Kenya exists given the available genetic and physical resources. However, its achievement requires review of policies aimed at accelerating development in the rangelands and empowerment of the producers, pastoralists included, to increase their production (Kahi et al., 2006).

2.2. Traits of economic importance in beef production

Beef cattle productivity is a function of many traits; production, fertility, survival and carcass composition (Vercoe and Frisch, 1992). The economic impact of these traits on a beef production enterprise is examined by considering their effects on profitability of the enterprise. Selecting the best cattle can lead to gains in genetic potential for profit. As the traits are related, breeding programmes incorporating most of the favourable traits would be more effective than those considering a particular trait category. Selection for improvement of these traits in a production system is influenced by the production environment, ease of expression and market conditions.

2.2.1. Production traits

Production performance is described by growth traits, which directly influence profitability in beef production (Baker and Morris, 1981; Johnston and Graser, 1998; Arango and Plasse, 2002). The traits include all growth characteristics measured as live weight and depend on the animal's inherent growth potential under given production circumstances (Dillard et al., 1980; Mackinnon et al., 1991; Davis, 1993; Campelo et al., 2004). In commercial cut-based beef cattle, production parameters related to growth are important because they determine the size of an animal at slaughter. Production traits are used in the computation of feed efficiency traits (Arthur et al., 2001).

Pre-weaning growth of calves is one of the most important parameters for evaluating beef cattle. Birth weight, ADG and WW are some of the common measures of this growth (Dillard et al., 1980; de Mattos et al., 2000; Arango and Plasse, 2002; Abdel-Aziz et al., 2003). These traits in beef cattle are important in selection programs (Ferreira et al., 1999). Weights at weaning give breeders useful information to test growth ability (Goyache et al., 2003). Genetic merit for growth of meat producing animals is generally assessed, treating records taken at different ages, or ranges of ages, as different traits (Arthur et al., 2001; Meyer, 2004). For the estimation of breeding values, weaner traits should be treated as different from yearling traits (Arthur et al., 2001). This is due to the fact that growth during the active growth phase (weaners) is characterised predominantly by muscle growth, while that during the slow growth phase (yearlings) is characterised by increased fat deposition. Early maturity in beef cattle may be important in the tropical environment with large seasonal variations where costs of production are minimised by marketing slaughter cattle at the end of a growing season and, therefore, avoid weight loss during an additional dry season (Koch et al., 1989). The efficiency with which feed, labour and capital are converted into beef forms an important component in determining profitability in beef cattle.

2.2.2. Fertility traits

In a beef production enterprise, high off-take is the ultimate goal. This involves animal movement out of the system as sale or slaughter animals. The goal is determined by fertility, among other factors. Normal fertility (i.e., the regular production of viable offspring) is the prerequisite to achieving high off-take. Fertility levels are measured using AFC, NSC, CI, DC, NR and calving rate/ calf crop (Branton, 1970; Johnston and Graser, 1998; MacGregory and Casey, 1999; Schaeffer, 2004). Losses from impaired fertility or reproductive failure constitute the greatest single cause of loss among beef cattle in the tropics (Branton, 1970).

The main reason for the relatively low reproductive efficiency of beef cattle in the tropics is recognized to be environmental (Haile-Mariam and Kassa-Mersha, 1994; Demeke et al., 2004).

High rates of fertility, i.e., the efficiency of cows in producing calves are directly related to profitability in beef cattle. Except for AFC, fertility traits are observed before every parturition and, therefore, there are observations on the same animal over a period of years (Schaeffer, 2004). Fertility traits generally have low heritability, indicating a strong influence of environmental factors such as herd management decisions (Haile-Mariam and Kassa-Mersha, 1994; Olori et al., 2002; Demeke et al., 2004; Schaefer, 2004). Age at first calving is negatively correlated with growth traits, signifying favourable relationships between growth and early fertility (Bourdon and Brinks, 1982). A delay in conception due to poor fertility prolongs intercalving interval, causing a shift in calving pattern, which can lead to culling. Calving interval as a measure of fertility can present a problem because only animals that survive to the next lactation have a CI. However, CI remains the principle measure of fertility efficiency in continuous breeding schemes (MacGregory and Casey, 2000).

2.2.3. Survival traits

The ability of an animal to grow and reproduce in a given management system is described by survival traits. The traits describe the potential of an animal to grow, reproduce and remain productive under given production conditions (Mackinnon et al., 1991). The more adapted an animal, the longer it will live and reproduce, such that more calf crop percentage can be realised. Survival is a trait observed daily in an animal's lifetime, but only at the point at which an animal dies or is culled is it usually recorded (Schaefer, 2004). At the beginning of the observation period, usually at birth or first calving, most animals are still alive so the phenotypic variance is close to zero.

Survival estimates vary widely under different environments, management systems and culling policies. Estimates of cow survival and associated statistics are useful in modelling herd-age structures in production systems (Hearnshaw et al., 2002). Herd life is a measure of the animal's adaptability to a particular production environment and is usually described as survival rate at various developmental stages measured in terms of tolerance to pathogenic parasites and mortality (Burrow, 2001). Longevity, the number of days a cow survives given an opportunity to stay in the herd after a first calving, is one of the traits that affect overall profitability and efficiency in beef production (Martinez et al., 2002 and 2004; Hearnshaw et al., 2002; Forabosco et al., 2004). Cows with long productive life increase

profits by decreasing annual cost of replacements (Hearnshaw et al., 2002; Forabosco et al., 2004) and, therefore, enhance rates of genetic gain (Hearnshaw et al., 2002). Genetic prediction of stayability of females represents an important opportunity for cost reduction and increased profits through selection for persistent fertility and productivity. Survival traits tend to have widely varied parameter estimates due to high environmental influences (Davis, 1993; Hearnshaw et al., 2002).

2.2.4. Carcass traits

The carcass constitutes 50-60% of the live weight of an animal. The loss comprises mainly offals, the hide and bones. Carcass merit of beef cattle forms an important attribute in beef marketing because it determines the amount and quality of saleable meat harvested from slaughtered animals, and the revenue generated thereof (Rewe et al., 2006b). The traits describe the characteristics of beef and can be divided into carcass quality and 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. Carcass measurements can be taken after slaughter of animals either at the same age or same weight. Carcass measurements at the same age reflect growth. Heritabilities of carcass traits are moderate to high in Polled-Hereford cattle (Meyer et al., 2004).

2.3. Performance of *B. taurus* beef cattle and their crosses

Beef cattle that are entirely dependent on natural range forage for growth and reproductive functions and therefore, exhibit a seasonal cyclicity in body weight and condition (Itulya et al., 1987). In the tropics, growth virtually ceases during the dry season and then resumes during the wet season. Consequently, poor correlations between weights before and after the wet season are expected (Itulya et al., 1987; Mackinon et al., 1991). Besides, climate, amount and quality of feed resources, and market requirements play key roles in determining the optimum level of performance (Koch et al., 1989).

The *B. taurus* beef breeds have acceptable milking ability and good adaptability to pasture grazing conditions, with reasonable growth and carcass weights. They are, therefore, used as purebreeds and in crossbreeding systems to maximise cow performance (Baker and Morris, 1981; Koch et al., 1989; Morris et al., 1993). In *B. taurus* x *B. indicus* breed crosses, there is more heterosis for performance traits (Gregory et al., 1984; Trail et al., 1984; Koch et

al., 1989), due to their diverse genetic backgrounds. Direct across-breed comparisons of individuals require joint knowledge of the relative genetic merits of breeds and individuals within breeds (Sullivan et al., 1999). Genetic merit for reproductive performance could change over time as well (Schaeffer, 2004). Tables 1 and 2 below show the growth and reproductive performances, respectively, of some *B. taurus* beef breeds and crosses in the temperate and tropical countries. There is very little published information on the traits of *B. taurus* breeds under Kenyan conditions.

2.3.1. Productive performance

Table 1 presents mean performances for some productive traits for *B. taurus* breeds. Performances of the *B. taurus* breeds and their crosses are variable. The variations may be attributed to differences in the population structures of the herds, herd management, breed, differences in selection strategies and the environment or climate where the data was obtained. However, the Charolais outperforms most of the breeds with regard to BW, WW, FW and ADG. This demonstrates superiority in performance of the Charolais over the other breeds. Generally, across the breeds, male calves weighed more than female ones and, on average, Charolais calves were heavier at birth and weaning, and grew faster than the other breeds. This could be attributed to the higher individual additive genetic influence on the growth of Charolais cattle relative to the other *B. taurus* breeds. Lunstra and Cundiff (2003) reported lower post-weaning weight gain and attainment of puberty in offspring of heat-adapted sire breeds compared to those of *B. taurus*-sire breeds. *Bos taurus*-sired bulls grew more rapidly after weaning than *B. indicus*-sired bulls. In that study, differences in growth patterns through yearling could be attributed to seasonal effects that could have favoured heat-adapted breeds during pre-weaning period (summer) but favouring temperate breeds during post-weaning period (winter). This shows the influence of the production environment on the growth performance of beef cattle. The *B. taurus* x *B. taurus* (i.e., Charolais x Hereford, Hereford x Angus) crosses tended to be lighter at weaning than the *B. taurus* x *B. indicus* (Charolais x Boran) crosses (Table 1). This could be attributed to greater heterotic effects in the *B. taurus* x *B. indicus* crossbred genotypes, owing to their diverse genetic backgrounds. Breed differences in performance characteristics are important genetic resources for improving efficiency of beef production, and crossbreeding is an acceptable means of incorporating desirable traits from various breeds (Meyer, 1993b; Lunstra and Cundiff, 2003). Weaning weight estimates within a genotype are highly variable (Table 1). This is because weaning weight is largely dependent on age at weaning (Goyache et al., 2003), which in turn

is dependent on the month of birth of the calf. In addition, this could be attributed to the calf rearing systems and environmental conditions of the production areas where the data used in the studies were obtained. Male animals were born and weaned heavier than female animals (Table 1). Sex of the animal affects all 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., 2000). Male cattle tend to be heavier than their female counterparts at all ages due to higher influence of testosterone hormone. It has been suggested that male calves had greater nutritional requirements to fully express their growth potential than their female contemporaries (Sharma et al., 1982; Itulya et al., 1987; Burrow, 2001).

Table 1. Productive performance of *B. taurus* beef cattle and their crosses

Genotype[b]	Trait[a]											Country	Source
	BW^m	BW^f	BW^a	WW^m	WW^f	WW^a	ADG^a	ADG^m	$ADGP^m$	YW	FW		
CH			38			206	0.82					„	Dillard et al. (1980)
			47			280						France	Phocas and Laloe. (2004)
			48			286						„	Fouilloux et al. (2002)
			42			229						Canada	Sullivan et al. (1999)
			41			259				344	454	Australia	Meyer (1993b)
								1.61	1.15			France	Arthur et al. (2001)
									1.41		728	„	Renand et al. (2002)
HF			32			157	0.61					USA	Dillard et al. (1980)
	44			252				1.04	1.30			„	Lunstra and Cundiff (2003)
			33			211	0.70					Australia	Arthur et al. (1994)
			33			206				324		„	Meyer (1992)
			32			228					410	„	Meyer (1995)
			38			228				344		„	Meyer (2004)
			40			198						Canada	Sullivan et al. (1999)
	35	33		206	193							USA	Itulya et al. (1987)
			36			203				313		„	Ferreira et al. (1999)
	36	34		221	184	278				422		„	Bourdon and Brinks (1982)
				222	188	194						„	Nadarajah et al. (1987)
RAN	34	32		233	200					276		USA	Bourdon and Brinks (1982)
Angus	34	32		244	198					280		„	„
				204	175	186						„	Nadarajah et al. (1987)
			38			211						Canada	Sullivan et al. (1999)
			33			168						New Zealand	Morris et al. (1993)
			28			187				207		Australia	Meyer (1992)
						211				404		Canada	Fan et al. (1995)
	43			254				1.06	1.33			USA	Lunstra and Cundiff (2003)
B	46			254				1.04	1.01			„	„
						194						Kenya	Gregory et al. (1984)
Tuli	39			242					0.99			„	Lunstra and Cundiff (2003)
F_1	44			251				1.04	1.16			„	„
CH x B						211						„	Gregory et al. (1984)
HF x CH			35			177	0.69					„	„
HF x Angus			32			172	0.69					„	Dillard et al. (1980)

[a]AFC= age at first calving (days); CI= calving interval (days); BW^m= birth weight for males (kg); BW^f= birth weight for females (kg); BW^a= average birth weight (kg); WW^m= weaning weight in males (kg); WW^f= weaning weight in females (kg); WW^a= average weaning weight (kg); ADG^a= average daily gain (kg); ADG^m=pre-weaning average daily gain in males (kg); $ADGP^m$= post-weaning average daily gain in males (kg); YW= yearling weight (kg); FW= Weight at 18 months (kg).

[b]CH= Charolais; HF= Polled-Hereford;; RAN= Red Angus; B= Boran; F_1= first generation crosses.

2.3.2. Reproductive performance

Increased fertility improves the profitability of beef production under most production/ marketing situations (Johnston and Graser, 1998). Cow reproductive performance is a more important objective for improvement than growth rate (Baker and Morris, 1981). However, improving cow fertility through female selection is expected to be slow and costly, owing to the low heritability and selection intensity associated with female reproductive traits (Mwansa et al., 2000). The success or failure of an insemination event can be viewed as a trait of the cow that is being inseminated (e.g., female fertility), or as a trait of the service bull (e.g., male fertility) (Waigel and Rekaya, 2000). Improvement by selection is more difficult for reproductive performance because of low heritabilities of reproductive traits. Fortunately, crossbreeding can substantially improve both cow fertility and maternal performance (Baker and Morris, 1981). Improvement in fertility has been found to be sensitive in most production systems because it will improve meat production (Peeler and Omore, 1997; MacGregory and Casey, 2000). The environment surrounding the animal plays a major role in its fertility. The environmental effects range from physical (i.e., climatic factors) to nutrition and general management (feeding and heat detection). Therefore supplementing animals with quality feeds during adverse seasons, employing prudent heat detecting and culling of cows that exhibit silent heat and those that do not conceive after repeated insemination could improve reproductive efficiency. High rates of fertility in a beef herd are directly related to the profitability of beef production (Johnston and Graser, 1998; MacGregory and Casey, 1999). Conversely, before fertility can be improved, it is essential that a suitable measure of fertility performance be found. The trait should be heritable, exhibit variation and be easy and cost effective to measure under field conditions (Baker and Morris, 1981; Johnston and Graser, 1998). Calving interval is currently used as a measure of fertility in many countries. However, it is not a suitable measure of reproductive ability when cows are mated during restricted breeding seasons owing to the negative effect of previous calving date on CI (MacGregory and Casey, 1999; Rust and Groeneveld, 2001). It is only available for cows from the second parity onwards, and can be computed from minimum data, but does not take into account information from the first parity or end of a cow's life span (Rust and Groeneveld, 2001). Calving interval is only available for cows that conceive and calf again (Olori et al., 2002). In addition, CI is under the influence of certain environmental factors, e.g., parity (Gregory et al., 1984; MacGregory and Casey, 1999), and the previous calving date

(MacGregory and Casey, 2000). In the present study, where year round mating took place for the majority of the period, CI appears to be a comparable measure of fertility. Cows with shorter CI's are the most fertile (Demeke et al., 2004) and, consequently, are selected in preference to those with longer CI's. Heritability estimates of CI for beef cattle are scarce in the literature due to the fact that either calving rate or calving date (days to calving) are considered to be appropriate measures of fertility in seasonal mating schemes (Haile-Mariam and Kassa-Mersha, 1994). On the other hand, AFC represents one component in the reproductive life of a cow, and it is only recorded for heifers. Furthermore, in a variable environment, AFC reflects management decisions to a greater extent than genetic merit (Rust and Groeneveld, 2001). Fertile cows have their first calves at an early age followed by short CI's thereafter (Demeke et al., 2004). A reduced AFC would increase the number of calves born for a given number of cows in a herd (Rust and Groeneveld, 2001). This index can be computed without additional data recording because birth date and the first calving of a cow are generally known.

Table 2 presents a summary of some reproductive performances for *B. taurus* and *B. indicus*, and their crosses. Age at first calving was variable, although *B. taurus* and composite breeds had shorter AFC compared to the *B. indicus* breeds. The Red Angus in the USA attained AFC earlier than the Boran in Ethiopia as the *B. taurus* x *B. indicus* crosses recorded shorter AFC than the purebred *B. indicus* (Gregory et al., 1984). The variation could be due to genotype by environment interactions. *B. taurus* x *B. indicus* crosses recorded shorter CI's compared to the *B. indicus*. Generally, *B. taurus* x *B. indicus* crosses have shorter CI's than purebred *B. indicus* (Table 2). This could be attributable to the effect of heterosis in the crossbred genotypes.

Table 2. Reproductive performances of *B. taurus* and *B. indicus* beef cattle and their crosses

Genotype	Trait[a]			Country	Source
	AFC	CI	CD		
Polled-Hereford	730			USA	Bourdon and Brinks (1982)
Red Angus	723			,,	,,
Angus	726			,,	,,
,,	930			Brazil	Teixeira et al. (2002)
Beef herd		377	87	South Africa	MacGregory and Casey (1999)
Boran	1271	442		Ethiopia	Haile-Mariam and Kassa-Mersha (1994)
,,	1275	473		,,	Demeke et al. (2004)
,,	1049	412			Gregory et al. (1984)
,,	1223	413		Kenya	Trail and Gregory (1981)
,,	1093	421		,,	Trail et al. (1984)
,,	1188	477		,,	Wasike (2006)
Composite breed	782	391		South Africa	van der Westhuizen et al. (2001)
Sahiwal	1259	469		India	Seithi et al. (1997)
,,	1345	468		Kenya	Ilatsia et al. (2007)
Charolais x Boran	1021	398		,,	Gregory et al. (1984)
Santa Gertrudis x Boran	1104	452		,,	,,
Red Poll x Boran		392		,,	,,

[a]AFC= age at first calving (days); CI= calving interval (days); CD= calving date.

