GENETIC PARAMETERS AND CORRELATIONS BETWEEN FEED EFFICIENCY AND GROWTH TRAITS FOR BORAN CATTLE IN KENYA

ANGELA AMONI MAJOYA

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DECLARATION AND RECOMMENDATION

Declaration

This thesis is my original work and has neither wholly or in part been presented nor concurrently been presented for the award of any degree in this or any other institution.

Signature: Majoya Date: ……01/10/2024…
Majoya Angela Amoni

KM 111/13626/19

Recommendation

This thesis has been submitted with our approval as University supervisors.

Signature….............................Date …….2nd October 2024...............

Dr. Thomas K. Muasya, PhD (*Dr. rer. agr)*
Department of Animal Sciences,
Egerton University, Njoro

Signature .. Date…….2nd October 2024...........
Dr. Ir. Joel Onyango Khobondo, PhD
Department of Animal Sciences
Egerton University, Njoro

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DEDICATION

This thesis is dedicated to my loving husband, the Majoya family, and all beef cattle farmers who inspired this study

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ABSTRACT

Selection for increased body weight leads to heavier animals which have higher feed and maintenance costs, ultimately reducing the profitability of beef enterprises. Measures of feed efficiency such as residual feed intake (RFI) and feed conversion efficiency (FCE) require individual animal feed intake records, leading to higher cost of production. Kleiber index (KI) and relative growth rate (RGR) are derived from already existing performance data. However, their genetic parameters and genetic correlations with growth traits are not known. This study aimed to estimate genetic parameters for feed efficiency and their genetic correlation with growth traits as well as investigating the impact of direct-maternal genetic correlation on estimated breeding values on weaning weight by analysing 2184 records of body weight adjusted (WA) to 205 (WA205), 365 (WA365) and 550 days (WA550), daily growth rate from birth to weaning (ADGB-205), yearling (ADG205-365) and 550 days (ADG365-550), Kleiber Index and relative growth rate at 205 days (KI205, RGR205), 365 days (KI365 and RGR365) and 550 days (KI550 and RGR550) via Bayesian inference in THRGIBBSF90 Software. Direct heritability estimates for ADG ranged from 0.12 to 0.27. Estimates for WA were in range of 0.05±0.05 at 205 days to 0.10±0.05 at 550 days. Estimates for KI were 0.13±0.05 at 205 days to 0.29±0.05 at 550 days. For RGR, estimated direct heritability at 205 days was 0.21±0.05, 0.19±0.04 at 365 days and 0.33±0.05 at 550 days. Genetic correlations between growth rate and feed efficiency traits were low at all ages. The direct-maternal genetic correlations for WA, ADG, KI and RGR at 205 days were between -0.30 and 0.90. The genetic correlations between WA365 and ADG were moderate to high (0.45 to 0.67) while WA550 had a low, positive (0.17±0.09) and negative (-0.30±0.08) genetic correlation with ADG205-365 and ADG365-550, respectively. The association between KI365 and RGR365 was strong and positive (0.78±0.04) while the genetic correlations between KI365 and RGR550 at 365 and 550 days were low (-0.34 to 0.02). Direct-maternal genetic correlation for weaning weight was strong and negative (-0.49±0.03), leading to significant re-ranking of animals for direct (r_{rank}=0.827) and maternal breeding values (r_{rank}=0.221) estimated by the model fitting direct-maternal genetic correlation and those without. KI and RGR had substantial heritability estimates, implying potential for improvement through selection. The genetic correlations of KI and RGR with growth traits and the direct-maternal genetic correlation indicate antagonistic relationships, therefore, a weighted index which also accounts for direct-maternal genetic effect should be implemented.

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CHAPTER ONE

INTRODUCTION

1.1 Background information

The principal aim of most beef production systems is to improve the profitability of the enterprise, which is dependent on both input and output costs. However, most genetic improvement programs have concentrated on output traits, such as growth and carcass traits, with little attention paid to input traits (Arthur & Herd, 2012; Hozáková *et al*., 2020; Matos *et al*., 2019).The interest in improving the profitability of beef cattle production systems has recently increased with focus shifting towards identifying animals that can efficiently utilize feed resources in order to reduce feeding costs (Mehrban *et al.*, 2021). Reduction in feed input is expected to substantially improve profitability of beef operations (Carstens, 2006), since feeds account for over 70% of the cost of production in beef enterprises. Measures of feed efficiency are becoming popular traits for genetic analyses because feed is a major component of variable costs (Pryce *et al*., 2014). This provides an avenue for exploiting genetic variation in feed efficiency.

Economic efficiency of beef cattle production systems is associated with the body weight and weight gain of cattle as well as efficiency of feed utilization (Hozáková *et al*., 2020). Rather than incur the additional cost of individual feed recording, traits derived from existing performance records such as differences in rate of gain have been used as an indicator of feed efficiency. Measures of feed efficiency which provide possible means for improving the profitability of beef cattle production systems include residual feed intake (RFI), feed conversion ratio (FCR), relative growth rate (RGR), and Kleiber index (KI) (Mehrban *et al.*, 2021). Estimated genetic parameters for efficiency traits, across multiple cattle populations suggest that inter-animal genetic differences do exist (Kelly *et al*., 2020).

The existence of genetic variation in feed efficiency suggests that genetic improvement can be made in beef cattle for feed efficiency (Arthur & Herd, 2012). Selection for improved feed efficiency will compliment cow performance traits due to the favourable genetic correlations that exist between the traits (Crowley *et al*., 2011). As such, cattle of superior total genetic merit are more feed efficient, lower residual feed intake, and greater residual gain, and have greater carcass weight (Kelly *et al*., 2020). Selection for KI and RGR can be considered as indirect feed utilization measures that can improve the feed efficiency traits with no individual record on feed intake (Mehrban *et al.*, 2021). On the other hand, the negative genetic correlation between FCR and cow BW, indicates that selection for FCR alone will, over time, lead to a heavier cow with possible unfavourable implications for the cost of maintenance (Crowley *et al*., 2011).

There are limited number of studies with estimates of genetic correlations between feed efficiency traits and other traits of economic importance, however some studies found that the genetic correlation between feed efficiency measured by residual feed intake and average daily gain, metabolic body weight is close to zero, furthermore, feed conversion ratio is negatively correlated with average daily gain (Arthur & Herd, 2012). The genetic correlation between feed efficiency measured by Kleiber index and weight gain in various age is similar hence selection for KI or weight gain has the same effect, this means, it selects the same animals and the same alleles (Matos *et al*., 2019).

In Kenya beef production is mainly carried out under arid and semi-arid land (ASAL) condition either under ranching or pastoral production systems (Rewe *et al*., 2006), in these conditions feed resources are usually limiting and production is mainly rain-driven. There is need to consider feed efficiency since beef cattle are reared under arid and semi-arid conditions (Mehrban *et al.*, 2021). The animals kept are the highly adapted indigenous Zebu (small East African Zebu and Boran) or exotic beef (for example, Hereford, Simmental, Charolais, Angus) breeds and their crosses kept mainly by the commercial ranchers (Kahi *et al.*, 2006).

The Boran is a large East African Zebu breed that is considered to have distinct groups of unimproved and improved Boran with an estimated population size of 580,570 (ILRI, 2011). The unimproved Boran is utilised in subsistence and semi-commercial systems of production in Ethiopia, Kenya and Somalia where it is commonly called Borana, Boran or Awai, respectively (Rewe *et al.*, 2006). The improved Boran or the Kenya Boran is reared by ranchers for commercial beef production (Muraya *et al.*, 2015; Mutembei *et al.*, 2015) due to its superior growth and reproductive performance compared to indigenous breeds and high adaptive performance compared with exotic beef breeds (Wasike *et al.*, 2009). The breed is used in crossbreeding programmes in Kenya, Ethiopia, Soth Africa and Australia due to its exemplary heterosis and high reproductive and maternal performance traits and longevity (Haile *et al.*, 2011; Muntean, 2011). The breeding objective of Boran cattle in Kenya aims to maximize beef production from 36-month-old steers and heifers at optimal sale weights on pastures without supplementation. Traits considered in the breeding objective were: direct sale weight, dressing percentage, consumable meat percentage, cow weaning rate, cow survival rate, cow weight, age at first calving, milk yield, feed intake and post weaning survival rate (Rewe *et al*., 2006).

It was therefore recommended that the beef cattle industry should incorporate selection for feed efficiency in its breeding programs (Herd *et al*., 1998).

1.2 Statement of the Problem

Genetic improvement of beef cattle in Kenya has focused primarily on improvement of body weight and growth rates under ASAL condition either under ranching or pastoral production systems. In the ASALs conditions feed resources are usually limiting and production is mainly rain-driven. Selection for increased body weights based on direct genetic estimated breeding values has led to heavier with higher feed requirements for maintenance and growth. Measures of feed efficiency have heritability estimates of between 0.20 to 0.45 meaning that animals that consume less feed or add more weight for the same amount of feed can be selected to improve efficiency of rate of gain in beef cattle. However, the inclusion of feed efficiency traits in selection is hampered by lack of their genetic parameters and genetic correlations with growth traits. Ignoring maternal genetic and permanent environmental effects in beef cattle selection leads to bias, inflation and low accuracy of estimated breeding values. Although several studies have reported on genetic variation and parameters estimates for growth performance in Boran cattle in Kenya no such estimates for feed efficiency traits are currently known for this breed.

1.3 Objectives

1.3.1 General objective

To contribute towards increased productivity of beef production in Kenya through estimation of genetic parameters for feed efficiency traits and their correlation with growth traits and evaluation of effect of maternal genetic effect on breeding values for weaning weight in Boran cattle in Kenya

1.3.2 Specific objectives

i. To estimate genetic variation and parameters of feed efficiency traits in Boran cattle in Kenya
ii. To estimate genetic correlations between feed efficiency and growth traits in Boran cattle in Kenya
iii. To evaluate the maternal genetic effect on estimated breeding values for weaning weight in Boran cattle in Kenya

1.4 Research questions

i. What are the genetic variation and parameters of feed efficiency traits in Boran cattle in Kenya?
ii. What is genetic correlation between feed efficiency and growth traits in Boran cattle in Kenya?
iii. What is the effect of maternal genetic effect on estimated breeding values for weaning weight in Boran cattle in Kenya?

1.5 Justification

The ultimate aim of any genetic improvement program is to optimize whole production system efficiency, of which feed efficiency plays a major part. It is therefore essential that the genetic relationships between feed efficiency and the economically important traits for beef production systems in ASALs be known. Estimates of genetic parameters for feed efficiency traits enable identification and selection of beef animals that are genetically efficient converters of feed to muscle under the feed limiting ASAL conditions. The genetic correlations between feed efficiency, growth and fertility traits will be used to develop an optimal selection index for Boran Cattle in Kenya. Inclusion of maternal genetic and permanent environmental effects lead to increased accuracy of estimated breeding values of selection candidates This will lead to improvement in the profitability of beef cattle enterprises also contribute to mitigation of climate change due to the lower emissions associated with animals with higher feed efficiency.

CHAPTER TWO

LITERATURE REVIEW

2.1 Introduction

Kenya’s average beef production is estimated at 408,000MT per annum of which 70% is mainly based on the Zebu cattle population found in the ASALs while the rest (30%) is from culls from the dairy herd (MOALFI, 2019). The demand for beef as a protein source is increasing worldwide, although in most countries beef accounts for considerably less than half of total meat consumption (Smith *et al*., 2018). Increasing demand in developing countries for animal sources of food including red meat is predicted to double by 2050 because of population growth, urbanization, economic progress and changing consumer preferences (Smith *et al*., 2018). Annual per capita meat consumption is expected to increase to an average of 44 kg or a total consumption of 326 million metric tonnes of meat in the developing countries by the year 2050 (Bett *et al*., 2012).