2.4. Factors influencing productive and reproductive performances

Productive and reproductive performances are normally influenced by fixed environmental factors and other continuous effects. Environmental factors greatly influence growth and reproductive performances of beef cattle in the tropics (Haile-Mariam and Kassa-Mersha, 1994; Wasike, 2006). These effects are usually included in models used for the analysis to adjust the data for any bias that would lead to under- or over-estimation of an animal's performance. The fixed effects are usually defined into classes comprising all the possible levels of interest. These include herd, year, season, sex, genotype and parity, and their interactions. Continuous effects are sources of variation usually not defined into class levels and have a continuous influence on the observation. They are usually fitted as covariables and include age related effects like age of the calf at weaning and age or weight of the cow at birth or calving (Dillard et al., 1980; van der Westhuizen, 2001; Goyache et al., 2003). It has been observed that age of calf at weaning was an important source of variation for WW, while age of dam affected both BW and WW (Maiwashe et al., 2002; Wasike, 2006).

Table 3 presents some of the factors and their effect on growth and fertility traits in beef cattle. Significant differences between sexes have been reported for BW and WW (Dillard et al., 1980; Goyache et al., 2003) (Table 1). Male calves weighed more than the heifers. Among the possible reasons for differences in performance of the breed groups are breed additive and breed maternal environment contributions to their performance (Dillard et al., 1980; Meyer, 1992). For example, the Charolais maternal ability (mainly dam's milk production) may exceed that of the Polled-Hereford and Angus for growth traits and, therefore, account for significant amounts of variation in BW and WW (Table 1). Galina and Arthur (1989) observed substantial evidence that certain breeds, particularly *B. taurus*, tend to have their first calving much earlier than the *B. indicus* and that crossing the two types generally improved the performances of the *B. indicus* breeds.

Significant herd x year interaction effects have been reported for BW and WW (Table 3) implying that year effects were not the same for both herds, i.e., changes in both management and climatic conditions would result in changes in productive performance (Dillard et al., 1980). Herd x year of birth interactions influence reproductive performance, e.g., animals born in herds under good management and favourable climatic conditions would calve down earlier and their CI's would be shorter and *vice-versa* (van der Westhuizen, 2001).

Genotype by environment interactions is a change in the relative performances of two or more genotypes measured in two or more environments (Mathur, 2002). Morris et al. (1993) reported greater genotype by environment interaction differences for reproductive than growth traits, and the *B. taurus* breeds excelled in most favourable environments than in harsh ones. In real life, both the environmental and genetic changes are happening and, therefore, it is necessary to improve on the total efficiency of a beef production system.

Table 3. Factors influencing productive and reproductive performances in beef cattle

Factor[a]	Traits[b]							Source
	BW	WW	ADG	ADG^P	FW	AFC	CI	
Fixed effects								
Herd		***						Goyache et al. (2003)
		**	**					Dillard et al. (1980)
			**		**			Mwandotto et al. (1988)
Sex	**	**	**					Dillard et al. (1980)
		***						Goyache et al. (2003)
	**	**	**					Abdel-Aziz et al. (2003)
						NS	NS	Haile-Mariam and Kassa-Mersha (1994)
	**	**	**					Sharma et al. (1982)
Parity							***	Demeke et al. (2004)
	*	*						Indetie et al. (2000)
Genotype	*	*						Arthur et al. (1994)
						***	***	Demeke et al. (2004)
	**	**	**					Abdel-Aziz et al. (2003)
	**	**	**					Dillard et al. (1980)
	***		**	***				Lunstra and Cundiff (2003)
	**	**	**	**	**			Sharma et al. (1982)
G x E	NS	NS						Arthur et al. (1994)
	*	*				*	*	Morris et al. (1993)
		***						Goyache et al. (2003)
	*	*						Indetie et al. (2000)
Y-Sob		**	**					Mwandotto et al. (1988)
						*		Demeke et al. (2004)
	**		NS	NS				Lunstra and Cundiff (2003)
							**	McGregory and Casey (1999)
						*	*	Haile-Mariam and Kassa-Mersha (1994)
	**	**	**					Abdel-Aziz et al. (2003)
	**							Koster et al. (1994)
H–Yob						***	***	van der Westhuizen (2001)
	**	**	**	**	**			Sharma et al. (1982)
	**	**						Dillard et al. (1980)
Continuous effects								
AWn		***						van der Westhuizen (2001)
		**						Abdel-Aziz et al. (2003)
		***						Goyache et al. (2003)
		**			**			Dillard et al. (1980)
		**						Mwandotto et al. (1988)
Age of dam	**	**	**					Dillard et al. (1980)
	**	**	**					Abdel-Aziz et al. (2003)
		*						Arthur et al. (1994)
	**	**	**		**			Sharma et al. (1982)
	*	*						Indetie et al. (2000)

[a]G x E= genotype x environment; Y-Sob= year-season of birth; H–Yob= herd-year of birth; Awn= age at weaning.
[b]BW =birth weight (kg); WW= weaning weight (kg); ADG = average daily gain (kg); ADG^P= post weaning average daily gain (kg); FW= weight at 18 months; AFC= age at first calving (days); CI= calving interval (days).
***P<0.001; **P< 0.01; *P<0.05; NS= not significant.

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2.5. Variance components

2.5.1. Genetic variance

Biological variation is an important aspect of genetic progress. The actions of individual genes are largely unknown. Consequently, quantitative methods based on the infinitesimal models have been designed to analyse the effects of genes and partition phenotypic variance into its components; genetic and environmental causes (Mrode, 2000). These components vary among populations for several reasons; due to changes on gene frequency, previous selection, environment and past history of the population (Kennedy et al., 1988; Bennett and Gregory, 1996). Estimates made in one population are, therefore, not recommended for application in another. Such estimates are available for European cattle breeds in the temperate regions (Kaps et al., 1999; de Mattos et al., 2000). However, estimates of (co)variance components for *B. taurus* beef cattle breeds reared in the tropics are scarce in the literature.

Direct additive genetic effects are effects on performance of an animal that can be attributed to its own genes. They are due to the average parental genes (Falconer and Mackay, 1996) and constitute the breeding value of the animal. These effects are heritable and, therefore, form the core component of genetic improvement due to their ability to be selected for. Maternal additive genetic effects refer to any contribution or influence on the offspring's phenotype attributable to its own dam and the sample of genes passed onto the offspring (Falconer and Mackay, 1996). Consequently, these effects are partly environmental and partly genetic. Growth in beef calves is determined not only by the animal's genetic potential for growth, but also by its dams' maternal ability (Meyer, 1992, 1993a and b). Negative additive-maternal genetic correlations have been reported (Baker, 1980; Dodenhoff et al., 1998; de Mattos et al., 2000; Maniatis, 2000). They indicate the genetic progress made in selection for beef traits where maternal effects exist. Faster genetic progress would be realised when the correlation is small (Baker, 1980). This is achievable when multi-trait models are used for genetic analyses because the models reduce the correlation owing 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 through the use of detailed pedigree data, in which a high proportion of the dams and maternal grand dams have their own records (Maniatis and Pollott, 2003). This is the main constraint in genetic evaluation in tropical Africa where performance and pedigree recording are not consistent. This limitation also hinders the partitioning of maternal effects into genetic and

permanent maternal effects, which require repeated records on individual dams and the presence of these dams in the data.

Maternal environmental contribution to calf growth comprises pre- and post-natal nutrition supplied by the dam as well as the behavioural interactions between the cow and the calf (Crow and Howell, 1982). The influence of age of dam on performance (mainly growth) traits of offspring is greatest during the pre-weaning period and lessens as the animal grows older post-weaning (Sharma et al., 1982; Arthur et al., 2001). Other effects known to influence performance include direct dominance and grand-maternal effects. According to Duangjinda et al. (2001), direct dominance effects (deviations originating from interactions between alleles at same loci at two homologous chromosomes) are important for weaning weight. Animals with high weaning weight due to direct dominance effects tend to have lower maternal ability due to maternal dominance effects. Knowledge of the proportion of the genetic variance attributable to direct additive and maternal contribution to the performance of the offspring is necessary in planning sound breeding programmes (Dillard et al., 1980; Arthur et al., 1994).

2.5.2. Environmental variance

This is a component of phenotypic variance resulting from the environment surrounding the animal. The effects range from physical (i.e., climatic factors) to nutrition and general management. Environmental variance is further partitioned into permanent, common and residual (measurement error) variances, each resulting from different effects. However, common environmental variance is evidenced in multiparous animals and, therefore, is not of interest in the current study. In successively recorded traits, more than one record/ observation is made on an individual. For example, weight records from an animal at different times in beef cattle, milk yield records in different lactations or same lactation in dairy cattle and successive calving intervals in the same animal are observations taken repeatedly on the same individual at different times (Meyer, 2000). The variations arising from such observations are partly related and, therefore, constitute a permanent variance that is attributed to the environment (Mrode, 2005). In analysis of growth and fertility traits, the environmental variance is partitioned for accurate estimation of residual variance, which estimates the effect of the environment on the measurement. Consequently, the permanent environmental effects are modelled as random effects as they apply to the animals in question. 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 and 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, therefore, the reliability of the results. All these components of variance are important in the estimation of genetic parameters for use in genetic improvement programmes, and their accuracy is necessary for high genetic progress.

2.6. Genetic and phenotypic parameters for *B. taurus* beef cattle and their crosses

Estimates of genetic and phenotypic parameters are needed for the genetic evaluation of animals and the design of effective breeding programmes (Dillard et al., 1980; Davis, 1993; Arthur et al., 1994; Lôbo et al., 2000). These parameters are essential and have to be continually estimated (Argentao et al., 2002). Table 4 below shows the estimates of genetic and phenotypic parameters for growth and reproductive traits for beef cattle. Genetic parameter estimates and information on the extent of within breed variation in the tropics is scarce (Haile-Mariam and Kassa-Mersha, 1994). Genetic and phenotypic parameter estimates are variable (Lôbo et al., 2000). The variability has been attributed to factors such as population history, data size and structure, the model of analysis used, breed, environmental effects and evolution (Meyer, 1992; Davis, 1993; Meyer, 1993a; Burrow, 2001; Hearnshaw et al., 2002; Rumph et al., 2002; Maniatis and Pollott, 2003). Estimates of genetic effects are useful in explaining differences in performance among genotypes (Arthur et al., 1994). Increases in beef productivity can occur only if based on improved techniques of animal breeding, nutrition, fertility and disease management (Souza et al., 1998, Lôbo et al., 2000). In Kenya, breed descriptions in terms of genetic parameters for traits affecting biological efficiency for the main *B. taurus* beef cattle are scarce and, therefore, the need to estimate these parameters for use in design and evaluation of breeding programmes.

Table 4. Estimates of genetic and phenotypic parameters for productive and reproductive traits for beef cattle

Population[a]	Trait 1[b]	Trait 2[b]	Model[c]	Parameter estimates[d]					Country	Source
				$h^2_{a\ trait\ 2}$	$h^2_{m\ trait\ 2}$	$r_{am\ trait2}$	$r_{a\ (1,2)}$	$r_{p\ (1,2)}$		
Charolais	WW	WW	AM	0.34	0.15	-0.47				Duangjinda et al. (2001)
	BW		,,	0.33	0.11	-0.41			France	Phacos and Laloe (2004) et al. (2004)
	,,		,,	0.22	0.11	-0.80	0.56	0.25	Australia	Meyer (1993b)
	,,	YW	,,	0.32	0.00		0.67	0.28	,,	,,
		WW	AMM	0.11	0.14	-0.12			USA	Dodenhoff et al. (1999)
	FW	ADGP[m]	AM	0.26			0.43		France	Renand et al. (2002)
	BW	WW	AMM	0.16		0.12			USA	Bennett and Gregory (1996)
	ADGP[a]	ADGP[a]	,,	0.46					,,	,,
Polled-Hereford	WW	WW	AM	0.23	0.12	-0.30			Canada	Duangjinda et al. (2001)
		,,	AMM	0.17	0.16	-0.37			USA	Dodenhoff et al. (1999)
	BW	BW	,,	0.41	0.08	0.05			Australia	Meyer (1992)
	WW	WW	,,	0.14	0.13	-0.59			,,	,,
	BW	BW	,,	0.35	0.14	-0.05			,,	Ferreira et al. (1999)
	,,	WW	,,	0.18	0.17	-0.34			,,	,,
	,,	YW	,,	0.30	0.08	-0.26			,,	,,
	,,	WW	AM	0.10			0.52	0.25	,,	Itulya et al. (1987)
	WW	,,	,,	0.24	0.16	-0.42			USA	de Mattos et al. (2000)
	BW	BW	AMM	0.45	0.10	0.15			,,	Dodenhoff et al. (1998)
		AFC		0.07					,,	Bourdon and Brinks (1982)
	ADGP[a]	ADGP[a]	AMM	0.39					,,	Bennett and Gregory (1996)
Angus	BW	WW	,,	0.20	0.14	0.22	0.76	0.51	Australia	Meyer (1993a)
	WW	YW	,,	0.25	0.15	-0.04	0.95	0.74	,,	,,
	BW	BW	,,	0.36	0.07	0.29			,,	Meyer (1992)
		,,	,,	0.53	0.18	-0.51			,,	Kaps et al. (1999)
		WW	,,	0.25	0.11	-0.15			USA	Dodenhoff et al. (1999)
	BW	,,	,,	0.25		0.34			,,	Bennett and Gregory (1996)
Composite	,,	,,	,,	0.17	0.34	-0.19	0.53	0.56	Australia	Burrow (2001)
		BW	,,	0.57	0.18	-0.25			,,	,,
		AFC		0.40					,,	van der Westhuizen et al. (2001)
	AFC	CI		0.01			-0.3		,,	,,
Mertolenga		,,	AM	0.03					Portugal	Matos et al. (2002)
Boran		AFC	,,	0.06					Ethiopia	Haile-Mariam and Kassa-Mersha (1994)
		CI	,,	0.04					,,	,,
Crosses	WW	YW	,,	0.25	0.14	-0.40	0.79	0.80	France	Meyer (1993a)
	BW	WW	AMM	0.58	0.36	-0.78			Australia	Meyer (1992)

[a]Crosses= *B. indicus* x *B. taurus*.

[b]BW= birth weight; WW= weaning weight; ADGP[a]= post-weaning average daily gain; ADGP[m]=post-weaning average daily gain for males; YW = yearling weight; FW= final weight; AFC= age at first calving; CI= calving interval.

[c]AM= simple animal model (random direct); AMM= animal maternal model (random direct and maternal genetic).

[d]h^2_a= direct heritability; h^2_m= maternal heritability; r_{am}= correlation between direct genetic and maternal genetic effects; $r_{a\ (1,2)}$= additive genetic correlation between traits1 and 2, $r_{p\ (1,2)}$= phenotypic correlation between traits 1 and 2.

2.6.1. Heritability

Heritability is the proportion of the total variance that is attributable to the average effects of genes (Falconer and Mackay, 1996). Information on heritability is important for selection because it determines the degree of resemblance between individuals. Traits with high heritability can be improved through selection where response to selection and genetic gain are expected to be great. The estimates are partitioned into maternal and direct heritability, attributed to maternal and individual animal genetic effects, respectively. Estimation of genetic parameters due to maternal effects in beef cattle has generally been restricted to traits describing growth until weaning (Meyer, 1992). In most studies, only additive genetic components have been considered.

Variations in heritability estimates of productive traits in *B. taurus* and their crosses in the temperate and the tropics have been reported (Table 4). These variations could be attributed to differences in the population structures of the herds, the model fitted in the estimation of genetic parameters, the breed and the environment where the data was obtained. For example, estimates obtained using AM were larger than those obtained using models that included AMM (Table 4). This was due to fitting of only one random effect (additive genetic effect) to account for all the genetic sources of variation. As a result, the effect of the dam on the growth of its offspring was not accounted for independently as in the latter model but lumped together with the individual genetic effect as genetic variance. When AMM was fitted, the estimate of direct heritability is drastically reduced due to partitioning of the genetic variance into direct and maternal genetic variance (Meyer, 1992). There were differences in heritability estimates between breeds (Table 4), owing to differing genetic potentials of different breeds for the various traits of interest, and the varying levels of selection subjected to different breeds (e.g., Ferreira et al., 1999). For instance, in Table 4, medium to high heritabilities for BW and low to medium heritabilities for WW imply that growth performance could be improved through selection on these traits. For most production traits, selection plays a major role in their improvement. Generally, the maternal genetic variance is smaller than the direct genetic variance, resulting in higher estimates of direct heritability than maternal heritability (Table 4). Low to medium maternal heritabilities for the growth traits (Table 4), indicate maternal influence on pre-weaning growth traits. Maternal heritability increased up to weaning after which the estimates decreased. However, Meyer (1993b) reported no carry-over of maternal effects until weaning on post-

weaning weights in the Charolais; the observed maternal genetic effects were not important for BW and were small for WW. 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 withdrawn and, therefore, the effects of this environment on variance decline as the calf grows and becomes independent (Meyer, 1992).

Fertility traits generally have low heritability (Table 4). This is because female reproductive traits are highly influenced by herd management and other environmental factors (Rege et al., 1991a and 1992a; Koots et al., 1994; van der Westhuizen et al., 2001). Heritabilities for AFC were low to medium, while for CI were low (Table 4). Low heritabilities for AFC and CI have been reported in Holstein in Ireland (Olori et al., 2002), and Boran (Wasike, 2006) and Sahiwal (Ilatsia et al., 2007) cows in Kenya. The wide range of heritability estimates in reproductive traits would be attributed to variation in environmental and other management factors. For example, short breeding season and the producer's habit to specify an age or weight to expose heifers to the first mate probably would reduce the additive variance and heritability of the traits (Ilatsia et al., 2007). Furthermore, variation in reproductive performance would be due to differences in growth rate, age at onset of puberty, regularity of oestrus circle and ability to conceive (Galina and Arthur, 1989). However, medium heritability estimates for AFC in composite breeds (Table 4), suggest that progress could be achieved through selection. Age at first calving is easy to measure because it does not require differential management to be obtained (Teixeira et al., 2002). A limitation for both AFC and CI as measures of fertility is that they exclude animals that are not calving (Haile-Mariam and Kassa-Mersha, 1994; Olori et al., 2002).