Beef continues to be the most popular red meat in Kenya, constituting up to 80% of the red meat consumed in the country with an annual consumption of 17 kg per person (Mwangi *et al*., 2020). The continued inability of producers to meet the increasing and changing market demand has been associated with several factors these factors include drought and erratic weather patterns affecting supply of feed and water, livestock diseases, poor management of pastures, lack of and/or weak delivery of extension and veterinary services, high cost of inputs, poor market infrastructure (Mwangi *et al*., 2020).

2.2 Traits of economic importance in beef cattle

All traits of economic value should be considered when selecting beef cattle, the major traits influencing productive efficiency of desirable beef are reproductive performance or fertility, growth rate, feed efficiency, longevity, carcass merit and conformation or structural soundness (Gadberry *et al.*, 2016). Various combinations of these traits are included in the breeding objective of different beef cattle breeding programs worldwide. For instance, in Kenya the breeding objective is composed of direct sale weight, dressing percentage, consumable meat percentage, cow weaning rate, cow survival rate, cow weight, age at first calving, milk yield, feed intake and post weaning survival rate (Rewe *et al*., 2006).

2.2.1 Fertility traits

Reproductive traits describe the animal’s ability to conceive, calve down and suckle the calf to weaning successfully (Haile, 2011). Female reproductive traits have been identified as the most economically important characters in many beef production systems (Pravia *et al*, 2014). Because of the economic importance of reproductive efficiency, much attention has been given to fertility traits and to their relationship with production over the years (Miglior *et al.*, 2017). Although female fertility traits are key components of the profitability of beef cattle production, these traits are difficult and expensive to measure, particularly under extensive pastoral conditions, and consequently, fertility records are in general scarce and somehow incomplete (Naya *et al*., 2017). Approximately one third of cows removed from the beef herd are eliminated because of reproductive failure thus, reproductive inefficiency is a limiting factor for the sustainability of beef cattle production systems that leads to financial losses to cattle producers (Moorey & Biase, 2020).

Main factors influencing reproductive efficiency in cattle include age at puberty and first conception, duration of post-partum anoestrus and total lifetime productivity (Burns *et al.*, 2010). Lifetime production, or total weight of calves weaned during a cow's lifetime, is the most important output component of efficiency in the cow–calf segment of beef production as it is a function of survival and reproductive performance of cows and of survival and growth rate of their offspring (Burns *et al*., 2010). Low heritability estimates for fertility traits have been reported for various cattle breeds in the tropics (Wasike *et al.*, 2006). The low additive genetic variances for fertility traits show that these traits are, to a large extent, influenced by environmental and other herd management policies and therefore little genetic progress could be expected through selection, improvement on fertility could be achieved through appropriate herd management policies (Orenge *et al.*, 2009).

2.2.2 Growth traits

Growth performance of an animal at various stages of the growth curve directly influences profitability in beef production systems. It is also the basis of selection in many of the genetic improvement programs due to their early expression and ease of measurement (Haile, 2011). Growth is an important economic trait hence should be included in any beef cattle breeding program, since it is directly related to higher productivity (Hozáková *et al.*, 2020). Good growth ability of calves is a decisive factor in the profitability of breeding of suckling cows and plays a key role in setting purchase prices. Therefore modern selection programs aim to increase adult weight and size of cattle (Hozáková *et al*., 2020). Factors affecting growth rate are age of the dam, sex, breed, effect of heard year season and age at weaning were confirmed in beef breeds (Krupa *et al*., 2005). Heritability estimates for weight gain in different ages are of moderate magnitude, indicating that these traits could respond to selection, improving genetically the weight gain for the corresponding period (Caetano *et al*., 2013).

2.2.3 Longevity

Longevity is the most important functional trait in selection of cattle worldwide and is defined as duration of life of a cow to her natural death (Olechnowicz *et al*., 2016). Direct selection for longevity may be limited due to the amount of time needed to obtain the measurement. Longevity can be measured up to a certain point in life, culling or death of the animal (Kern *et al*., 2014) and is characterized by low heritability (0.03 to 0.10), particularly when assessed by a linear model (Kern *et al*., 2014). The overall value of a beef female is calculated as the sum of all cash earned over her lifetime minus all expenses. While considerable economic inputs are required to develop replacement heifers, the calves produced throughout a cow's productive lifespan may repay the costs of development and annual maintenance (Moorey & Biase, 2020).

2.2.4 Carcass merit

Carcass traits are of great interest to producers due to increasing demands for quality in the consumer market (Yokoo *et al*., 2009). High-quality beef that meets consumer expectations can only be produced in beef and crossbred cattle herds characterized by high productivity (Nogalski *et al*., 2017). High quality carcasses should have adequate bone: muscle ratio and good fat coverage (Pires *et al*., 2016). Both carcass and meat quality traits are paramount for optimizing the profitability of the beef cattle industry. These traits are influenced by diet and feeding practices, pre- and post-slaughter management, and meat processing and storage methods (Grigoletto *et al.*, 2020). Other factor affecting meat quality are species, breed, sex, individual, age and weight at slaughter (Guerrero *et al*., 2013). The heritability of carcass traits is moderate and vary greatly due to differences in breeds groups, method of estimation effect of model and number of observation sex and managements (Rios *et al*., 2004).