2.6.2. Repeatability

When several measurements are taken on an individual animal for a particular trait, e.g., daily milk recorded in a lactation of dairy cattle and weekly weight gains taken in beef cattle, these constitute repeated measurements. Since these measurements are related, they constitute a covariance between them due to permanent environmental factors (Mrode, 2005). This covariance in measurements is accounted for as a component of phenotypic variance, by estimating a parameter called repeatability (Lynch and Walsh, 1998). It is treated as within individual variance and computed as a 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.

2.6.3. Correlations

Phenotypic, genetic and environmental correlations are measures of the strength of the relationship between animal performance among traits, breeding values and environmental effects between traits. Genetic and environmental causes of correlation combine together to give the phenotypic correlation (Falconer and Mackay, 1996). Correlations are important as they aid in the prediction of response to selection in one trait due to selection in another. Table 4 shows some genetic and phenotypic correlations for various traits in beef cattle. Moderate to high genetic correlations between body weight measurements at various points imply that genetic improvement in weight at older ages could be achieved by selection at younger ages. Further, this could allow for early culling of unwanted animals and, therefore, save on feed resources. For example, improvement in WW and YW would be achievable when selection is done on the basis of BW. However, this may not be desirable since continual increase in BW as a correlated response to selection for increased post-weaning weights could eventually lead to dystocia as has happened in the temperate areas (Davis, 1993). Nonetheless, the high heritability of BW for Zebu-derived cattle (Table 4) indicates that selection against high BW could limit this problem.

As alluded to earlier, in the tropics growth nearly ceases during the dry season and resumes during the wet season. Selection for rapid growth rate when nutrition is unlimited should, therefore, focus on growth measured in the animal during the periods in its life when nutrition is least limiting. There exist antagonistic relationships between or among traits. For example, favourable genetic relationships between carcass traits of males, and growth and reproductive traits of females have been reported (Splan et al., 1998). However, undesirable relationships could also exist, e.g., calving difficulty has favourable genetic correlations with hot carcass weight and retail product percentage. To deal with economically important but antagonistic traits in beef cattle selection indices that incorporate female productivity and male carcass value may be one solution, while producers could choose to restrict change in some traits as they improve on others. That is, progeny of females with high reproductive values could be managed after weaning to reduce fat deposition (Splan et al., 1998). Milk yield of the cow can be

considered as a trait influenced by the calf (through demand for milk and nursing frequency) and the cow (Miller and Wilton, 1999). High (0.76) genetic correlations between maternal weaning gain and cow milk yield have been reported by Miller and Wilton (1999). That study suggested that maternal weaning gain evaluations are good predictors of a cow's potential for milk yield. Milk yield is a trait of economic importance in beef production and can effectively be selected for in a breeding programme indirectly through maternal weaning gain.

Negative genetic correlations between direct genetic and maternal effects for BW and WW in beef cattle have been reported (Dodenhoff et al., 1998; de Mattos et al., 2000) caused by sire x year interaction (i.e., when a large proportion of sires are introduced into the population/ imported each year) and the dam-offspring covariance (fatty udder syndrome). The negative genetic correlations suggest genetic antagonism between direct and maternal effects for WW of beef cattle (Bennett and Gregory, 1996; de Mattos et al., 2000; Lee and Pollak, 2002; Campelo et al., 2004), and explain why selection in traits subject to maternal influence could be ineffective (Baker, 1980). Therefore, fitting a random maternal effect in models for genetic evaluation is recommended (Meyer, 1997). The antagonism observed between direct and maternal effects requires that knowledge of the maternal influence on pre-weaning weights and of the correlation between these effects are fundamental for achieving unbiased heritability estimates. However, difficulties have been encountered in reliable estimation of such correlations arising because direct and maternal effects are partially confounded in an animal's performance (Crow and Howell, 1982; Pelicioni et al., 2002; Phocas and Laloe, 2004). Meyer (1997) observed that direct-maternal covariance in the Polled-Hereford was environmental rather than genetic, and reported breed differences in the relative importance of genetic and environmental maternal effects on WW of beef cattle. Other important correlations are those between different values of the same trait (e.g., the correlation between maternal and additive effects).

Favourable genetic correlations between growth and fertility traits have been reported (Bourdon and Brinks, 1982; Davis, 1993). Selection for increased live weight would result into improved female fertility. Bourdon and Brinks (1982) reported low (0.07) heritability for AFC, negative genetic correlations between AFC and growth traits in the Red Angus, Angus and the Polled-Hereford, and concluded that there was a favourable relationship between growth and early fertility. Generally, heritability estimates for fertility traits are much less than for growth traits. These require larger data sets for genetic estimation with reasonable accuracy (Baker,

1980). Mercadante et al. (2003) pointed out that selection of young animals based on body weights promoted high and consistent weight and height responses, both at yearling and later ages, without compromising the reproductive performance of cows with respect to days to calving (i.e., there are no negative effects of selection for growth on the fertility of females in beef cattle). While such estimates have been obtained for European breeds in temperate environments, knowledge is still limited on such estimates under tropical environments. Consequently, strategies for genetic improvement of growth in a tropical environment require knowledge of both the extent of this genetic variation, and the genetic and phenotypic correlations among the traits involved (Dillard et al., 1980; Mackinnon et al., 1991).

2.7. Models for genetic evaluation of growth and fertility traits

Statistical models applied to data obtained from animals attempt to describe biological processes and effects quantitatively. The aim is to describe the biological situation as explicitly as possible (Kennedy et al., 1988). In animal breeding, animal models are used to predict breeding values, and estimation of selection responses and genetic parameters. A common feature exhibited by these models is their use of the additive genetic relationship matrix directly or indirectly (Kennedy et al., 1988). The models include univariate and multivariate models (Haile-Mariam and Kassa-Mersha, 1994; Khombe et al., 1995; Rumph et al., 2002; Demeke et al., 2003; Campelo et al., 2004).

2.7.1. Univariate models

These models are used in estimating genetic parameters considering a single trait at a time or as a repeated measure on the same animal. As a result, univariate models are unable to account for relationships between traits, leading to biases in estimates due to selection and their inefficiency in data utilization. The advantages of fitting univariate models in estimating genetic parameters is due to the reduced computational demands and accounting for individual permanent environmental effects because of repeated measures on the same animal (Meyer, 2004).

2.7.2. Multivariate models

Multivariate models can estimate parameters of many traits simultaneously. The models involve the concurrent evaluation of animals for two or more traits, making use of phenotypic and genetic correlations between the traits (Mrode, 2000). Estimates resulting from such models are more accurate than those from univariate analysis. This enhanced accuracy is due to the ability of the model to account for relationships between the traits and better connections in the data due to residual covariance between traits (Mrode, 2005). The univariate models, unlike multivariate models, account for the effect of selection on variance, and environmental factors.

2.7.3. Random regression models

Genetic evaluation of performance is conventionally done using univariate and multivariate animal models (finite models), which assume constant variances between traits. However, growth as a biological process is continuous. The assumption of constancy in the variance component estimates is, therefore, not valid (Kirkpatrick and Heckman, 1989). It is on this principle that a RRM, which is more flexible and employs CFs between observations on the trait, was developed for application in genetic evaluation of traits that vary continuously along a trajectory (Kirkpatrick and Heckman, 1989). For example, in evaluating growth traits in beef animals, weight is taken on the same individual at various times from birth to maturity (Schaeffer, 2004). These constitute records often referred to as longitudinal data or repeated records (Meyer and Hill, 1997). Consequently, the pattern of animal growth over time can be modelled by random regressions.

Random regression models provide a means of estimating genetic parameters for all ages without correcting the observations to certain landmark ages (Albuquerque and Meyer, 2001; Lewis and Brotherstone, 2002; Nobre et al., 2003). Furthermore, they are intended to model deviations around the phenotypic trajectories (Schaeffer, 2004). 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, therefore, assume a particular covariance structure (Meyer, 1998; Schaeffer, 2004). Random regression models are a special case of CFs by which covariance function coefficients are estimated directly by REML (Meyer and Hill, 1997; Albuquerque and Meyer, 2001). These 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).

2.8. Genetic and environmental trends

Genetic and environmental trends measure the changes that take place in a population or herd and are the ultimate indicators of sustainable progress (Nadarajah et al., 1987; Musani and Meyer, 1997). Evaluation of genetic progress for economic traits is an essential part of successful planning for the future, and allows documentation of progress from past selection (Nadarajah et al., 1987). It allows assessment of the effectiveness of selection procedures and gives the opportunity for monitoring management conditions such as nutrition and health status (Kovac, and Groeneveld, 1990). However, this requires separation of the genetic and environmental portions of the total phenotypic trend (Nadarajah et al., 1987).

The genetic level of a herd in a particular year is the average of the breeding values of the animals with a calving in that year (Pollak and Quaas, 1998; Martinez et al., 2004). Phenotypic and genetic trends are estimated from averages of cow performance and cow estimated breeding values, respectively, within year, and regressing the annual average on year (Nadarajah et al., 1987; Rege, 1991b; Haile-Mariam and Kassa-Mersha, 1994; Cunningham and Klei, 1995; Musani and Meyer, 1997; Martinez et al., 2004). Although the phenotypic trend in performance can be estimated by regression of actual performance records on time (Nadarajah et al., 1987; Cunningham and Klei, 1995), unbiased estimates of either genetic or environmental trends are difficult to obtain because of potential confounding of changes in the environment with changes in genotype (Nadarajah et al., 1987). Breed differences in genetic trends also cause breed merit differences to change over time (Sullivan et al., 1999).

Positive genetic and environmental trends in beef cattle herds are indicators of favourable selection methods and good management (Plasse et al., 2002). Negative genetic trends reflect the failure of the selection programme in place, while negative environmental trends point to poor management within a herd (Rege and Wakhungu, 1992b; Khan et al., 1999; Ebangi et al., 2000). Seasonal variation in animal performance in the tropics is expected to be primarily a manifestation of variation in feed quantity and quality (Rege, 1991a). Haile-Mariam and Kassa-Mersha (1994) observed no environmental trend for CI in Boran cattle despite considerable

variation in the year, and suggested that the significance of the year effects was mainly due to random annual fluctuations in rainfall and, therefore, food availability. Cunningham and Klei (1995) estimated positive genetic trends for BW and WW in Simmental cattle in North America, and concluded that the increased performance of WW over time was due to increases in average genetics and the environment.

Two breeds can be described as overlapping genetically if selection candidates of equal genetic merit can be found in either breed (Sullivan et al., 1999). Consideration is, therefore, required for across-breed performance in order to maximize opportunities for genetic change and commercial production efficiency. Breed overlap provides an indication of the potential for breed rankings to change with differing breed improvement goals. A study by Mercadante et al. (2003) showed that subsequent to selection of Nelore cows for growth, positive genetic trends in YW (1.65-2.33 kg/ year and 1.78-2.39 kg/year) for males and females, respectively, occurred without compromising the reproductive performance of heifers. In the same study, non-significant annual genetic trends of days to calving (–0.33-0.19 days/year) were reported. Bourdon and Brinks (1982) reported negative environmental correlations between weaning traits and gain after weaning, and suggested some environmentally caused compensatory growth.

CHAPTER THREE

MATERIALS AND METHODS

3.1. Data source

Data on growth and reproductive traits were collected from the ADC's Chepchoina Farm and Solio Ranch Limited. Both farms maintain purebred stud herds registered with the Kenya Studbook.

Solio Ranch Ltd. lies at about 0^0S37^0E East of Greenwich, 130 km to the south of Rumuruti town, 30 km west of Nyeri town and 70 km east of Nyahururu town in Laikipia district of Rift Valley province, and 255 km to the North of Nairobi. The Ranch is in agro-ecological zone 4 on an altitude of 3680 m above sea level on clay-loam soils. The temperatures range between 9^0C (minimum) and 34^0C (maximum). It receives an average of between 700-800 mm of rainfall in a bimodal distribution (Figure 2). The long rains fall in March-May as the short rains come in October-December with dry spells in between, i.e., January-February and June-September (Figure 3). The Ranch occupies a total of 23,880 hectares (59,000 acres) of which cattle are extensively managed on 16,800 hectares (41,500 acres) of rain fed natural pastures comprising red oat (*Themeda triandra)* grasses. The remaining 7,085 hectares (17,500 acres) are under wild game. Trees found on the farm include Leleshwa *(Tarchonathem camphorates)* and *Acacia* species.

Chepchoina Farm is a government of Kenya farm, located in Endebess division, 70 km west of Kitale town in Trans-Nzoia district of the Rift Valley province, and 450 km to the North-west of Nairobi, at 1^0N35^0E East of Greenwich. The farm is in agro-ecological zone 3 on an altitude of 2,108 m above sea level on medium to heavy red loam volcanic soil. The temperatures range between 10^0C (minimum) and 32^0C (maximum). Figure 2 shows the annual rainfall distribution in the study area for the years 1977 to 2003. The area receives a bimodal rainfall averaging 1,053 mm annually (Figure 3). Long rains fall between March and August while short rains come between September and November (MoA, 2003).. The farm occupies a total of 135 hectares (334 acres) on which cattle are extensively managed on rain fed improved Boma Rhode pastures. The farm was founded with the vision to be a prime mover of agricultural development in Eastern Africa by producing and providing quality crop seed and livestock to farmers.

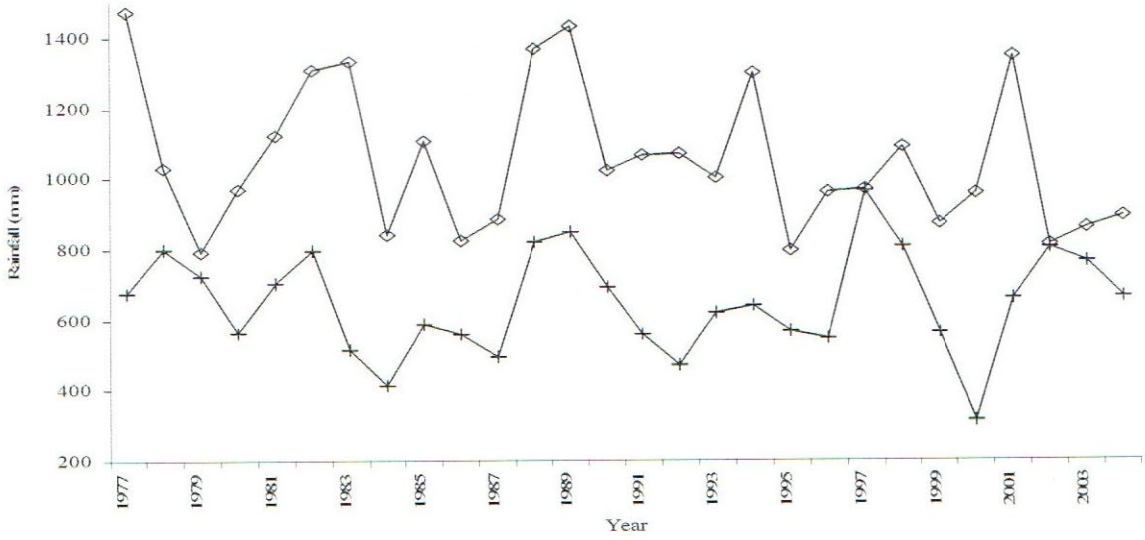


Figure 2. Annual rainfall distribution (mm) for Solio Ranch Ltd. (+) and the ADC Chepchoina (◊) farms.

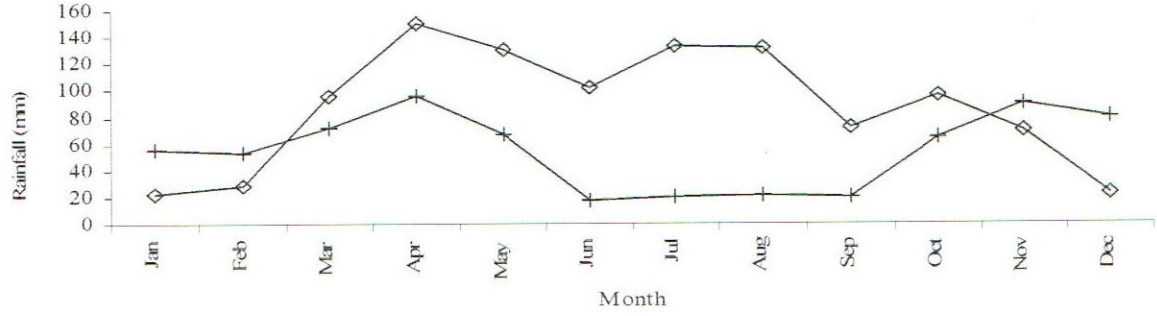


Figure 3. Monthly rainfall distribution (mm) for Solio Ranch Ltd. (+) and the ADC Chepchoina (◊) farms.

3.2. Herd management

The ADC Chepchoina farm comprised the two beef breeds, i.e., the Polled-Hereford, being the predominant breed, and the Charolais. Solio Ranch Ltd. exclusively raised the Charolais breed. At Chepchoina farm, both breeds were managed as a single herd. In both farms, the cattle were extensively grazed on natural pastures and supplemented with mineral licks *ad libitum*. In addition, stored Boma Rhodes hay was provided during dry seasons at Chepchoina farm. Calves were weighed and identified within 48 hours of birth and left to run with their dams

until weaning (approximately 9 months). Tattooing and debudding was done in calves when they were 2 weeks old, while branding was done at weaning. Bull calves not intended for breeding were castrated at weaning and raised as beef steers. Weaners were herded together away from the older stock until 17 months of age, when bulls were dispersed to various commercial breeding herds. At Solio Ranch Ltd., young bulls (weaning to 17 months) intended for breeding were placed on a feeding programme of supplementation (i.e., 2 kg magic steers, 260 gm of mixed salt and dicalcium phosphate, 0.7 kg molasses and 0.7 kg cotton seed cake per bull a day).

Disease management was mainly prophylactic through the control of ecto- and endo-parasites, and routine vaccinations against endemic diseases such as Foot and Mouth disease, Rinderpest, Black quarter, Anthrax and Lumpy skin disease. However, specific treatment was administered to sick animals. To control ticks and other ecto-parasites, cattle were sprayed every 4-5 days at Solio Ranch, while dipping was done once every week at ADC Chepchoina Farm. Control of endo-parasites was done at the onset of the rains and at the start of the dry period at ADC Chepchoina farm. At Solio Ranch ltd., this was done only once, i.e., at weaning.

Artificial insemination was exclusively used in both farms. However, at Solio Ranch Ltd., cows that did not conceive after two consecutive inseminations were exposed to a bull for natural mating. Heifers were served at an age of 18–24 months when they were about 380 kg body weight. Pregnancy diagnosis, through rectal palpation was done after two months by trained inseminators. Bulls were allowed to serve at 17 months of age when they were about 500 kg body weight. For bull service, near random mating was practised, avoiding sire-daughter, dam-son and full-sib matings. In both herds, calving was all year round. Selection of breeding animals was done at weaning, based on physical appraisal of growth performance and conformation. Selection and voluntary culling was more stringent at the ADC Chepchoina farm than at the Solio Ranch Ltd. This was because more sires were needed to crossbreed with the Boran cows in the commercial herd of the Ranch. Sire selection was subjective and was based on a combination of weaning performance and visual evaluation for soundness/ conformation. 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 at both farms. Culling of cows was determined by their reproduction efficiency rather than age. Initial culling of animals was done at weaning

where all animals with poor conformation were culled. Solio Ranch Ltd. maintained an average of 6,700 head of cattle, of which about 2,000 were Charolais breeding cows and bulls, the rest were the commercial herds of Boran, and Charolais x Boran crosses. An annual average of 1,800 head of cattle was sold yearly from the commercial herd. The Ranch operates by crossbreeding the French Charolais with the Kenyan Boran, capitalizing on the Charolais's rapid growth and the Boran's resistance to drought and disease. The grass-fed steers attained an average weight of 470 kg in about two and half years of age. At the ADC Chepchoina farm, cows and heifers were all reared in a similar environment with constant management over the years. However, at Solio Ranch Ltd., the cattle were divided into four herds; (a) observing herd (dry cows and cows with over 3-month old calves), (b) heifer herd (heifers 9 months old to first calving), (c) young bulls (9–17 months old) under a feeding programme, and (d) maternity herd (comprised of heavily pregnant cows, i.e., 7 months in-calf to 3 months post-calving). The Charolais bulls were used to crossbreed with the Boran cows/ heifers in the commercial herd and the resulting progenies were terminal (i.e., destined for slaughter for beef).

3.3. Description of traits and data characteristics

Data on growth and fertility traits were extracted for cows with at least a first calving during the period 1968 through 2004. Records were available from 1968 to 2004 and from 1973 to 2004 for fertility and growth traits, respectively. Growth traits considered were birth weight (BW, kg), pre-weaning average daily gain (ADG, kg/day) and weaning weight (WW, kg). For WW, only calves between 125 days to 275 days of age at weaning (AWn) were included. Fertility traits were CI (days), and AFC (days). Data were edited for consistency of pedigree information and correct dates of birth, calving and weighing. The pedigree file was traced back to 1968. Records with anomalies in pedigree information and dates were discarded. Table 5 below presents the data structure and summary statistics for growth and fertility traits.

Table 5. Data structure and summary statistics for growth and reproductive traits for the Charolais and Polled-Hereford beef cattle breeds

	Charolais					Polled-Hereford				
Trait	BW	ADG	WW	AFC	CI	BW	ADG	WW	AFC	CI
No. records	1685	972	972	487	1096	1100	897	897	375	1021
Mean	40.24	0.78	243.60	1193.60	509.30	36.10	0.59	191.30	1200.70	420.10
SD	6.68	0.19	49.90	251.40	189.75	5.97	0.13	34.87	211.80	124.03
CV (%)	12.26	16.26	13.23	18.25	35.09	14.13	17.23	13.72	10.71	26.41
No. of animals in ped file	3334	3334	3521	3335	3334	3333	3333	3333	3335	3334
No. of sires	96	79	79	67	63	54	53	53	49	58
No. of progeny per sire	17.60	12.30	12.30	7.30	17.40	20.40	17	17	7.60	17.60
No. of dams	507	392	392	283	225	355	321	320	140	180
No. of progeny per dam	3.30	2.50	2.50	1.70	4.90	3.00	2.80	2.80	2.70	5.70

[a]BW= birth weight (kg); WW= weaning weight (kg); ADG= average daily gain (kg); AFC= age at first calving (days) and CI= calving interval (days).

3.4. Data analysis

3.4.1. Factors influencing growth and fertility traits and mean performance estimates

Analyses of variance were conducted for different traits in order to assess the non-genetic factors influencing growth and fertility traits using PROC GLM of SAS (1998). The fixed effects fitted in the model for the analyses of growth traits included sex of calf, breed, year-season of birth/ calving, and dam parity. A maximum of nine parities were allowed in the analyses. Table 6 below shows the type of fixed effects fitted as well as the corresponding levels of significance for the various traits. Herd and breed were fitted for all traits studied in the between-breed analysis for the ADC Chepchoina farm. In addition, age at weaning was fitted as a linear covariate for ADG and WW. Herd-year-season of calving and parity were fitted for CI, while year-season of birth and WW were fitted for AFC. The year of birth and weaning were from 1974 to 2004 and 1973 to 2003, respectively, while the AFC were, correspondingly, from 1974 to 2002 and 1974 to 2000 for the Charolais and the Polled-Herefords. The years of calving were from 1974 to 2004. In Chepchoina farm, each year consisted of three seasons; the primary wet season (March-August), the secondary wet season (September-November) and the dry season (December-February). Each year in Solio Ranch Ltd. consisted of four seasons; the primary wet season (March-May), secondary wet season (October-December) and the primary dry season (January-February), and the secondary dry season (June-September).

3.4.2. Univariate analysis

(Co)variance components and genetic parameters for individual traits were estimated using single-trait animal models within the DFREML programme (Meyer, 1998). The fixed part of the model consisted of effects that significantly influenced growth and fertility performances determined in section 3.4.1.

To identify the best model to fit the growth traits, preliminary analyses were conducted using different univariate models, each with different combinations of direct additive, maternal genetic and maternal environmental effects, and covariances between additive direct and maternal genetic effects. Likelihood ratio tests were conducted to determine the most suitable model for each growth trait in a univariate analysis. Analyses were terminated when the change in variance of the function values (-2log likelihood) fell below 10^{-4}. These analyses showed that the best model (based on maximum log likelihood) that fitted the growth data was a model with three random effects, i.e., direct additive genetic, maternal genetic and maternal environmental effects. The model also assumed a covariance structure between direct additive and maternal genetic effects. Although it is always desirable to include maternal environmental effects in genetic evaluation of beef breeding programmes, the data structure and the number of dams and grand dams with records are important determinants in estimating maternal effects (Meyer, 1992; Maniatis and Pollott, 2003; Solanes et al., 2004). For example, there seemed to be no maternal genetic influence on ADG and WW in Charolais (Table 7), a fact that could be attributed to the data structure (Table 5). A simple animal model (AM) with additive genetic effects as the only random effect was fitted for fertility traits. The structure of the models used in the final analyses is shown in Table 6. The general mixed model fitted in this case was:

$$y = Xb + Z_1c + Z_2a + Z_3m + e \qquad \text{cov}(a, m) \neq 0 \qquad (1)$$

where **y** is a vector of observations on the specific trait of the animal; b, a, m and c vectors of fixed effects, including covariables, direct additive genetic, maternal additive and maternal permanent environmental effects, respectively, X, Z_1, Z_2 and Z_3 are the corresponding incidence matrices relating the effects to y, and e the vector of residual error.

The phenotypic variance (σ^2_p) was calculated as the sum of direct additive genetic variance (σ^2_a), maternal genetic variance (σ^2_m), direct additive by maternal genetic covariance (σ_{am}), maternal permanent environmental (σ^2_c) and error variances (σ^2_e). The direct heritability

(h^2), maternal heritability (m^2) and the permanent environmental effect (c^2) were computed as σ^2_a/σ^2_p, σ^2_m/σ^2_p, and σ^2_c/σ^2_p, respectively. Total heritability (h^2_T) was estimated by summing all the genetic effects as a proportion of the phenotypic variance ($\sigma^2_{total\text{-}additive}/\sigma^2_p$), i.e., ($\sigma^2_a$+ $0.5\sigma^2_m$+$1.5\sigma_{am}$)/σ^2_p. The random effects were assumed to follow a normal distribution with zero mean and (co)variance structure:

$$Var\begin{bmatrix} c \\ a \\ m \\ e \end{bmatrix} = \begin{bmatrix} I\sigma_c^2 & 0 & 0 & 0 \\ 0 & A\sigma_a^2 & A\sigma_{am} & 0 \\ 0 & A\sigma_{am} & A\sigma_m^2 & 0 \\ 0 & 0 & 0 & I\sigma_e^2 \end{bmatrix}$$

where **A** and **I** represent the additive genetic relationship and identity matrix, respectively.

3.4.3. Bivariate analysis

The traits considered in bivariate analysis included BW, WW, ADG, AFC and CI. An animal model similar to model 1 above, but ignoring additive maternal and maternal permanent environmental effects, was used to carry out a series of bivariate analyses to estimate genetic and phenotypic correlations among all the traits studied.

3.4.4. Estimation of annual trends

Using univariate analyses, breeding values were predicted. To estimate the genetic and environmental trends, back solutions for EBVs and solutions for fixed effects were obtained. Genetic trends were estimated by regressing the EBVs in the particular trait on the year of birth. Year-season effects were regressed on year to obtain the annual environmental trends for various traits. The environmental trends were expressed as deviations from the overall mean.

CHAPTER FOUR

RESULTS

4.1. Environmental sources of variation

Table 6 presents levels of significance for the various sources of variation on growth and fertility traits in the Charolais and Polled-Hereford breeds. All main effects fitted significantly ($P<0.001$) affected BW. Sex significantly ($P<0.001$) affected BW but was not significant for all other traits studied. Age at weaning significantly ($P<0.001$) influenced ADG and WW. Dam parity significantly ($P<0.001$) affected BW, since earlier parity calves were lighter than later parity ones for both breeds. Dam parity also significantly ($P<0.05$) influenced WW in both breeds, and ADG in Charolais (Table 6). Herd effect was fitted for Charolais because the breed appeared in both herds and it significantly ($P<0.001$) affected BW, ADG and WW but was not significant for AFC and CI. Generally, animals at Solio Ranch Ltd. recorded heavier weights for growth traits than those at Chepchoina Farm. Year-season of birth interaction significantly ($P<0.001$) affected all traits studied except CI. Year-season of weaning significantly ($P<0.01$) affected WW in both breeds. Similarly, year-season of calving significantly ($P<0.001$) influenced CI. Weaning weight as a covariate significantly ($P<0.05$) affected AFC in both breeds.

4.2. Mean performance estimates

Estimates of breed means for growth and fertility traits are given in Table 6. The Charolais calves were generally born on average 4.14 kg heavier than those of the Polled-Hereford. Male calves were born heavier than their female counterparts for both breeds. Generally, calves at Solio Ranch Ltd. were born heavier than those at Chepchoina farm (not shown) and calves born of later parities were heavier than those born of first parity. Charolais calves gained weight 0.19 times faster than the Polled-Hereford calves (Table 6). Consequently, Charolais weaned higher weights than Hereford calves; the mean WW were 243.6 and 191.3 kg for Charolais and Polled-Hereford, respectively (Table 6).

Table 6. Structure of the models used in the final analyses, levels of significance, means and coefficients of variation for growth and fertility traits[a]

		Charolais					Polled-Hereford				
		BW	ADG	WW	AFC	CI	BW	ADG	WW	AFC	CI
Factors	Type[b]										
Sex	F	***	ns	ns	-	-	***	ns	ns	-	-
Dam parity	F	***	*	*	-	-	***	ns	**	-	-
YS of birth	F	***	***	***	***	-	***	***	***	***	-
YS calving	F	-	-	-	-	***	-	-	-	-	***
YS of weaning	F	-	-	***	-	-	-	-	**	-	-
Herd	F	***	***	***	ns	ns	-	-	-	-	-
BW	C	-	**	***	ns	-	-	***	***	-	-
WW	C	-	-	-	**	-	-	-	-	*	-
Age at weaning	C	-	***	***	-	-	-	***	***	-	-
Direct genetic	A	√	√	√	√	√	√	√	√	√	√
Maternal genetic	A	√	√	√	-	-	√	√	√	-	-
Maternal environmental	A	√	√	√	-	-	√	√	√	-	-
Direct-maternal effects	R	√	√	√	-	-	√	√	√	-	-
No. of records		1685	972	972	487	1096	1100	897	897	375	1021
Mean		40.24	0.78	243.60	1193.6	509.30	36.1	0.59	191.3	1166.7	420.1
Minimum		20	0.22	105	645	301	18	0.24	105	626	302
Maximum		65	1.86	380	1900	1488	63	1.21	335	1702	1153
SD		6.68	0.19	49.90	251.4	189.75	5.97	0.13	34.87	211.8	124.03

[a] YS= year season of birth/ calving/ weaning; BW= birth weight (kg) ; WW = weaning weight (kg); ADG= average daily gain (kg); AFC= age at first calving (days) and CI= calving interval (days).

[b] Type of factors: F= fixed factor; C= linear covariate; A= random factor with relationship matrix; R= random factor.

$^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$, ns = not significant.

√= fitted; - = not fitted.

Overall, Polled-Hereford heifers tended to calf down earlier than those of the Charolais. The mean AFC were, correspondingly, 1193.6 and 1166.7 days for the Charolais and Polled-Hereford (Table 6). However, Charolais cows at Solio Ranch Ltd. tended to have longer AFC than those at Chepchoina farm. Generally, the Charolais had prolonged CI (89.2 days) than the Polled-Hereford cows. The mean CIs were 509.3 and 420.1 days for the Charolais and Polled-Hereford, respectively (Table 6).

4.3. Estimate of (co)variance components, and genetic and phenotypic parameters

4.3.1. Estimates from univariate analyses

Estimates of variance components and genetic parameters for growth and fertility trait are shown in Table 7 below. The direct heritability estimates for BW were 0.36 and 0.21 for the Charolais and Polled-Hereford cattle, respectively. Heritability estimates for the growth traits in the Polled-Hereford ranged from 0.10 to 0.21. The corresponding heritabilities for the Charolais were moderate. Direct heritability estimates for the fertility traits were low (0.00 to 0.16) for both breeds. Estimates of total heritability (h^2_T) were low to moderate for the growth traits and low for the fertility traits. Additive genetic effects accounted for a small proportion of total variation in the fertility traits. However, the corresponding estimates of residual error variance were high (Table 7). This resulted in very low heritability estimates for the fertility traits, i.e., 0.0 to 0.05 for CI and 0.06 to 0.16 for CI and AFC, respectively.

For WW, maternal genetic effects accounted for a higher proportion of total variation than direct additive genetic effects in the Polled-Hereford (Table 7). However, the converse was true for the Charolais. Direct-maternal genetic correlations were moderate to unity, and negative for the growth traits analysed except for BW in the Polled-Hereford, which was positive (Table 7).

Table 7. Estimates of (co) variance components and genetic parameters for growth and fertility traits[a] from univariate analyses

	Charolais					Polled-Hereford				
Estimates[b]	BW	ADG	WW	AFC	CI	BW	ADG	WW	AFC	CI
σ^2_c	1.08	0.00	0.00			3.11	1180.23	0.00		
σ^2_a	9.57	4150.61	247.20	2923.80	0.02	5.34	982.75	87.47	2671.94	619.37
σ^2_m	3.08	3067.55	178.60			0.17	1.03	116.46		
r_{am}	-0.46	-0.51	-0.47			1.00	-1.00	-0.39		
σ_{am}	-2.51	-1831.79	-98.72			0.94	-31.90	-39.34		
σ^2_e	15.51	11261.01	731.78	44526.10	30482.54	15.50	7846.41	531.26	13858.05	11687.77
σ^2_p	26.73	16647.37	1058.90	47449.90	31936.84	25.07	9978.52	695.85	16529.99	12307.15
C^2	0.04	0.00	0.00			0.12	0.12	0.00		
h^2	0.36	0.25	0.23	0.06	0.00	0.21	0.10	0.13	0.16	0.05
m^2	0.11	0.18	0.17			0.01	0.00	0.17		
h^2_T	0.27	0.08	0.09	0.06	0.00	0.27	0.09	0.12	0.16	0.05

[a]BW= birth weight; WW= weaning weight; ADG= average daily gain; AFC= age at first calving; CI= calving interval.
[b]σ^2_a= additive genetic variance; σ^2_m= maternal genetic variance; σ^2_e= error variance; σ^2_p= phenotypic variance; σ_{am}= direct-maternal covariance; h^2= direct heritability; m^2= maternal heritability; r_{am}= direct maternal genetic correlation; h^2_T= total heritability.

4.3.2. Estimates of correlations from bivariate analyses

Estimates of genetic and phenotypic correlations for growth and fertility traits from bivariate analyses are presented in Table 8. Due to limitations in the size and structure of the data (Table 6), other combinations within fertility trait category and between fertility and growth trait categories were not estimable. Estimates of genetic variances for the Polled-Hereford from bivariate analyses for the growth traits were higher than those from univariate analyses (not shown). However, the corresponding estimates for fertility traits (AFC and CI) were lower for bivariate analyses than those from univariate analyses for the Polled-Hereford. For the Charolais, bivariate genetic variance estimates for fertility traits were greater than those from univariate analyses. The additive genetic and phenotypic variances for BW in CH were generally comparable in both the univariate and bivariate analyses.