2.2.5 Growth and reproduction traits

Growth and reproduction are relevant economical traits that should be included in a sound breeding program. Therefore, the knowledge of the genetic parameters and the relationship between them are required before a selection program could be implemented (Del Carmen *et al*., 2016). Beef cattle selection programs should include both fertility and productivity traits, but often the possibility of using a total herd reporting system under extensive conditions is limited (Santana *et al*., 2013). For effective breeding programs to be implemented, especially under pasture conditions, the genetic parameters for growth and reproductive traits are crucial, particularly considering the impact that selection for growth may have on production efficiency (Pardo *et al*., 2020). Parameters such as pre-weaning average daily gain (PWG),weaning to first calving average daily gain (WFCG), age at first calving (AFC), cow weight at weaning (CWW), cow average annual productivity (CAAP) have been studied (Lopes *et al*., 2017; Pardo *et al.,* 2020; Pires *et al*., 2016). Heritability estimates for CWW (predictor of mature weight) and WFCG were higher than those for PWG, AFC and CAAP the amount of genetic variability estimated for CAAP makes it feasible to incorporate this trait as a selection criterion (Pardo *et al*., 2020).

Some genetic evaluation systems use fertility indicators or indexes of overall cow productivity. In one such system, the average annual productivity of the cow is expressed as kg of calf weaned per cow per unit of time (Pardo *et al*., 2020). Herds in which cows remain for a longer period of time and calve regularly require a lower portion of primiparous females than herds in which cows have a greater chance of not getting pregnant and therefore being culled earlier (Santana *et al*., 2013). Reproduction is one of the important components for productive efficiency, but the number of kilograms of weaned calves is the main factor of concern. The length of time a cow stays in the herd is therefore not only related to sexual precocity and cow fertility but also to calf weaning weight. This index takes into account the quantity of weaned calves (kg) and the length of time necessary for their production (Santana *et al*., 2013). Eler *et al*. (2008) used the same index called COWPROD which is defined as the amount (in kilograms) of weaned calves produced yearly by one cow during her remaining time in herd ignoring an initial fixed period of 365 days. Another trait related to cow reproduction and production that has been evaluated in some beef cattle breeding programs is stayability in the herd for at least 6yr (Santana *et al*., 2013). The stayability in the herd for at least 6 years has been reported as a feature related to the fertility of the adult female. In general, the reproductive management of beef cattle is based on the culling of females which do not calve in the breeding season or of those that wean a very light calf (Eler *et al*., 2008) The use of an index including cow productivity instead of STAY is advantageous because a productivity index permits the evaluation of the genetic merit of females with only 1 or few calving as well as the evaluation of young bulls (Santana *et al*., 2013).

2.2.6 Feed efficiency traits

Feed efficiency (or its inverse, feed conversion), is described as units of feed/forage consumed divided by the units of animal weight gain over a specific time period (Lamb & Maddock, 2009). Feed intake is an economically important trait that is difficult to measure in the all production systems (Talebi, 2012). Approximately 55 to 75% of the total costs associated with beef cattle production are feed costs (Lamb & Maddock, 2009). As feed is a major cost in beef production, improvement of the output of beef per unit of feed used over the whole production system (hereafter referred to as 'production system feed efficiency) would be of significant economic benefit to the beef industry (Archer *et al.*, 1999). In commercial production systems emphases is being placed on improving feed efficiency as it is a notable strategy for reducing GHG emission (Llonch *et al.*, 2017). Many factors influence feed/forage efficiency including age, diet type, environmental temperature, breed, growth promotants, and many other management and environmental variables (Lamb & Maddock, 2009)

Various measures of feed efficiency are available, e.g. residual feed intake (RFI), residual gain (RG), feed conversion ratio (FCR) and Kleiber index (KI) (Van Marle-Köster *et al.*, 2018). Selection for feed efficiency in cattle has traditionally been accomplished by indirect procedures and various management strategies (i.e., not direct selection) (Lamb & Maddock, 2009). Kleiber index, is expressed as post-weaning average daily gain/mature mass$^{0.75}$, could be used as an indirect selection parameter for feed conversion (Talebi, 2012). Kleiber index, defined as growth rate/live weight$^{\mathbf{0.75}}$, has been suggested to be a useful indicator of growth efficiency and an indirect selection criterion for feed conversion (Talebi, 2012). Kleiber described another feed efficiency Index, called the Kleiber Index (KI), which does not need individual measurement of intake and is used to identify animals with improved growth efficiency regarding their body size (Matos *et al.*, 2019). The Kleiber index can be used as a reliable indication of efficiency, especially for gain and feed efficiency under feedlot conditions also increasing Kleiber index in post weaning can be lead to improve the feed efficiency and gain (Talebi, 2012). The heritability estimates for Kleiber index in different age is moderates hence, the Kleiber index could be applied in selection for increasing the efficiency of growth (Koster *et al.*, 1991).

Kleiber index is highly correlated ($r = 0.81$) with feed conversion efficiency in beef cattle (Talebi, 2012). Mehrban *et al.* (2020) also found the genetic correlation between ADG and KI to be positive and high (0.70 ± 0.05). In the same study, the genetic correlation between KI and RGR were very high (0.92 ± 0.02). Cattle of superior total genetic merit were also more feed efficient (i.e., had a lower energy conversion ratio, lower residual feed intake, and greater residual gain), had a greater proportion of their liveweight as carcass weight (Kelly *et al.*, 2020). The improvements in efficiency described represents only feed efficiency during the finishing period prior to slaughter; in national breeding objectives, feed efficiency across the entirety of the animal's life should also be considered (Kelly *et al*., 2020). For beef cattle, especially Boran cattle, KI and possible biological consequences of the selection for this trait are still scarce. There is need therefore to evaluate the extend of genetic variation for feed efficiency traits that do not require additional recording e.g. RGR and KI to provide understanding of the potential responses to selection for these traits. Estimation of the genetic correlations are crucial in determining whether selection heavier animals led to reduced feed efficiency or vice versa.