The heritability estimates for growth and fertility traits from univariate analyses in the Charolais were comparable to those obtained from bivariate analyses. However, higher heritability estimates (close to 1) were obtained from bivariate analyses for WW and ADG traits in the Polled-Hereford. The change in magnitude of heritability estimates was most pronounced for WW, and ADG, which increased from 0.13 to 0.98 for the Polled-Hereford. However, no marked changes were seen for fertility traits.

The correlations between the growth traits were variable and positive in magnitude except for those between BW and ADG, and ADG and WW, which were negative (Table 8). Generally, genetic correlations between the traits were more variable and stronger (absolute values) than the corresponding phenotypic correlations. For example, the genetic correlations between the growth traits ranged from -0.06 to 1.00 while the corresponding phenotypic correlations ranged from 0.00 to 0.28. Strong genetic correlations (1.00) were estimated between BW and ADG in the Charolais. Low (–0.16 to 0.12) phenotypic correlations between growth and fertility traits were estimated (Table 8) but the corresponding genetic correlations were strong. For the Charolais, the genetic correlation was strong and positive (1.00) while the phenotypic correlation was low and positive (0.11) (Table 8). The corresponding correlations between WW and AFC were low and negative (-0.06) for the Polled-Hereford. The genetic correlation between AFC and CI was strong and negative (-0.99), but there seemed to be no phenotypic correlation between the traits in both breeds (Table 8).

Table 8. Estimates of genetic and phenotypic correlations[a] for growth and fertility traits[b] in the Charolais and the Polled-Hereford breeds from bivariate analyses

		Charolais		Polled-Hereford	
Trait 1	Trait 2	r_g	r_p	r_g	r_p
BW	ADG	1.00	0.07	-0.06	0.00
,,	WW	0.27	0.09	0.07	0.02
,,	AFC	-	-	0.13	0.12
,,	CI	0.99	0.00	-0.07	0.00
ADG	WW	0.20	0.20	-0.99	0.28
,,	AFC	-0.99	-0.02	-	-
,,	CI	1.00	0.00	-1.00	-0.16
WW	AFC	1.00	0.11	-0.06	-0.06
,,	CI	-	-	-1.00	-0.16
AFC	,,	-0.99	0.00	-0.99	0.00

[a] r_g = genetic correlations; r_p = phenotypic correlations.
[b] BW= birth weight; WW= weaning weight; ADG= average daily gain; AFC= age at first calving; CI= calving interval.

4.4. Genetic and environmental trends in growth and fertility traits

Genetic and environmental trends for BW, ADG and WW are presented in Figures 4, 5 and 6, respectively. Generally, genetic and environmental trends fluctuated over the years for all traits in both breeds. Save for the earlier years (i.e., 1973-1982, BW; 1974-1978, ADG and WW), in subsequent years the trends were consistently negative for all the traits studied. The coefficients of change in environmental trends for BW, ADG and WW were -0.300 and -0.198 kg/yr, –12.99 and –7.43 g/yr, -3.56, and -2.17 kg/yr for the Charolais and the Polled-Hereford, respectively.

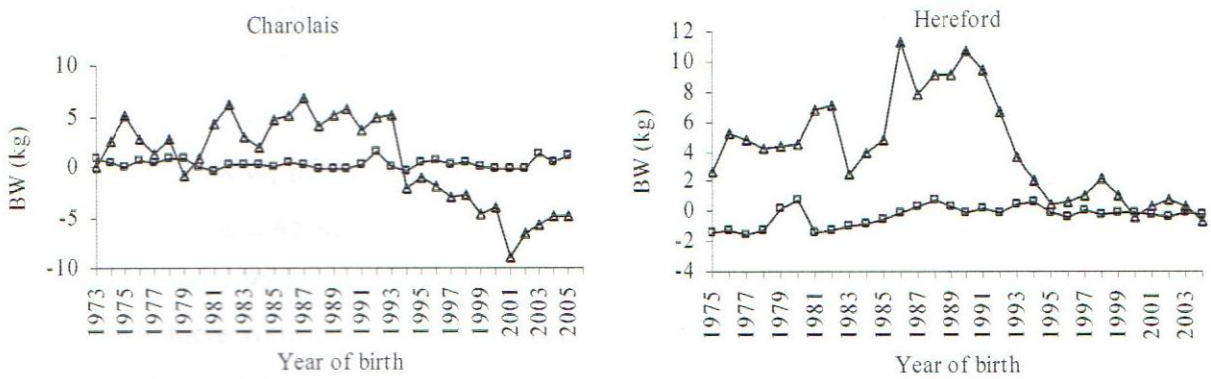


Figure 4. Genetic (□) and environmental (Δ) trends for birth weight (kg) in the Charolais and the Polled-Hereford beef cattle breeds. The environmental trends are expressed as deviations from the overall mean.

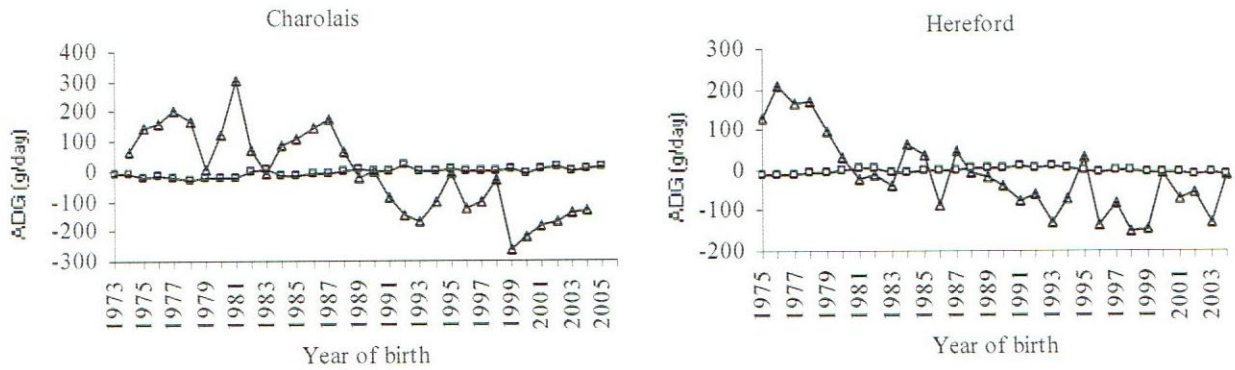


Figure 5. Genetic (□) and environmental (Δ) trends for average daily gain (kg) in the Charolais and the Polled-Hereford beef cattle breeds. The environmental trends are expressed as deviations from the overall mean

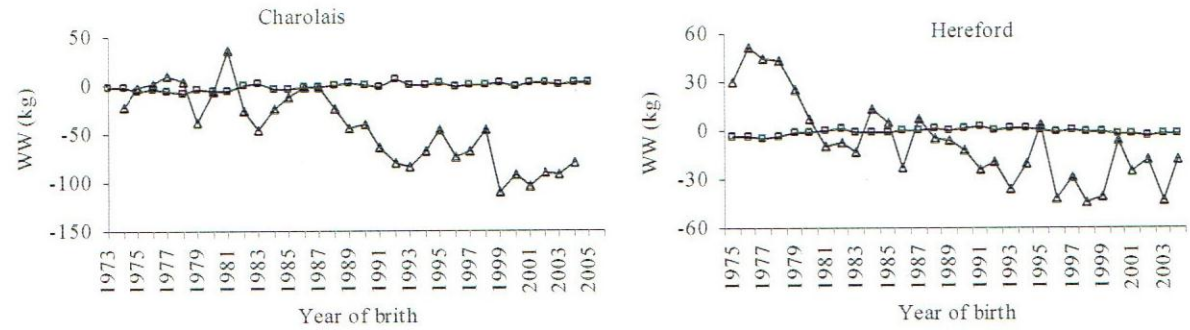


Figure 6. Genetic (□) and environmental (Δ) trends for weaning weight (kg) in the Charolais and the Polled-Hereford beef cattle breeds. The environmental trends are expressed as deviations from the overall mean

Generally, the performance in BW fluctuated between 1.60 kg/yr and –0.40 kg/yr with a peak performance of 1.57 kg/yr in 1992 followed by 1.36 kg/yr in 2003 for the Charolais. For the Polled-Hereford, performance fluctuated between –1.54 kg/yr and 0.9 kg/yr with a peak of 0.82 kg/yr in 1988. For WW, the performance fluctuated between –7.80 kg/yr and 6.50 kg/yr with a peak performance of 6.45 kg/yr in 1992 for Charolais. For the Polled-Hereford, it fluctuated between –4.30 and 1.95 kg/yr with a peak of 1.91 kg/yr in 1991. Similar trends were seen for ADG. Overall, there were positive trends in growth traits for both breeds. The coefficients of genetic progress for BW, WW and ADG were, correspondingly, –0.001 and 0.036; 0.866 and -0.044; 0.229 and 0.035 kg/yr, for the Charolais and the Polled-Hereford breeds.

Genetic and environmental trends for fertility (AFC and CI) traits are presented in (Figures 7 and 8). Fluctuations in environmental trends were evident in both breeds, with high

environmental fluctuations in the earlier than later years for the Charolais. However, the environmental trends improved over the years for the Polled-Hereford. The coefficients of change in environmental trends were –1.8 and 16.0 days/yr for AFC, and –4.8 and 3.3 days/yr for CI in the Charolais and Polled-Hereford, respectively. Negative (favourable) trends were observed for AFC in the Charolais, but no discernable genetic trends were evident for CI. The coefficient of change in genetic trends were, correspondingly, -0.5 yr and 0.0 days/yr for AFC and 0 days/yr for CI in the Charolais and the Polled-Hereford. The environmental trends are expressed as deviations from the overall mean.

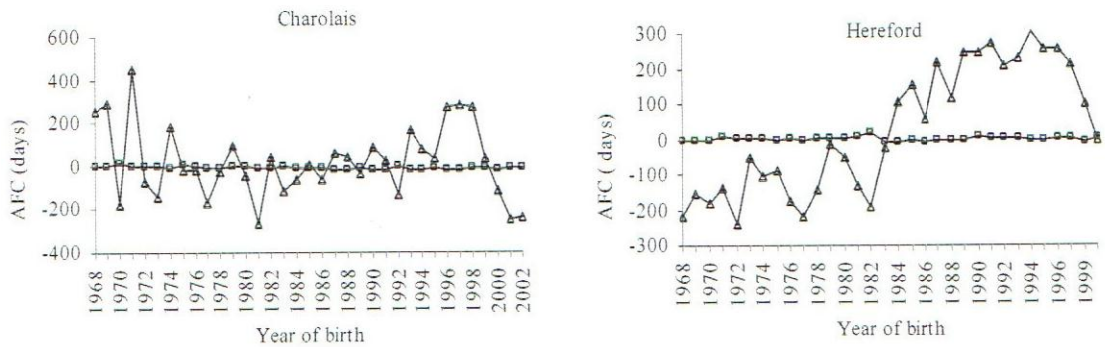


Figure 7. Genetic (□) and environmental (Δ) trends for age at first calving (days) for the Charolais and the Polled-Hereford beef cattle breeds. The environmental trends are expressed as deviations from the overall mean

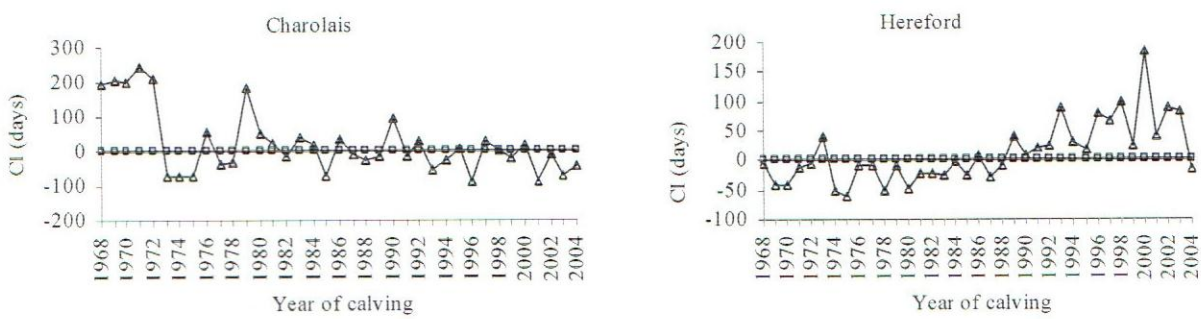


Figure 8. Genetic (□) and environmental (Δ) trends for calving interval (days) for the Charolais and the Polled-Hereford beef cattle breeds. The environmental trends are expressed as deviations from the overall mean

CHAPTER FIVE

DISCUSSION AND CONCLUSIONS

5.1. Aim of the study

Genetic analysis of traits of economic importance is important in determining the effectiveness of any genetic improvement programme. Genetic improvement programmes comprise a number of components; i.e., definition of breeding objectives, choice of selection criteria, performance recording and evaluation, selection and design of mating systems (Ponzoni and Newman, 1989; Rewe et al., 2006a and b). Consequently, the efficiency and effectiveness of a breeding programme is dependent on the choice of breeding objective traits for improvement and accuracy in genetic evaluation. Genetic evaluation has evolved systematically overtime, from use of simple least square methods to more complex maximum likelihood procedures in the estimation of (co)variance components and genetic parameters (Lynch and Walsh, 1998). Unlike in the temperate and other tropical countries, genetic evaluation of beef cattle breeding programmes in Kenya based on recent animal models has not been fully achieved. As a result, selection of animals is based on phenotypic appraisal of an individual's performance rather than objectively determined genetic merit. The objective of the current study was to genetically evaluate growth and fertility performance of the Polled-Hereford and Charolais beef cattle breeds in Kenya. The specific objectives were to: (i) determine factors affecting performance and obtain mean estimates for growth and fertility traits of the Polled-Hereford and the Charolais beef cattle breeds, (ii) estimate genetic and phenotypic parameters for growth and fertility traits of the Charolais and Polled-Hereford beef cattle breeds, and (iii) to estimate the genetic and environmental trends in the growth and fertility traits of the Charolais and the Polled-Hereford cattle over the years.

In line with the foregoing objectives, three hypotheses were tested; (i) environmental factors were not the causes of observed variation in growth and fertility traits, (ii) genetic and phenotypic parameters for growth and fertility traits in the Charolais and the Polled-Hereford cattle were comparable and (iii) no genetic and environmental improvements had occurred in the Charolais and the Polled-Hereford cattle in Kenya over the years.

5.2. Performance of *B. taurus* beef cattle breeds

5.2.1. Non-genetic factors influencing performance

Environmental effects influencing performance of tropical beef cattle have been reported under various production conditions (e.g., Johnston and Graser, 1998; Lôbo et al., 2000; van der Westhuizen et al., 2001). This is a prerequisite to formulation of management policies and production decisions on beef production enterprises. This study indicated significant effects of year-season on growth, as manifested by the effect of climatic conditions on the performance of the beef cattle. However, the absence of a correlation between the inter-annual rainfall distribution and the least square means for growth traits in this study, suggested that the significance of year-season effects was mainly due to random annual fluctuations in rainfall and, therefore, pasture availability.

Parity significantly ($P<0.001$) influenced BW of calves (Table 6). It can be speculated that in young dams, the nutrient competition between fertility and maintenance needs of the animals is high than in older dams, a fact that could lead to low BW. This is in agreement with the literature (e.g., Bourdon and Brinks, 1982; Okeyo et al., 1998; Indetie et al., 2000; Wasike, 2006) that have reported significant influence of parity and age of the dam on BW of calves. Sex significantly ($P<0.001$) influenced BW (Table 6). Bull calves were born heavier than the heifers. This was due to sexual dimorphism, a physiological phenomena arising from higher levels of testosterone hormone in males, which accelerates muscle deposition and, therefore, faster growth compared to females. Sexual dimorphism in growth performance has been reported in the Boran and Sahiwal cattle in the ASALs (Trail and Gregory, 1981; Mwandotto et al., 1988; Wasike, 2006). Environment (year-season of birth/ calving) significantly ($P<0.001$) influenced AFC and CI, respectively, in both breeds (Table 6). In a wet year, unlike a dry one, heifers/ cows had better nutrition; probably this would lead to faster growth and, consequently, earlier ovarian cycling (post-partum), allowing for prominent and regular oestrus expression and, therefore, lead to short AFC and CI. Conversely, failure to detect heat either because of nutritionally-induced silent heat, sub-standard supervision or sheer lack of experience in heat detections, is likely to be responsible for the long AFC and/ or CI in the environments the two breeds were kept. For trends in CI, discernible fluctuations were observed throughout the period (Figure 8). The fluctuations could be as a result of poor management emanating from poor heat detection, leading to many repeat services per conception.

5.2.2. Mean performance estimates

Charolais calves were born 4.14 kg heavier than the Polled-Hereford's (36.10 kg) (Meyer, 1992; Meyer, 1993b; Arthur et al., 1994; Meyer et al., 2004). Preliminary results (not shown) revealed stable trends in least squares means for BW, an indication of the ability of the Charolais and the Polled-Hereford dams to provide a neutral prenatal environment for calf growth irrespective of the fluctuations in the environmental conditions. In addition, it appears the farms were cognisant of BW and its relationship to dystocia such that many of their breeding decisions were based on the trait, particularly when selecting bulls to breed to virgin heifers.

Discernable fluctuations in WW performances across the years (Figure 6) were indicative of the sensitivity of calves to post-natal stress, possibly due to exposure of nursing dams to nutritional stress during droughts that lead to reduced milk production and, subsequently, depriving calves of nutrients. Generally, the Charolais weighed 52.3 kg heavier than the Polled-Hereford (191.3 kg) at weaning (Table 6). However, higher WW for the Charolais have been reported in France (Fouilloux et al., 2002; Phocas and Laloe, 2004), Canada (Duangjinda et al., 2001) and Australia (Meyer, 1993b). Similarly, lower weights have also been reported by Dillard et al. (1980) and Sullivan et al. (1999) in Canada and the USA, respectively. The difference could be attributed to variations in climatic conditions, quality of pastures and breeding objectives between temperate and tropical countries. For the Polled-Hereford, similar WW as in this study have been reported (Ferreira et al., 1999) in the USA, whereas higher WW have been reported in the USA (Bourdon and Brinks, 1982) and Australia (Meyer, 1992; Arthur et al., 1994; Meyer, 2004). However, lower WW have been reported in the USA (Dillard et al., 1980; Nadarajah et al., 1987) and Canada (Fan et al., 1995; Sullivan et al., 1999). The effect of age at weaning on WW was found to be significant (Table 6), an indication of the potential bias in decisions to select or cull animals based on performance parameter estimates from analyses where their ages were not accounted for. For example, if age at weighing is not accounted for, selection would tend to favour older animals.