2.3 Methodological aspects of genetic evaluation of beef cattle traits of importance

To obtain accurate genetic values for mature weight, good estimates of variances and covariance's are required (Costa *et al*., 2011). Several methods have been used to evaluate growth rate these are repeatability model which seems to be the simplest way to obtain estimates for repeated measures, however, with this model the genetic correlation between successive weights is assumed to be one, whereas several authors observed that it did not happen with real data (Costa *et al*., 2011). Using multiple-trait model (MTM) and random regression models (RRM) provides similarities between RRM and MTM for most estimates of variance components and genetic trends but choosing MTM for genetic evaluation seems simpler (Khorshidi *et al*., 2020). Multiple-trait models seem to be a good alternative because of their robustness and ability to account for differences in the (co)variance and correlation structure along the growth curve(Costa *et al*., 2011). Genetic parameter estimates for indigenous African beef breeds have been estimated considering mainly direct genetic effects and to some extent maternal effects. In a few studies of genetic evaluation of growth performance where they were considered, highly negative direct- maternal genetic covariance estimates were reported (Wasike *et al*., 2006).

CHAPTER THREE

GENETIC VARIATION AND PARAMETERS FOR GROWTH AND FEED EFFICIENCY TRAITS IN BORAN BEEF CATTLE IN KENYA

Abstract

A major drawback of improving feed efficiency in beef cattle enterprises is to identify measures of feed efficiency which do not require feed intake information on an individual animal basis. Kleiber Index, (KI) and relative growth rate (RGR) are alternative measures which do not need individual measurement of intake and can be used to select for improved feed and growth efficiency in relation to their body size. The aim of the study was to estimate genetic parameters for measures of feed efficiency and growth traits for Boran beef cattle in Kenya. A total of 1,348, 2,209, 2,183 and 2,184 weight records were available for birth, weaning, yearling and 550-day weight records, respectively, were available for animals born between 1973 and 2019. The traits derived were growth rate from birth to 205 days (ADGB-205) and from weaning to 365 days (ADG205-365), adjusted weight (WA) at 205 days (WA205) and 365 days (WA365), KI and RGR at weaning at 205 days (KI205 and RGR205), yearling (KI365 and RGR365) and 550 days (KI550 and RGR550). Genetic parameters were estimated using a maternal genetic effects model. Direct heritability estimates for WA205, WA365, WA550, ADGB-205, ADG205-365, ADG365-550, 0.05±0.05, 0.05±0.03, 0.10±0.05, 0.27±0.05, 0.12±0.04, 0.18±0.05, respectively. Estimates of heritability for KI205, KI365 and KI550 were 0.13±0.05, 0.26±0.08 and 0.29±0.05, respectively. For RGR estimate of direct heritability at 205 was 0.21±0.05, 0.19±0.04 at 365 and 0.33±0.05 at 550 days. The direct-maternal genetic correlations for WA, ADG, KI and RGR at 205 days were -0.30±0.05, -0.30±0.04, 0.90±0.05 and -0.72±0.04, respectively. Maternal heritability estimates for WA205, ADGB-205, KI205, RGR205 were 0.12±0.06, 0.05±0.05, 0.38±0.06, 0.07±0.05, respectively. The estimates of direct heritability for growth and feed efficiency traits indicate the traits can be improved through selection. Maternal effects had medium heritability estimates and were unfavourable correlated with growth and feed efficiency traits. The unfavourable direct-maternal genetic correlations for all traits indicate the need to include maternal effects in selection.

3.1 Introduction

Feed provision in beef cattle enterprises is a major economic factor influencing the profitability of beef enterprises since feeds account for up to three-quarters of total direct costs (Kenny *et al.*, 2018). A strategy that is increasingly being adopted to reduce feed cost is to improve feed efficiency through selection (Matos *et al.,* 2019). Generally, feed efficiency is defined as the ratio between product (product) and feed intake (costs) in the form of mass or energy value of product per kilogram of dry matter intake (DMI) (Lovendahll *et al.*, 2018). Heritability estimates for feed efficiency related traits range from 0.28 (Mehrban *et al.,* 2021) to 0.53 (Ceacero *et al.,* 2016), meaning that animals that can efficiently make use of feed resources can easily be identified (Mehrban *et al.,* 2021).

Measures of feed efficiency include feed conversion ratio (FCR) which is defined as the ratio of feed intake to weight gain (Robinson & Oddy, 2004) or residual feed intake (RFI) which is the difference between actual and predicted intake based on its body weight and growth rate over a time period is another measure of feed efficiency (Berry & Crowley, 2013). Both RFI and FCR require feed intake information which is difficult to measure in most livestock production systems (Talebi, 2012). Kleiber Index, (KI) and relative growth rate (RGR) are measures of feed efficiency which do not need individual measurement of intake and can be used to identify and select animals with improved growth efficiency in relation to their body size (Berry & Crowley 2013; Matos *et al.,* 2019; Mehrban *et al.,* 2021; Pitchford, 2004). Kleiber index is defined as the ratio of rate of gain to metabolic body weight. Metabolic body weight is the weight of the animal scaled to the power of 0.75 (Matos *et al.,* 2019). Relative growth rate is obtained as the logarithm of rate of daily gain multiplied by 100 (Matos *et al.,* 2019; Mehrban *et al.,* 2021). As such the two traits can easily be derived from data that is routinely recorded in most beef cattle production enterprises.