In cow-calf beef production systems, high off-take is the ultimate goal. Calves with high growth rates attain slaughter weights early and, therefore, optimise off-take, resulting in higher profits. The Charolais calves gained weight faster than those of the Polled-Hereford (Table 6), implying higher feed conversion ability for the Charolais compared to the Polled-Hereford.

Generally, the gains were within the range of estimates reported in the literature (e.g., Dillard et al., 1980; Arthur et al., 1994).

Increased herd fertility improves the profitability of a beef production system. As reported by Rust and Groeneveld (2001), for example, reduced AFC and short CI would increase the number of calves born for a given number of animals. This would ensure a higher calf crop in the productive life of a cow. In less profitable systems, performance of animals is usually lower than in more profitable systems. Generally, the estimates for AFC and CI (Table 6) were higher than those reported for the Polled-Hereford in the USA (Bourdon and Brinks, 1982) and in Charolais x Boran crosses in Kenya (Gregory et al., 1984).

5.3. Estimate of (co)variance components and genetic parameters

5.3.1. Estimates from univariate analyses

The direct heritability estimates for BW for the Charolais (0.36) and the Polled-Hereford (0.21) (Table 7), were lower than reported for Hereford and Angus beef cattle in Australia and the USA. However, the maternal heritability estimates for the Charolais (0.11) and the Polled-Hereford (0.01) were within the range of those reported in other studies (e.g., Meyer, 1992; Dodenhoff et al., 1998; Ferreira et al., 1999; Kaps et al., 1999). Generally, maternal effects accounted for less variation than direct genetic effects in BW. This is in agreement with other results on tropical beef cattle in which maternal influence were observed (Meyer, 1992 and 1993b; Haile-Mariam and Kassa-Mersha, 1995; Dodenhoff et al., 1998; Ferreira et al., 1999; Duangjinda et al., 2001; Burrow, 2001; Demeke et al., 2003). No maternal influence was reported for BW in the Boran beef cattle in Kenya (Wasike, 2006). Maternal effects at birth are almost entirely non-genetic, and are attributed to the pre-natal maternal environment and cytoplasmic effect (Meyer, 1993b; Maniatis, 2000). Maternal influence on BW as evidenced in the current study could be an indicator of variability in the uterine environment provided for the Charolais and the Polled-Hereford offsprings during embryonic development. The estimates of direct-maternal genetic correlations reported in this study for the Charolais and the Polled-Hereford were higher (absolute values) than reported elsewhere (Meyer, 1992; Dodenhoff et al., 1998; Ferreira et al., 1999; Burrow, 2001), but were within the range of estimates reported for Angus in Australia and Simmental cattle in South Africa by Rust et al. (1998) and Kaps et al. (1999), respectively. Differences between the estimates may be attributed to genetic variations

between populations, structures of the pedigree and selection policies. A negative estimate of direct-maternal genetic correlation indicates an antagonistic relationship between these components, such that omitting the direct-maternal genetic covariance in analyses where maternal effects are important (for Charolais in this study) would result into overestimation of direct and maternal heritability (Meyer, 1997).

The direct heritability estimates for WW were similar to ADG (Table 7). They were low to moderate (0.1-0.25) for the Charolais and the Polled-Hereford (Table 7). The implication is twofold; genetic improvement could be achieved through selection on the traits, and that ADG could be used to select calves meant for breeding earlier before weaning age. For the Charolais, the direct heritability was within the range of what has been reported for the breed in the USA (Duangjinda et al., 2001), but was higher than estimates for several other breeds in the tropics (e.g., Meyer, 1992, 1993a and b; Dodenhoff et al., 1998; 1999; Ferreira et al., 1999; de Mattos et al., 2000; Duangjinda et al., 2001; Phocas and Laloe, 2004). For the Polled-Hereford, the direct heritability was within the range of estimates reported in the literature (Meyer, 1992; Dodenhoff et al., 1999) in Australia and the USA, respectively. However, higher estimates have been reported for various beef breeds in the tropics and subtropics (e.g., Meyer, 1993a and b; Dodenhoff et al., 1998 and 1999; Ferreira et al., 1999; de Mattos et al., 2000; Duangjinda et al., 2001; Phocas and Laloe, 2004). Differences between estimates may be attributed to varying levels of genetic variation between populations, differences in selection strategies and use of different models in estimating these parameters.

Maternal effects were more pronounced at weaning in the Polled-Hereford (Table 7). They accounted for a higher proportion of total variation (116.46) than direct additive genetic effects (87.47). The maternal heritability was low (0.17) for both breeds. Generally, these estimates were comparable with estimates reported in the literature (e.g., Meyer, 1992, 1993a and b; Bennet and Gregory, 1996; Dodenhoff et al., 1998 and 1999; Rust et al., 1998; Ferreira et al. 1999; de Mattos et al., 2000; Duangjinda et al., 2001; Phocas and Laloe, 2004).

The heritability estimates for fertility traits were low (Table 7). Similar findings have been reported for Boran cattle in Ethiopia (Haile-Mariam and Kassa-Mersha, 1994) and in Kenya (Wasike, 2006). Low heritability estimates for fertility traits have been reported for various cattle breeds in the tropics (e.g., Bourdon and Brinks, 1982; van der Westhuizen et al., 2001; Rust and Groeneveld, 2001; Olori et al., 2002; Demeke et al., 2004). Moderate (0.31) and low (0.11)

average heritability estimates for AFC and CI, respectively, have been reported for beef cattle in the tropics (Lôbo et al., 2000). The low heritability estimates could be attributed to high phenotypic variance arising from high environmental variations, such as management decisions taken by the breeder (Olori et al., 2002) and, consequently, slow response to selection would be expected. As suggested by Haile-Mariam and Kassa-Mersha (1994) and van der Westhuizen et al. (2001), much of the improvement in fertility traits could be achieved through improvement of the production environment rather than selection. Producers should, therefore, opt for a long-term strategy of achieving change in these traits, which should incorporate improvement of the production environment, e.g., proper feeding, accurate heat detection and timely insemination, and control of reproductive disorders. Notwithstanding the low additive genetic variance for fertility traits, some progress in these traits could be achieved through selection strategies such as culling cows that do not conceive after a number of inseminations, culling heifers with extended AFC or selecting for higher body weight at one year of age in heifers (Ilatsia et al., 2007).

Based on the pedigree information, the number of dams and grand-dams with progeny records were adequate to estimate the direct-maternal correlations (Table 7). The correlation in BW was moderate and negative for the Charolais but was strong and positive for the Polled-Hereford. Direct-maternal genetic correlations in ADG and WW were negative and strong to moderate for the Charolais (-0.51 to -0.47) and the Polled-Hereford (-1.0 to -0.39) (Table 7). These estimates depict an antagonistic relationship between the effects of an individual's genes for growth and those of the dam. Similar findings have been reported by Lee et al. (1997) and de Mattos et al. (2000). Medium and negative (-0.25) correlations have been reported for WW in the Polled-Hereford and Boran breeds, respectively (Dodenhoff et al., 1998; Wasike, 2006). Differences in direction and magnitude of direct-maternal correlations have been associated with data structure and pedigree information (Gutierrez et al., 1997; Maniatis and Pollot, 2003; Wasike, 2006). A positive relationship between genetic effects implies that they can be selected for simultaneously. The results of the present study demonstrate the necessity of including maternal effects in genetic models for early growth traits. Ignoring maternal effects where they are important inflates direct heritability estimates in growth traits (Meyer, 1992).

5.3.2. Estimates from bivariate analyses

Table 8 shows genetic and phenotypic correlations between traits. Apart from correlations between BW and ADG, and ADG and WW in the Polled-Hereford, the genetic correlations between BW and other growth traits were positive and ranged from 0.07 to unity. Similar estimates have been obtained for beef cattle in the tropics (Burrow, 2001; Meyer et al., 2004). This implies that improvement of BW is achievable when selection is done on the basis of other growth traits. However, this may not be desirable since selection, for instance, on the basis of WW could result into calving difficulties due to increased BW. For Charolais, the strong positive relationship between BW and ADG would suggest that selection for low BW would result into slow growth rate.

The strong and negative genetic correlation between AFC and ADG for the Charolais (Table 8) indicates a favourable relationship between breeding values for the early weight gain and AFC. Increased selection based on ADG would result in early onset of puberty. This would be desirable in most beef production enterprises since early AFC would increase the number of calvings per cow in a herd. This agrees well with results presented by Rust and Groeneveld (2001). However, the strong positive genetic relationship between WW and AFC (Table 8) suggest that younger Charolais heifers weaned lighter calves, and given the positive correlations between WW and other growth traits for the breed, selection for early AFC would result in diminished growth performance. Therefore, as an improvement strategy, producers should put their Charolais heifers in the bullying herds on the basis of weight rather than age.

The negative correlations between early growth traits and CI for the Polled-Hereford (Table 8) indicate favourable relationships between breeding values for early growth traits and CI, such that selection for high growth (BW, WW and ADG) traits could result into animals with short CI. This would normally be desirable since shorter CI would translate to high reproductive efficiency (MacGregory and Casey, 1999). However, owing to the effects of dystocia, care should be exercised when selection is to be based on BW, as continuous selection on high BW could predispose Polled-Hereford cows to dystocia. Similar relationships have been reported in the Polled-Hereford and Angus breeds (Bourdon and Brinks, 1982). However, it should be noted that CI is a trait that has many other components, and being a time between two successive calvings, it is only available from the second parity onwards and does not take into account information from the first parity or the end of a cow's lifespan (Rust and Groeneveld, 2001;

Olori et al., 2002). High and negative genetic correlations estimated between AFC and CI (Table 8) indicate unfavourable relationships between the two traits, such that selecting for short AFC could result into cows with prolonged calving intervals and *vice versa*. Low and negative genetic correlations between AFC and CI have been reported in the Kenya Boran (Wasike, 2006). In a different study, Haile-Mariam and Kassa-Mersha (1994), investigating AFC and CI for Boran cattle in Ethiopia, reported low genetic correlations between the two traits. However, a positive genetic relationship between AFC and CI has recently been reported for the Sahiwal breed (Ilatsia et al., 2007).

5.4. Genetic and environmental trends

5.4.1. Genetic trends

The genetic trend for BW was generally low and negative for the Charolais, but it was positive for the Polled-Hereford (Figure 4). At Chepchoina farm, the management would have, over the years, taken cognizant of the possible dystocia problems that would result from heavy Charolais calves and, therefore, selected against the trait. The pattern of genetic trends in BW for the Polled-Hereford was comparable to those reported for Gudali and Wakwa cattle breeds in Cameroon (Ebangi et al., 2000). High genetic progress has been reported for various beef breeds in the temperate countries (Cunningham and Klei, 1995; Sullivan et al., 1999). There is generally high response to selection for growth traits in light breeds, resulting in more genetic progress in these breeds (Sullivan et al., 1999). Consequently, beef cattle breeders with lighter calves at birth tend to put a lot of selection emphasis on weaning and yearling weights than would breeders of beef cattle breeds with heavier calves at birth. This is so because increased BW is less of a concern for breeds that are already light. Apparently, the breeders have been cognizant of BW and its undesirable relationship to dystocia such that their breeding decisions are based on BW, among other factors.

The steady and positive genetic trends in ADG and WW for both the Charolais and the Polled-Hereford indicate genetic progress (Figures 5 and 6). This could arise from intense selection that is based on WW. There was faster genetic progress for WW in the Charolais than the Polled-Hereford (Figure 6). The low genetic progress in ADG for both breeds indicates less selection emphasis for this trait. Generally, low genetic progress in fertility (AFC and CI) traits for both the Polled-Hereford and the Charolais were observed (Figures 7 and 8). Genetic trends

in CI were close to zero; this was to be expected because little effort was directed towards fertility traits in the selection process at both farms. Despite this, favourable genetic trends in AFC (-0.48 and -0.04days/ year) were evident for the Charolais and the Polled-Hereford, respectively. Generally, the annual trends for CI in the Charolais breed were close zero. This would be considered undesirable for the enterprise since the number of calves born per cow would be reduced. This also shows that there was little selection effort to reduce on CI. Low genetic progress in fertility traits has been reported in Zebu cattle breeds in the tropics (Haile-Mariam and Kassa-Mersha, 1994; Wasike, 2006; Ilatsia et al., 2007).

5.4.2. Environmental trends

Fluctuations in environmental trends for BW (Figure 4) imply environmental influence on the trait. However, considerably high and negative environmental trends observed in ADG and WW (Figures 5 and 6) could suggest strong nutritional inadequacies influencing these traits. The environmental trends in BW were negative for both breeds but were more pronounced in the Charolais than in the Polled-Hereford (Figure 4). Negative environmental trends observed in pre-weaning growth traits (Figures 4, 5 and 6) could be attributed to deteriorating management on the farms over the period, coupled with changing climatic conditions that would lead to poor and inadequate livestock nutrition, in addition to disease/ parasite incidences. The influence of environmental factors on fertility traits was apparent (Figures 7 and 8). The annual difference in these traits could be attributed to random inter-annual fluctuations in climatic conditions, which result in variability in feed availability, both in quantity and quality. The somewhat increase in mean AFC over the years up to 1998 for the Polled-Hereford (Figure 7), would suggest that there might have been deliberate changes in age at first exposure for breeding in the breed. Although there was a general understanding for heifers to be first mated at 18 months, this rule could have been broken, especially if heifers were found underweight then. Fluctuations were observed in the environmental trends in AFC and CI (Figures 7 and 8). The effect of the environment under which the animals were performing was undesirable in 1968 to 1989 for the Polled-Hereford. Due to the low additive genetic variance in fertility traits, very little genetic progress would be expected. In this case, the management should adopt stringent management strategies such as supplementing their animals with quality feeds during adverse seasons, employing prudent heat detecting strategies in order to achieve favourable cow reproductive performance. Culling of

cows that exhibit silent heat and those that do not conceive after repeated insemination could also improve reproductive efficiency on both farms. The negative environmental trends as observed for the Charolais reproductive performance would indicate deteriorating management of the herd over time.

5.5. Prospects for genetic improvement of *B. taurus* beef cattle breeds in Kenya

5.5.1. Breeding objectives and selection strategies

Tropical environments are characterised by poor nutrition, high disease challenges and ambient temperatures. Breeding strategies to improve beef production should, therefore, be based on beef cattle breeds that are of high growth potential and relatively adapted to the tropical conditions (Cunningham and Syrstad, 1987). *Bos taurus* beef breeds have been reared under tropical conditions for decades and it is assumed that some of them have evolved to tolerate some of the environmental extremes. Consequently, breeding programmes should be designed to guarantee the continued utilisation of these breeds under such conditions.

One of the major approaches to improving the production efficiency of *B. taurus* beef cattle breeds under the prevailing tropical conditions is through the design of appropriate breeding programmes. Effective genetic improvement depends on appropriate selection and mating decisions for particular breeding objectives based on population specific genetic and phenotypic parameters (Hill and Mackay, 1989). In the context of the Kenya highlands, improvement in production efficiency would seem likely to be achieved through the improvement of exotic beef cattle breeds. Breeding objectives for Zebu cattle breeds in Kenya have been developed (Rewe et al., 2006a); genetic and phenotypic parameters for the breed are also in place (Wasike, 2006). Constraints and prospects for research and development in beef cattle production in Kenya have recently been discussed (Kahi et al., 2006). With regard to beef production in the Kenyan highlands, prospects for improved productivity have been hampered by lack of genetic and phenotypic parameters for production and reproductive traits to aid in the design of appropriate breed improvement strategies. Results in Chapter 4 provide useful information on the general performance levels, population specific (co)variance components and genetic parameter estimates which would be used in the development and evaluation of breeding goals aimed at improved growth and reproductive performance of the Charolais and the Polled-Hereford in Kenya. Selection processes on most farms are usually based on physical appraisal

rather than genetic merit. Selection of sires and dams based on a well-defined breeding objective would ensure improvement in both the biological and economic efficiency in beef production enterprises that utilise the Charolais and the Polled-Hereford genetic resources. For example, a breeding objective for the *B. taurus* beef breeds should be based on increased beef production efficiency because such a goal would represent an efficient and realistic objective for its improvement. In addition, it might also be necessary to consider including reproductive traits in the breeding objective. Given that tropical environments would present a greater challenge, especially for *B. taurus* breeds, it would also be important to consider adaptive alongside productive and fertility traits in the breeding goal.

5.5.2. Organisation of *B. taurus* beef cattle breeding schemes

There are no effective genetic improvement programmes for *B. taurus* beef breeds in Kenya (Kahi et al., 2006). Sound beef cattle improvement programmes should have clear mechanism of timely dissemination of superior genes to the intended population so as to enjoy the benefits accrued thereof (Smith, 1988; Bondoc and Smith., 1993; Ponzoni and Newman, 1989). Currently, the ADC and commercial ranches, e.g., Solio Ranch Ltd. are the custodians of majority of the purebred Charolais and Polled-Hereford beef cattle in Kenya and, therefore, they should take centre stage in genetic improvement programmes. The ADC farms are strategically placed because they are formed on a dispersed structure with various herds located in several parts of the country. Such geographically dispersed herds offer an option of enjoying the full benefits of nucleus breeding schemes. However, the challenge still remains to be inadequate performance and pedigree recording given that such information is key in genetic evaluation, selection and mating. For this reason, use of nucleus breeding schemes in *B. taurus* beef breeds is recommended because they concentrate investment within centralised herds (Smith, 1988). Furthermore, an open nucleus breeding scheme would be recommended owing to the small population size of these breeds and poor performance recording as evidenced in the study. Development of this scheme requires knowledge on the extent of variance for economically important traits, genetic and phenotypic parameters. Results in Chapter 4 provide useful information on these estimates. These estimates will form the basis of designing breeding schemes that can be implemented for genetic improvement of *B. taurus* beef breeds in Kenya. The estimates when used in genetic improvement programmes of *B. taurus* cattle breeds, will

result in higher rate of genetic gain in the breeding objective traits and translate to high economic returns in the entire scheme.

Logistics of operating open nucleus breeding schemes and the various migration policies have been discussed (Smith, 1988; Bondoc and Smith, 1993; Kahi et al., 2004). Owing to the small population of *B. taurus* beef cattle breeds in Kenya, a two-tier breeding structure, comprising of a nucleus (breeding unit) and a commercial population sector, would seem feasible. As a beginning, the ADC farms could act as nucleus centres, and because these farms already have the exotic stock of the beef cattle breeds, they could adopt occasional importation of semen from merited bulls to be used in the nucleus to broaden the genetic base. The beef ranches that will source breeding bulls from the nucleus herds would represent the commercial sector. Initially, selection would be kept simple with selection on individual or index merit for the main economic traits (Kahi et al., 2006). As the breeding scheme develops, selection would be designed to maximize the genetic response in economic merit subject to constraints on levels of inbreeding (Smith, 1988). Close involvement of the ADC and the private ranchers should be emphasised to keep the breeding schemes relevant to both stakeholders. The ADC herd would be involved in performance recording and sire and dam selection aimed at generating desired genetic gain. This nucleus scheme would be expected to offer wide selection base where exceptionally good genetic material from the private ranches could be used and, therefore, reduce levels of inbreeding. Some form of performance recording could also be practised in the commercial herds to aid in the selection process. In this case, it would be assumed that part of the profits derived from sale of animals would be used in running a recording scheme.

5.6. Conclusions

The demand for beef is predicted to increase and, therefore, there is need to exploit efficient beef breeds for high beef output. General improvement in beef cattle performance will be realised through the design of appropriate breeding programmes. The latter requires knowledge on genetic parameters such as trait means, heritabilities and repeatabilities, and genetic and phenotypic correlations for traits to include in the selection index and the breeding objective.

The genetic parameter estimates from the current study fall within the range of reports in the temperate beef cattle breeds. Potential for selective breeding for improvement of growth

traits exists, as indicated by the magnitude of the additive genetic variances for these traits. However, for higher response to selection to be realised, uniformity in the production environment is mandatory. Unfavourable environmental effects tend to obscure genetically superior animals if an evaluation procedure does not effectively adjust for these effects. Given that the heritability estimates for AFC and CI were low, and the high and negative genetic correlation between the two traits, improvement of these traits through selection is limited. Improvement of fertility performance would possibly be achieved with emphasis on improving the production environment, including better recording, timely culling of cows with long AFC and CI, use of bulls with known semen characteristics, and high intensity of selection among the breeding females when their numbers improve. Although the Charolais performed better in most traits than the Polled-Hereford, the mean performance for both breeds showed their potential to meet the ever-increasing demand for beef and beef products in Kenya. The relatively low annual genetic progress registered in both beef breed reflects the actual lack of consistent directional selection for clear selection goals. Genetic and phenotypic parameters were only estimated for early growth and fertility traits; this was so because of the records available at the time. It is, therefore, important to obtain estimates for other economically important traits such as later growth, carcass, body condition score and survival traits when the information will be available. This would allow for the design of effective breeding programmes that will ensure faster genetic improvement rates within the Charolais and the Polled-Hereford breeds. However, in general and based on results from the current study, genetic improvement of the two breeds in Kenya could be achieved by formulation of good breeding strategies that would incorporate good herd management and replacement policies.

REFERENCES

Abdel-Aziz, M., Schoeman, S.J., Jordaan, G.F., 2003. Estimation of additive, maternal and non-additive genetic effects of pre-weaning growth traits in a multibreed beef cattle project. Journal of Animal Science **74**: 169-179.

Albuquerque, L.G., Meyer, K., 2001. Estimates of covariance functions for growth from birth to 630 days of age in Nelore cattle. Journal of Animal Science **79:** 2776-2789.

Arango, J., Plasse, D., 2002. Cow weight in a closed Brahman herd. In: Proceedings of the Seventh World Congress on Genetics Applied to Livestock Production, August 19-23, 2002, Montpellier, France, CD ROM, Communication No. 02-30.

Argentao, C., Filho, M., Souza, E.M., Eler, J.P., Ferraz, J.B.S., 2002. Genetic and phenotypic parameters of growth and carcass traits of a male line of broilers raised in tropical conditions. In: Proceedings of the Sixth World Congress on Genetics Applied to Livestock Production, vol. 30, January 12-16, 1998, Armidale, Australia, pp. 333-336.

Arthur, P.F., Hearnshaw, H., Kohun, P.J., Barlow, R., 1994. Evaluation of *Bos indicus* and *B. taurus* straightbreds and crosses. III. Direct and maternal genetic effects on growth traits. Australian Journal of Agricultural Research **45**: 807-818.

Arthur, P.F., Renand, G., Krauss, D., 2001. Genetic parameters for growth and feed efficiency in weaner versus yearling Charolais bulls. Australian Journal of Agricultural Research **52**: 471-476.

Baker, R.L., 1980. The role of maternal effects on the efficiency of selection in beef cattle – a review. Proceedings of the New Zealand Society of Animal Production **40**: 285-303.

Baker, R.L., Morris, C.A., 1981. Breeding plans for beef producers. In: Proceedings of the Ruakura Farmers' Conference, 1981, Ruakura, New Zealand, pp. 1-11.

Bennett, G.L., Gregory, K.E., 1996. Genetic (co)variances among birth weight, 200-day weight, and post weaning gain in composites and parental breeds of beef cattle. Journal of Animal Science **74**: 2598-2611.

Berry, S., 1993. Understanding Agricultural Policy in Africa: The Contributions of Robert Bates. World Development **21**: 1055-1062.

Bett, C.R., 2005. Developing Breeding Goals for the Kenya Dual-Purpose Goat. M.Sc. Thesis. Egerton University, Njoro, Kenya, 115 pp.

Blair, H.T., Garrick, D.J., 1994. How relevant are current and emerging genetic technologies to the beef breeding cow? Proceedings of the New Zealand Society of Animal Production **54**: 337-343.

Bondoc, O.L., Smith, C.H., 1993. The effects of genotype by environment interactions in dairy cattle open nucleus-breeding schemes. Journal of Animal Breeding and Genetics **110**: 186-193.

Bourdon, R.M., Brinks, J.S., 1982. Genetic, environmental and phenotypic relationships among gestation length, birth weight, growth traits and age at first calving in beef cattle. Journal of Animal Science **55**: 543-553.

Branton, C., 1970. Measures of fertility. In: Cattle Production in the Tropics. Tropical Agricultural Series 1, pp. 263-325.

Burrow, H.M., 2001.Variances and covariances between productive and adaptive traits and temperament in a composite breed of tropical beef cattle. Livestock Production Science **70**: 213-233.

Campelo, J.E.G., Lopes, P.S., Torres, R.A., Silva, L.O.C., Euclydes, R.F., Araujo, C.V., Pereira, C.S., 2004. Maternal effects on the genetic evaluation of Tabapua beef cattle. Genetic and Molecular Biology **27**: 517-521.

Creek, M.J., 2003. The Kenya Feedlot Project. UNDP Special Fund Project, Nakuru, Kenya. Selected Articles from the World Animal Review, pp.1-10.

Crow, G.H., Howell, W.E., 1982. Genetic parameters of the maternal grandsire contribution to beef cattle weaning weights. Canadian Journal of Animal Science **62**: 1057-1062.

Cunningham, E.P., 1980. Methods for Recording, Evaluation and Selection in Adverse Environments, FAO/UNEP Technical Consultation on Animal Genetic Resources Conservation and Management, Rome, Italy.

Cunningham, B.E., Klei, L., 1995. Performance and genetic trends in purebred Simmental for regions of the United States. Journal of Animal Science **73**: 2540-2547.

Cunningham, E.P., Syrstad, O., 1987. Crossbreeding *Bos indicus* and *B. taurus* for Milk Production in the Tropics. FAO. Animal Production and Health. Paper No. 68; Food and Agricultural Organization of the United Nations, Rome, Italy.

Davis, G.P., 1993. Genetic parameters for tropical beef cattle in Northern Australia: a review. Australian Journal of Agricultural Research **44**: 179-198.

De Mattos, D., Misztal, I., Bertrand, J.K., 2000. Variance and covariance components for weaning weight for Polled-Herefords in three countries. Journal of Animal Science **78**: 33-37.

Demeke, S., Neser, F.W.C., Schoeman, S.J., 2003. Variance components and genetic parameters for early growth traits in a mixed population of purebred *Bos indicus* and crossbred cattle. Livestock Production Science **84**: 11-21.

Demeke, S., Neser, C.W., Schoeman, S.J., 2004. Estimates of genetic parameters for Boran, Friesian and crosses of Friesian and Jersey with the Boran cattle in the tropical highlands of Ethiopia: reproduction traits. Journal of Animal Breeding and Genetics **121**: 57-65.

Dillard, E.U., Oswaldo, R., Robinson, O.W., 1980. Estimation of additive and non-additive direct and maternal genetic effects from crossbreeding beef cattle. Journal of Animal Science **50**: 653-663.

Dodenhoff, J., van Vleck, L.D., Gregory, K.E., 1999. Estimation of direct, maternal and grand maternal genetic effects for weaning weight in several breeds of beef cattle. Journal of Animal Science **77**: 840-845.

Dodenhoff, J., van Vleck, L.D., Kachman, S.D., Koch, R.M., 1998. Parameter estimates for direct, maternal and grand maternal genetic effects for birth weight and weaning weight in Polled-Hereford cattle. Journal of Animal Science **76**: 2521-2527.

Duangjinda, M., Bertrand, J.K., Misztal, I., Druet, T., 2001. Estimation of additive and non-additive variances in Polled-Hereford, Gelbvieh and Charolais by method ℜ. Journal of Animal Science **79**: 2997-3001.

Ebangi, A.L., Erasmus, G.J., Neser, F.W.C., Tawah, C.L., 2000. Genetic trends for growth in the Gudali and Wakwa cattle breeds of Cameroon. South African Journal of Animal Science **30**: 36-37.

Falconer, D.S., Mackay, T.F.C., 1996. Introduction to Quantitative Genetics. 4th Edition, Longman Group, England.

Fan, L.Q., Bialey, D.R.C., Shannon, N.H., 1995. Genetic parameter estimation of post-weaning gain, feed intake and feed efficiency for Polled-Hereford and Angus bulls fed two different diets. Journal of Animal Science **73**: 365-372.

Ferreira, G.B., MacNeil, M.D., van vleck, L.D., 1999. Variance components and breeding values for growth traits from different statistical models. Journal of Animal Science **77**: 2641-2650.

Forabosco, F., Groen, A.F., Bozzi, R., van Arendonk, J.A.M., Filippini, F., Boettchers, P., Bijma, P., 2004. Phenotypic relationships between longevity, type traits, and production in Chianina beef cattle. Journal of Animal Science **82**: 1572-1580.

Fouilloux, M.N., Renand, G., Laloe, D., 2002. Genetic evaluation using commercial carcass data in French beef cattle. In: Proceedings of the Seventh World Congress on Genetics Applied to Livestock Production, August 19-23, 2002, Montpellier, France, CD ROM, Communication No. 02-20.

Galina, C.S., Arthur, G.H., 1989. Review of cattle reproduction in the tropics. Part 1. Puberty and age at first calving. Animal Breeding Abstracts **57**: 583-590.

Garrick, D.J., 1990. Maternal effects on growth in beef cattle: estimation of additive and non-additive variances in Polled-Hereford. Journal of Animal Science **79**: 2997-3001.

Garrick, D.J., 1993. The importance of industry structure. In: Blair, H.T., McCutcheon, S.N. (Eds.), Proceedings of A.L. Rae Symposium on Animal Breeding and Genetics, Massey University, New Zealand, pp. 110-119.

Gibson, J.P., Dekkers, J.C.M., 2003. Design and Economics of Animal Breeding Strategies. Available from *j.gibson@cgiar.org* and *jdekkers@iastate.edu.*

Goyache, F., Fernandez, I., Royo, L.J., Alvarez, I., Gutterrez, J.P., 2003. Factors affecting actual weaning weight, preweaning average daily gain and relative growth rate in Australian de Los Valles beef cattle breed. Archives of Animal Breeding **46**: 235-243.

Gregory, K.E., Trail, J.C.M., Sandford, J., Durkin, J., 1984. Crossbreeding cattle in beef production programmes in Kenya. I. Comparison of purebred Boran and Boran crossed with the Charolais, Ayrshire and Santa Getrudis breeds. Tropical Animal Health and Production **16**: 181-186.

Gutierrez, J.P., Canon, J., Oyache, F., 1997. Estimation of direct and maternal genetic parameters for preweaning traits in the Austriana de Los Valles beef cattle breed through animal and sire models. Journal of Animal Breeding and Genetics **114**: 261-266.

Haile-Mariam, M., Kassa-Mersha, H., 1994. Genetic and environmental effects on age at first calving and calving interval of naturally bred Boran (zebu) cows in Ethiopia. Journal Animal Production **58**: 329-334.

Haile-Mariam, M., Kassa-Marsha, H., 1995. Estimates of direct and maternal (co)variance components of growth traits in Boran cattle. Journal of Animal Breeding and Genetics **112**: 43-52.

Harris, D.L., Stewart, T.S., Arboleda, C.R., 1984. Animal Breeding Programs: Systematic Approach to their Design. Publication AAT-NC-8, Agricultural Research Service, U.S. Department of Agriculture, 14 pp.

Hearnshaw, H., Archer, J.A., Barlow, R., 2002. Evaluation of Polled-Hereford and first-cross cows on three pasture systems: cow survival and reasons for disposal under different culling regimes. Livestock Production Science **75**: 183-197.

Ilatsia, E.D., Muasya, T.K., Muhuyi, W.B., Kahi, A.K., 2007. Genetic and phenotypic parameters and annual trends for milk production and fertility traits of the Sahiwal cattle in semi arid Kenya. Tropical Animal Health and Production **39**: 37-48.

Indetie, D., Kinyua, J.M., Gachanja, P.M., 2000. Environmental factors contributing to pre-weaning performance of beef cattle in Kenya. In: Proceedings of the Seventh Biennial KARI Conference, KARI Hqs., Loresho, Nairobi, Kenya, pp. 39-43.

Irungu, K.R.G., Ouda, J.O., 2001. Beef production and finishing systems in Kenya. In: Proceedings of the Beef Industry Stakeholders' Workshop, 19-20 April 2001, Nakuru, Kenya, pp. 1-2.

Itulya, S.B., Ray, D.E., Roubicek, C.B., Benson, C.R., 1987. Genetic parameters, maternal ability and related selection criteria for unsupplemented Polled-Hereford range cows. Journal of Animal Science **64**: 1630-1637.

Johnston, D.J., Graser, H.U., 1998. Genetic evaluation of fertility for Australian beef cattle. In: Proceedings of the Sixth World Congress on Genetics Applied to Livestock Production, vol. 23, January 12-16, 1998, Armidale, Australia, pp. 157-160.

Kahi, A.K., Nitter, G., Gall, C.F., 2004. Developing breeding schemes for pasture based dairy production systems in Kenya. II. Evaluation of alternative objectives and schemes using a two-tier open nucleus and the young bull system. Livestock Production Science **88**: 179-192.

Kahi, A.K., Wasike, C.B., Rewe, T.O., 2006. Beef production in the arid and semi-arid lands of Kenya: constraints and prospects for research and development. Outlook on Agriculture **35**: 217-225.

Kaps, M., Herring, W.O., Limbers, W.R., 1999. Genetic and environmental parameters for mature weight in Angus cattle. Journal of Animal Science **77**: 569-574.

Kennedy, B.W., Schaeffer, L.R., Sorensen, D.A., 1988. Genetic properties of animal models. Journal of Dairy Science **71**: 17-26.

Khan, U.N., Dahlin A., Zafar A.H., Saleem M., Chaudhry M.A., Philipsson, J., 1999. Sahiwal cattle in Pakistan: genetic and environmental causes of variation in body weight and reproduction and relationship to milk production. Animal Science **68**: 97-108.

Khombe, C.T., Hayes, J.F., Cue, R.I, Wade, K.M., 1995. Estimation of direct additive and maternal additive genetic effects for weaning weight in Mashona cattle of Zimbabwe using an individual animal model. Journal of Animal Science **60**: 41-48.

Kilungo, J.K., Mghenyi, E., 2001. Marketing and economics of beef production: the past, present and future outlook. In: Proceedings of the Beef Industry Stakeholders' Workshop, April 19-20, Nakuru, Kenya, pp. 9-27.

Kinyamario, J.I., Ekaya, W.N., 2001. Mechanisms of drought management by African pastoralists. In: Proceedings of The Animal Production Society of Kenya Symposium, pp 117-122.

Kirkpatrick, M., Heckman, N., 1989. A quantitative genetic model for growth, shape, reaction norms and other infinite-dimensional characters. Journal of Mathematical Biology **27**: 429-450.

Koch, R.M., Cundiff, L.V., Gregory, K.E., 1989. Beef cattle breed resource utilization. Brasilian Genetics **12.3** (Supplement): 55-80.

Koots, K.R., Gibson, J.P., Smith, C., Wilton, J.W., 1994. Analyses of published genetic parameter estimates for beef production traits. 1. Heritability. Animal Breeding Abstracts **62**: 309-338.

Kosgey, I.S., Baker, R.L., Udo, H.M.J., van Arendonk, J.A.M., 2005. Successes and failures of small ruminant breeding programmes in the tropics: a review. Small Ruminant Research **61:** 13-28.