In the wake of climate change selection for improved feed efficiency can be used as mitigating strategy to reduce methane gas (CH_4) production hence play an important role in decreasing the environmental impact by means of minimizing the area needed for grazing and production of residues, such as manure and methane (Matos *et al.,* 2019) . Reduction of the amount of feed needed for a given body weight by improving feed efficiency minimizes the emissions arising from both feed and manure management (Leinonen & Kyriazakis 2016) . Efforts are now being directed towards developing animal husbandry approaches that lower enteric CH_4 emissions (Beauchemin *et al.,* 2010). Feed efficiency traits can help to complement the efforts to reduce the negative impacts of animal production on the environment by reducing carrying capacity while achieving the same or higher productivity per unit of land (Gidenne *et al.,* 2017). Therefore it is possible and practical to improve profitability and reduce environmental impacts by selecting for higher feed efficiency and lower methane (CH4) emission traits in livestock farms (Lovendahll *et al.,* 2018) . Therefore, this study aimed to estimate genetic parameters for feed efficiency trait such as relative growth rate RGR, the

Kleiber Index, average daily weight gain for a broader understanding of potential responses to selection for these traits.

3.2 Materials and Methods

Production Environment

Records of growth from body weight records of animals born between 1973 and 2019 from the National Beef Research Centre of the Kenya Agricultural and Livestock Research Organisation, Ol Pajeta and Mugwooni ranches. These ranches maintain improved Boran cattle stud herds which are registered with the Kenya Stud Book and are members of the Kenya Boran cattle Breeders Society (KBCBS). The three ranches are located in agro-ecological zone (AEZ) IV, which is classified as arid and semi-arid land (ASAL). The National Beef Research Station receives an average annual rainfall of 800 mm. Ol Pejeta ranch covers 90,000 acres (360km^2), and lies between Mt. Kenya and the Aberdare Mountains (0°7.288'N, 36°42.384'E and 0°8.634'N, 37°0.605'E) (0°1.831'S, 36°46.578'E and 0°5.7025'S 37°2.492'E), at an average altitude of 1810m, mean annual rainfall of 739mm, mean maximum and minimum temperatures of 28°C and 12°C respectively (Kavwele *et al.,* 2017). Mugwooni Ranch, lies between longitude 360 4' West and 370 27' East and between latitude 00 17' South and 00 45' North. The annual rainfall ranged from 600 to 900mm. The vegetation is predominantly Savannah with scattered acacia and shrubs (Njiru *et al.,* 2001). The rainfall pattern for the three ranches is bimodal, with the long rains falling in March to June and the short rains occurring in September to October with dry seasons in between. The hottest and the driest month in all the herds are January and February (Wasike *et al.,* 2006).

3.3 Performance and Pedigree Records

Birth weight records were recorded at the National Beef Research Station herd only. Pedigree data consisted 3,306 animals born between 1974 and 2018 with a maximum pedigree depth of 8 generations. The pedigree of each individual was traced as far back as possible from the records. Performance records of each individual included birth weight (BW) and weaning weight (WWT) as well as the animal's sex, order of birth number (parity), age of dam at calving and dates of birth and weaning. An animal was retained for further analyses if it had both birth and weaning weights and the respective dates of weighting. Based on these criteria, a total of 1,348, 2,209, 2,183 and 2,184 weight records (animals) for birth, weaning, yearling and 550-day weight records, respectively, were available for analysis.

3.4 Derivation of Growth and Feed Efficiency Traits

The age intervals were pre-established to obtain adjusted body weights at 205 days (WA205), 365 days (WA365) and 550 days (WA550) as follows (Matos *et al.,* 2019) as:

$$WA = \left[\frac{(BW_f - BW_i)}{DS}\right] C + BW_i$$

where BW_f and BW_i are the final body weight and initial body weight, respectively; DS is the interval between weights while C is the standard age in days corresponding to 205, 365, or 550 days.

Relative growth rate at 205 days (RGR205), 365 days (RGR365) and 550 days (RGR550) were calculated as (Mehrban *et al.,* 2021):

$$RGR = \left(\frac{logBW_f - logBW_i}{age_{max} - age_{min}}\right) \times 100$$

where age_{min} and age_{max} are the minimum and maximum recorded ages for each animal.

Kleiber Index (KI) at 205 days (KI205), 365 days (KI365) and 550 days (KI550) were calculated as (Arthur *et al.,* 2001a):

$KI = \frac{ADG}{MBW}$, where ADG is the rate of growth for the pre-established ages and MBW is $LW^{0.75}$ (for Live weight (LW) at weaning, yearling and 550 days). The PROC GLM of SAS (SAS, 2002) was used to test the effect of systematic fixed factors on the traits. The factors included year-season of birth or weaning, sex, parity and dam weight at birth or weaning.

3.5 Estimation of Genetic Parameters

A univariate animal model analyses for each model was fitted to estimate genetic and phenotypic variances and heritability estimates for all the traits. The following general model was used:

$$\mathbf{y} = \mathbf{X\beta} + \mathbf{Za} + \mathbf{Mmg} + \mathbf{Wpe} + \mathbf{e}$$

where **y** is a vector of observations; $\boldsymbol{\beta}$ is a vector of fixed effects (sex, year-season of birth or weaning); **a**, **mg**, and **pe** are vectors of random direct genetic, maternal genetic and permanent maternal environmental effects, respectively; **e** is a vector of random residual effects. **X**, **Z**, **M** and **W** are incidence matrices relating $\boldsymbol{\beta}$, **a**, **m**, and **pe**, respectively, to **y**.

The assumptions for the models where applicable were E(**y**)=$\mathbf{X}\boldsymbol{\beta}$; E(**a**)=0; E(**mg**)=0; E(**pe**)=0; and E(**e**)=0. The variances were var(**a**)=$\mathbf{A}\sigma_a^2$; var(**mg**)= $\mathbf{A}\sigma_{\mathrm{mg}}^2$ var(**pe**) $\mathbf{I}_{\mathrm{d}}\sigma_{\mathrm{pe}}^2$; var(**e**) = $\mathbf{I}_{\mathrm{nb}}\sigma_{\mathrm{e}}^2$ and cov(**a**,**mg**)= $\mathbf{A}\sigma_{\mathrm{a,mg}}$, where **A** is the additive genetic relationship matrix; $\mathbf{I}_d$ and $\mathbf{I}_n$ are identity matrices of number of dams (d) and total number of observations (n); σ_{a}^2 is the direct additive genetic variance; σ^2_{mg} is the maternal genetic variance; $\sigma_{a,mg}$ is the covariance between direct and maternal genetic effects; σ^2_{pe} is the variance of maternal permanent environment; and σ^2_e is the residual variance. Variance components and genetic parameter estimates were estimated using the BLUPF90 family of programmes (Aguilar *et al.*, 2018).

3.6 Results

The least square means for growth and feed efficiency traits are shown in Table 3.1. Average daily gain was highest from birth to weaning (0.51±0.11 kg/day) and slowed down until 0.36±0.17kg/day) at 550 days of age. Kleiber index and relative growth rate were highest

Table 3.1: Number of records (N), least square means (LSMeans)±standard deviation (SD) and coefficient of variation (CV%) for growth and feed efficiency traits in improved Boran cattle in Kenya

Traits	N	LSMean ± SD	CV, %
WA205, kg	1348	129.92±23.54	18.12
ADGB-205, kg/day	1348	0.51±0.11	22.41
KI205, kg/kg$^{0.75}$	1348	1.24±0.15	12.55
RGR205, kg/day	1348	0.32±0.05	15.80
WA365, kg	2182	248.59±39.02	15.70
ADG205-365, kg/day	2183	0.39±0.19	49.61
KI365, kg/kg$^{0.75}$	2144	0.04±0.03	71.3
RGR365, kg/day	2169	0.05±0.03	67.6
WA550, kg	2150	319.19±47.84	15.0
ADG365-550, kg/day	2174	0.36±0.17	47.42
KI550, kg/kg$^{0.75}$	2150	0.49±0.19	38.24
RGR550, kg/day	2109	0.07±0.04	49.3

WA205=weaning weight adjusted to 205 days; ADGB-205=pre-weaning average daily gain; KI205=Kleiber index at 205 days of age; RGR205=relative growth rate at 205 days; WA365=weight at 1 year adjusted to 365 days; ADG205-365=average daily gain from weaning to yearling; KI365=Kleiber index at 365 days; RGR365=relative growth rate at 365 days; WA550=adjusted weight at 550 days; ADG365-550=average daily gain from yearling to 550 days; KI550=Kleiber index at 550 days; RGR550=relative growth rate at 550 days

Variance components due to additive genetic, maternal genetic and maternal permanent environmental effects, estimates of direct and maternal (where applicable) heritability and common environmental effects and direct-maternal genetic correlation for growth and feed efficiency traits are shown in Table 3.2. Direct heritability estimates were higher for ADGB-205 than for ADG205-305 and ADG365-550 (Table 3.2). For adjusted weight (WA), direct heritability was higher at 550 daysthan at 205 days and 365 days. Estimates of direct heritability for KI increased with age from 0.13±0.05 at 205 days to 0.29±0.05 at 550 days. For RGR direct heritability at 205 days was 0.21±0.05 which decreased to 0.19±0.04 at 365 days before increasing to 0.33±0.05 at 550 days. The ratio of variance due to maternal permanent environment effects to phenotypic variance for WA205, ADGB-205, KI205 and RGR205 were 0.12±0.06, 0.05±0.05, 0.38±0.06 and 0.07±0.05, respectively (Table 3.2).

Table 3.2: Variance components for direct (σ_a^2) and maternal σ_{mg}^2) genetic, permanent environment due to dam (σ_{pe}^2) and direct genetic (h_a^2) and maternal heritability (h_{mg}^2), Maternal permanent environment effect (c^2) covariance ($\sigma_{a,mg}$) and correlation ($r_{g_{a,mg}}^2$) between direct genetic and maternal genetic effects for growth and feed efficiency trait in improved Boran cattle in Kenya

Traits	σ_a^2	σ_{mg}^2	σ_{pe}^2	$\sigma_{a,mg}$	σ_e^2	h_a^2	h_{mg}^2	c^2	$r_{g_{a,mg}}^2$
WA205, kg	26.18	19.12	57.66	-0.19	378.96	0.05±0.05	0.04±0.03	0.12±0.06	-0.30
ADGB-205, kg/day	0.64	0.67	0.11	-0.13	0.91	0.27±0.05	0.29±0.03	0.05±0.05	-0.30
KI205, kg/kg$^{0.75}$	0.12	0.13	0.36	0.10	0.37	0.13±0.05	0.10±0.04	0.38±0.06	0.90
RGR205, kg/day	0.38	0.41	0.12	-0.21	0.87	0.21±0.04	0.23±0.04	0.07±0.05	-0.72
WA365, kg	35.02				687.73	0.05±0.03			
ADG205-365, kg/day	$1.57\text{x}10^{-2}$				$1.21\text{x}10^{-2}$	0.12±0.04			
KI365, kg/kg$^{0.75}$	$1.57\text{x}10^{-4}$				$5.56\text{x}10^{-4}$	0.26±0.08			
RGR365, kg/day	$5.7\text{x}10^{-5}$				$2.39\text{x}10^{-4}$	0.19±0.04			
WA550, kg	59.91				565.39	0.10±0.05			
ADG365-550	$1.17\text{x}10^{-3}$				$5.31\text{x}10^{-3}$	0.18±0.05			
KI550, kg/kg$^{0.75}$	$2.46\text{x}10^{-3}$				$5.88\text{x}10^{-3}$	0.29±0.05			
RGR550, kg/day	$1.14\text{x}10^{-4}$				$2.3\text{x}10^{-4}$	0.33±0.05			