Koster, E., van der Westhuizen, J., Erasmus, G.J., 1994. Heritability estimates for different Kleiber ratios obtained from growth performance data in a Polled-Hereford herd. South African Journal of Animal Science **24**: 71-72.

Kovac, M., Groeneveld, E., 1990. Genetic and environmental trends in German swine herd book populations. Journal of Animal Science **68**: 3523-3535.

Lee, C., Pollak, E.J., 2002. Genetic antagonism between body weight and milk production in beef cattle. Journal of Animal Science **80**: 316-321.

Lee, C., van Tassell, C.P., Pollak, E.J., 1997. Estimation of genetic variance and covariance components for weaning weight in Simmental cattle. Journal of Animal Science **75**: 325-330.

Lewis, R.M., Brotherstone, S., 2002. A genetic evaluation of growth in sheep using random regression techniques. Animal Science **74**: 63-70.

Lôbo, R.N.B., Madalena, F.E., Vieira, A.R., 2000. Average estimates of genetic parameters for beef and dairy cattle in tropical regions. Animal Breeding Abstracts **68**: 433-462.

Lunstra, D.D., Cundiff, L.V., 2003. Growth and pubertal development in Brahman-, Boran-, Belgian Blue-, Polled-Hereford- and Angus-sired F1 bulls. Journal of Animal Science **84**: 1414-1426.

Lynch, M., Walsh, B., 1998. Genetics and Analysis of Quantitative Traits. Sinauer Associates Inc, Sunderland, U.S.A., pp. 980.

MacGregory, R.G., Casey, N.H., 1999. Evaluation of calving interval and calving date as measures of reproductive performance in beef herd. Livestock Production Science **57**: 181-191.

MacGregory, R.G., Casey, N.H., 2000. The effects of maternal calving date and calving interval on growth performance of beef calves. South African Journal of Animal Science **30**: 70-76.

Mackinnon, M.J., Meyer, K., Hetzel, D.J.S., 1991. Genetic variation and covariation for growth, parasite resistance and heat tolerance in tropical cattle. Livestock Production Science **27**: 105-122.

Maiwashe, A.N., Bradfield, M.J., Theron, H.E., van Wyk, J.B., 2002. Genetic parameter estimates for body measurements and growth traits in South African Bonsamara cattle. Livestock Production Science **75**: 293-300.

MALDM. 2000. Ministry of Agriculture, Livestock Development and Marketing, Annual Report, Animal Production Division, Nairobi, Kenya.

Maniatis, N., 2000. Quantitative Genetic Analyses of Growth Traits in Sheep Under Different Models of Inheritance. Ph.D. Thesis, University of London, United Kingdom. pp. 159.

Maniatis, N., Pollott, G.E., 2003. The impact of data structure on genetic (co)variance components of early growth in sheep, estimated using an animal model with maternal effects. Journal of Animal Science **81**: 101-108.

Martinez, G.E., Koch, L.V., Cundiff, K.E., Gregory, S.D., Kachman, S.D., van Vleck, L.D., 2002. Genetic parameters and genetic trends for staybility in Polled-Herefords. In: Proceedings of the Seventh World Congress on Genetics Applied to Livestock Production, August, 19-23, 2002, Montpellier, France, CD ROM, Communication, No. 02-32.

Martinez, G.E., Koch, R.M., Cundiff, L.V., Gregory, K.E., van Vleck, L.D., 2004. Genetic parameters for six measures of length of productive life and three measures of lifetime production by year after first calving for Polled-Hereford cows. Journal of Animal Science **82**: 1912-1918.

Mathur, P.K., 2002. Methods for estimation and use of genotype by environment interactions. In: Proceedings of the Seventh World Congress on Genetics Applied to Livestock Production, August, 19-23, 2002, Montpellier, France, CD ROM, Communication No. 18-01.

Matos, C.A.P., Carolino, N., Bettencourt, C.M.V., Gama, L.T., 2002. Genetic variability for calving interval and growth traits in Mertolenga cattle. In: Proceedings of the Seventh World Congress on Genetics Applied to Livestock Production, August, 19-23, 2002, Montpellier, France, CD ROM, Communication No. 25-31.

Mercadante, M.E.Z., Packer, I.U., Razook, A.G., Cyrillo, J.N.S.G., Figueiredo, L.A., 2003. Direct and correlated responses to selection for yearling weight on reproductive performance of Nelore cows. Journal of Animal Science **81**: 376-384.

Meyer, K., 1992. Variance components due to direct and maternal effects for growth traits of Australian beef cattle. Livestock Production Science **31**: 179-204.

Meyer, K., 1993a. Estimates of direct maternal correlations among growth traits in Australian beef cattle. Livestock Production Science **38**: 91-105.

Meyer, K., 1993b. Estimates of covariance components for growth traits of Australian Charolais cattle. Australian Journal of Agricultural Research **44**: 1501-1508.

Meyer, K., 1995. Estimates of genetic parameters for mature weight of Australian beef cows and its relationship to early growth and skeletal measures. Livestock Production Science **44**: 125-137.

Meyer, K., 1997. Estimates of genetic parameters for weaning weight of beef cattle accounting for direct-maternal environmental covariances. Livestock Production Science **52**: 187-199.

Meyer, K., 1998. Modelling 'repeated' records: Covariance functions and random regression models to analyse animal breeding data. In: Proceedings of the Sixth World Congress on Genetics Applied to Livestock Production, vol. 25, January 12-16, 1998, Armidale, Australia, pp. 517-520.

Meyer, K., 2000. Random regressions to model phenotypic variation in monthly weights of Australian beef cows. Livestock Production Science **65**: 19-38.

Meyer, K. 2001. Estimates of direct and maternal covariance functions for growth of Australian beef calves from birth to weaning. Genetic Selection and Evolution **33**: 487-514.

Meyer, K., 2004. Scope for a random regression model in genetic evaluation of beef cattle for growth. Livestock Production Science **86**: 68-83.

Meyer, K., Hill, W.G., 1997. Estimation of genetic and phenotypic covariance functions for longitudinal or 'repeated' records by restricted maximum likelihood. Livestock Production Science **47**: 184-200.

Meyer, K., Johnston, D.J., U-Graser, H., 2004. Estimates of the complete genetic covariance matrix for traits in multi-trait genetic evaluation of Australian Polled-Hereford cattle. Australian Journal of Agricultural Research **55**: 195-210.

Miller, S.P., Wilton, J.W., 1999. Genetic relationships among direct and maternal components of milk yield and maternal weaning gain in a multibreed beef herd. Journal of Animal Science **77**: 1155-1161.

MoA, 2003. Ministry of Agriculture, Annual Report, Nairobi, Kenya.

MoARD, 1998. Ministry of Agriculture and Rural Development, Annual Report, Animal Production Division, Nairobi, Kenya.

Morris, C.A., Baker, R.L., Hickey, S.M., Johnson, D.L., Cullen, N.G., Wilson, J.A., 1993. Evidence of genotype by environment interaction for reproductive and maternal traits in beef cattle. British Society of Animal Production **56**: 69-83.

Mrode, R.A., 2000. Linear Models for the Prediction of Animal Breeding Values. CAB International Publishing, London, UK, 187 pp.

Mrode, R.A., 2005. Linear Models for the Prediction of Animal Breeding Values. 2nd Edition, CAB International Publishing, Oxon, UK.

Mucuthi, M.M., Munei, K., 1996. Some constraints to small ruminant production among small-scale farmers in Laikipia West. In: Proceedings of the Third Biennial Conference of the African Small Ruminant Research Network, UICC, Kampala, Uganda, pp. 83-86.

Musani, S.K., Mayer, M., 1997. Genetic and environmental trends in a large commercial Jersey herd in the Central Rift Valley, Kenya. Tropical Animal Health and Production **29**: 108-116.

Mwandotto, B.A.J., Carles, A.B., Cartwright, T.C., 1988. Weaning and 18-month weights of Boran, East African Shorthorn Zebu and Sahiwal breeds or crosses in Kenya. Tropical Agriculture (Trinidad) **65**: 257- 264.

Mwansa, P.B., Kemp, R.A., Crews Jr., D.H., Kastelic, J.P., Bailey, D.R.C., Coulter, G.H., 2000. Comparison of models for genetic evaluation of scrotal circumference in crossbred bulls. Journal of Animal Science **78:** 275-282.

Nadarajah, K., Notter, D.R., Marlowe, T.J., Eller, A.L. Jr., 1987. Evaluation of phenotypic and genetic trends in weaning weight in Angus and Polled-Hereford populations in Virginia. Journal of Animal Science **64**: 1349-1361.

NDP, 1997. National Development Plan, The Government of Kenya Development Plan for the Period 1997-2001. Government Printer, Nairobi, Kenya.

Nobre, P.R.C., Misztal, I., Tsuruta, S., Bertrand, J.K., Silva, L.O.C., Lopes, P.S., 2003. Analyses of growth curves of Nellore cattle by multiple-trait and random regression models. Journal of Animal Science **81**: 918-926.

Okeyo, A.M., Mosi, R.O., Lang'at, L.K.I., 1998. Effects of parity and previous parous status on reproductive and productive performance of the Kenya Boran cows. Tropical Agriculture (Trinidad) **75**: 384-389.

Olori, V.E., Meuwissen, T.H.E., Veerkamp, R.F., 2002. Calving interval and survival breeding values as measures of cow fertility in a pasture-based production system with seasonal calving. Journal Dairy Science **85**: 689-696.

Pariacote, F., van Vleck, L.D., Hunsley, R.E., 1998. Genetic and phenotypic parameters for carcass traits of American Shorthorn beef cattle. Journal of Animal Science **76**: 2584-2588.

Peeler, E.J., Omore, A.O., 1997. Manual of Livestock Production Systems in Kenya. 2nd Edition, National Veterinary Research Centre, Kikuyu, Kenya, pp. 23-57.

Pelicioni, L.C., de Queiroz, S.A., de Albuquerque, L.G., 2002. Estimates of genetic parameters for body weights of Guzerat cattle. In: Proceedings of the Seventh World Congress on Genetics Applied to Livestock Production, August, 19-23, 2002, Montpellier, France, CD ROM, communication, No. 02-77.

Phocas, F., Laloe, D., 2004. Genetic parameters for birth and weaning traits in French specialized beef cattle breeds. Livestock Production Science **89**: 121-128.

Plasse, D., Omar, V., Arango, J., Comaripano, L., Fossi, H., Romero, R., Rodriguez, M.C., Rumbos, J.L., 2002. (Co)variance components, genetic parameters and annual trends for calf weights in a Brahman herd kept on floodable savannah. Genetic and Molecular Research **1**: 282-297.

Pollak, E.J., Quaas, R.L., 1998. Multibreed genetic evaluation of beef cattle. In: Proceedings of the Sixth World Congress on Genetics Applied to Livestock Production, vol. 23, January 12-16, 1998, Armidale, Australia, pp. 81-88.

Ponzoni, R.W., Newman, S., 1989. Developing breeding objectives for Australian beef cattle production. Animal Production **49**: 35-47.

Prettejohn, G., Retief, R.M., 2001. 'Farmers perspective of the beef industry'. In: Proceedings of the Beef Industry Stakeholders' Workshop, 19–20 April 2001, Nakuru, Kenya. pp. 28-29.

Quintanilla, R., Lalo D., Renand, G., 2002. Heterogeneity of variances across regions for weaning weight in Charolais breed. In: Proceedings of the Sixth World Congress on Genetics Applied to Livestock Production, vol. 32, January 12-16, 1998, Armidale, Australia, pp. 367-370.

Rege, J.E.O., 1991a. Genetic analysis of reproductive and productive performance of Friesian cattle in Kenya. I. Genetic and phenotypic trends. Journal of Animal Breeding and Genetics **108**: 412-423.

Rege, J.E.O., 1991b. Genetic analysis of reproductive and productive performance of Friesian cattle in Kenya. II. Genetic and phenotypic trends. Journal of Animal Breeding and Genetics **108**: 424-433.

Rege, J.E.O., Lomole, M.A., Wakhungu, J.W., 1992a. An evaluation of a long-term breeding programme in a closed Sahiwal herd in Kenya. I. Effects of non-genetic factors on performance and genetic parameter estimates. Journal of Animal Breeding and Genetics. **109**: 364-373.

Rege, J.E.O., Wakhungu, J.W., 1992b. An evaluation of a long term breeding programme in a closed Sahiwal herd in Kenya. Genetic and phenotypic trends and levels of inbreeding. Journal of Breeding and Genetics **109**: 374-384.

Renand, G., Fouilloux, M.N., Mhissier, F., 2002. Genetic improvement of beef production traits by performance testing beef bulls in France. In: Proceedings of the Sixth World Congress on Genetics Applied to Livestock Production, vol. 29, January 12-16, 1998, Armidale, Australia, pp. 517-520.

Rewe, T.O., Indeite, D., Ojango, J.M.K., Kahi, A.K., 2006a. Breeding objectives for the Boran breed in Kenya: Model development and application to pasture based production systems. Animal Science **77**: 163-177.

Rewe, T.O., Indeite, D., Ojango, J.M.K., Kahi, A.K., 2006b. Economic values for production and functional traits and assessment of their influence on genetic improvement in the Boran cattle in Kenya. Journal of Breeding and Genetics **123**: 23-36.

Rumph, J.M., Koch, R.M., Gregory, K.E., Cundiff, L.V., van Vleck, L.D., 2002. Comparison of models for estimation of genetic parameters for mature weight of Polled-Hereford cattle. Journal of Animal Science **80**: 583-590.

Rust, T., Groeneveld, E., 2001. Variance component estimation on female fertility traits in beef cattle. a review. South African Journal of Animal science **31**: 132-141.

Rust, T., Groeneveld, E., Mostert, B.E., 1998. A comparison between multi-variate direct and maternal (co)variate components for growth traits in the South African Simmental beef cattle and those estimated on other continents. In: Proceedings of the Sixth World

Congress on Genetics Applied to Livestock Production, vol. 23, January 12-16, 1998, Armidale, Australia, pp. 125-128.

SAS, 1998. The Statistical Analysis System. Version 8 for Windows. Cary North Carolina, USA: SAS Inc.

Schaeffer, L.R., 2004. Application of random regression models in animal breeding. Livestock Production Science **86**: 35-45

Seithi, C.P., Khan, F.H., Singh, A., 1997. Genetic studies of calving interval in Sahiwal. Journal of Indian Veterinary **74**: 144-146.

Sharma, A.K., Willms, L., Hardin, R.T., Berg, R.T., 1982. Sex of calf and age of dam adjustments for some performance traits in two populations of beef cattle. Canadian Journal of Animal Science **62**: 699-708.

Simm, G., Conington, J., Bishop, S.C., Dwyer, C.M., Pattinson, S., 1996. Genetic selection for extensive production conditions. Applied Animal Behaviour Science **49**: 47-59.

Smith, C., 1984. Rates of genetic change in farm livestock. Research and Development in Agriculture **1**: 79-85.

Smith, C., 1988. Genetic improvement of livestock using nucleus-breeding units. World Animal Review **65**: 2-10.

Solanes, F.X., Grandinson, K., Rydhmer, L., Stern, S., Andersson, K., Lundeheim, N., 2004. Direct and maternal influences on the early growth, fattening performance, and carcass traits of pigs. Livestock Production Science **88**: 199-112.

Souza, J.C., Ramos, A.A., Silva, L.O.C., Euclides, F., Alencar, M.M., Wechsler, F.S., Gadini, C.H., van Vleck, L.D., 1998. Effect of genotype X environment interaction on weaning weight of Nellore calves raised in four different regions of Brazil. In: Proceedings of the Sixth World Congress on Genetics Applied to Livestock Production, vol. 23, January 12-16, 1998, Armidale, Australia, pp. 193-196.

Splan, R.K., Cundiff, L.V., van Vleck, L.D., 1998. Genetic parameters for sex-specific traits in beef cattle. Journal of Animal Science **76**: 2272-2278.

Sullivan, P.G., Wilton, J.W., Miller, P.S., Banks, L.R., 1999. Genetic trends and breed overlap derived from multiple-breed genetic evaluations of beef cattle for growth traits. Journal of Animal Science **77**: 2019-2027.

Taneja, G.C., 1982. Breeding goats for meat production. In: Proceedings of the third International Conference on Goat Production and Disease, 10-15 January 1982, Tucson, Arizona, U.S.A., pp. 27-30.

Teixeira, R.A., Dias, L.T., Albuquerque, L.G., 2002. Estimates of genetic parameters for age at first calving and scrotal circumference in a beef cattle crossbred population. In: Proceedings of the Seventh World Congress on Genetics Applied to Livestock Production, August 19-23, 2002, Montpellier, France, CD ROM, Communication, No. 02-60.

Trail, J.C.M., Gregory, K.E., 1981. Characterisation of the Boran and Sahiwal breeds of cattle for economic characters. Journal of Animal Science **52**: 1286-1293.

Trail, J.C.M., Gregory, K.E., Durklin, J., Sandford, J., 1984. Crossbreeding cattle in beef production programs in Kenya. II. Comparison of purebred Boran and Boran crossed with the Red Poll and Santa Getrudis breeds. Tropical Animal Health and Production **16**: 191-200.

Van der Westhuizen, R.R., Schoeman, S.J., Jordaan, G.F., van Wyk, J.B., 2001. Genetic parameters for reproductive traits in a beef herd estimated using multitrait analysis. South African Journal of Animal science **31**: 41-48.

Vercoe, J.E., Frisch, J.E., 1992. Genotype (breed) and environment interaction with particular reference to cattle in the tropics. Australian Journal of Animal Science **5**: 401-409.

Waigel, K.A., Rekaya, R., 2000. Genetic parameters for reproductive traits of Holstein cattle in California and Minnesota. Journal of Dairy Science **83**: 1072-1080.

Wasike, C.B., 2006. Genetic Evaluation of Growth and Reproductive Performance of the Kenya Boran Cattle. M.Sc. Thesis, Egerton University, Njoro, Kenya, 108 pp.

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