WA205=weaning weight adjusted to 205 days; ADGB-205=pre-weaning average daily gain; KI205=Kleiber index at 205 days of age; RGR205=relative growth rate at 205 days; WA365=weight at 1 year adjusted to 365 days; ADG205-365=average daily gain from weaning to yearling; KI365=Kleiber index at 365 days; RGR365=relative growth rate at 365 days; WA550=adjusted weight at 550 days; ADG365-550=average daily gain from yearling to 550 days; KI550=Kleiber index at 550 days; RGR550=relative growth rate at 550 days

3.7 Discussion

The more or less similar maternal and direct genetic heritability estimates for ADGB-205 (0.29±0.02 and 0.27±0.02), WA205 (0.05±0.02 and 0.04±0.02), KI205 (0.10±0.02 and 0.13±0.02) and RGR205 (0.21±0.02 and 0.23±0.04) (Table 3.2) indicate that the two effects are equally important in determining the performance of an animal at weaning. Direct heritability of 0.27±0.02 for ADGB-205 was below the estimates reported previously for various beef cattle populations of 0.34 to 0.38 (Arthur *et al.,* 2001b; Crowley *et al.,* 2010; Goyache *et al.,* 2003). However, WA205 had a lower estimate (0.05±0.05) compared to 0.24±0.02 for Brahman cattle (Matos *et al.,* 2019). For ADGB-205, the heritability of 0.27±0.02 found in the current study was similar to estimate of 0.21±0.02 (Matos *et al.,* 2019) but lower than those reported by Crowley *et al.* (2010), Hoque *et al.* (2005), Mehrban *et al.* (2021), and Takeda *et al.* (2018) which were in the range of 0.33 to 0.54. Average daily gains from 205 days to 365 days and from 365 days to 550 days had direct heritability estimates similar to those reported by Matos *et al.* (2019).

For feed efficiency traits, the heritability estimates for KI205 and RGR205 of 0.13±0.02 and 0.21±0.02, respectively, were lower than estimates of 0.40 (Arthur *et al.,* 2001a), 0.43 (Crowley *et al.,* 2010), 0.53 (Ceacero *et al.,* 2016; Grion *et al.,* 2014) and 0.28 (Mehrban *et al.,* 2021). The direct heritability estimate for KI365 (0.26) was similar that of Brahman cattle of 0.26 while KI550 had higher value (0.29 vs 0.12) (Matos *et al.,* 2019). These reported differences could be as a result of the differences in the number of animals considered, breed, the completeness of the pedigree, precision of recording, environmental variation, and statistical models used for analyses (Mehrban *et al.,* 2021). In general, the estimates of direct heritability for growth and feed efficiency traits which ranged from 0.05 to 0.33, and maternal heritability (0.04 to 0.29) indicate sufficient additive genetic variability, therefore improvement of all the studied traits may be explored in the selection process.

Direct heritability estimates for RGR and KI can be used to select for animals that require less feed per unit of liveweight gain (Lovendahll *et al.,* 2018). Animals with high values of Kleiber Index at weaning and lower values at subsequent ages are expected to have lower maintenance requirements, leading to higher growth rate without increasing maintenance requirements (Bullock *et al.,* 1993; Hoog, 1991). This has the added and desirable advantage of minimising greenhouse gas emissions from both feed and manure management, apart from reducing the cost of producing a unit of beef (Beauchemin *et al.,* 2010; Leinonen & Kyriazakis

2016; Lovendahll *et al.,* 2018). This attempt at complementing the efforts to reduce the negative impacts of animal production on the environment (Gidenne *et al.,* 2017) would be achieved without incurring extra recording costs since these traits utilise already existing routine records (Mehrban *et al.,* 2021).

3.8 Conclusion

Heritability estimates of Kleiber Index and residual growth rate ranged from 0.13±0.05 to 0.29±0.05 and 0.19±0.04 to 0.33±0.05, respectively. Adjusted weight had heritability estimates of 0.05±0.05 to 0.10±0.05 while those for ADG ranged from 0.12±0.04 to 027±0.05. The low to medium estimates of heritability for the feed efficiency and growth traits implying potential for improvement through selection. The traits with the highest direct genetic heritability were ADG2045, WA550, KI550, and RGR550 were at 550 days and 205 days for ADG. These traits can be used to select animals with desirable feed efficiency and growth traits to improve profitability. Additionally, animals with better feed efficiency are associated with lower greenhouse gas emissions.

CHAPTER FOUR

GENETIC CORRELATIONS AMONG MEASURES OF FEED EFFICIENCY AND GROWTH TRAITS IN BEEF CATTLE IN A NATURAL PASTURE GRAZING ECOSYSTEM IN THE TROPICS

Abstract

Efforts to improve feed efficiency have focused on traits such as residual feed intake (RFI), feed conversion efficiency (FCE) and Feed intake (FI) which require recording of individual animal feed intakes, leading to higher cost of production and time investment. Kleiber index (KI) and relative growth rate (RGR) are alternative measures feed efficiency which can be derived from already existing performance data. However, their genetic parameters and correlation with growth traits are lacking. The objective of this study was therefore to estimate genetic parameters for KI and RGR and their correlation with growth traits in Boran cattle in Kenya. A seven-trait animal model was fitted to 1348, 2182, 2150, 1348, 2174, 2144, 2150, 2144 and 2109 records of WA205, WA365, WA550, ADG205-365, ADG365-550, KI365, KI550, RGR365, and RGR550, respectively, to estimate heritability and genetic correlations among the traits via Bayesian inference in THRGIBBSF90 Software. The basic model for each trait included fixed effects and random effects due to direct and maternal genetic effects and maternal permanent environmental effects. The latter two effects were fitted for WA205 only. The heritability estimates for WA205, WA365, KI365, RGR365, W550, KI550 and RGR550 were 0.45±0.01, 0.16±0.02, 0.29±0.03, 0.24±0.01, 0.12±0.03, 0.23±0.01 and 0.31±0.02, respectively. WA205 had a strong relationship with WA365 (0.98±0.06) and a negative correlation with W550 (-0.68±0.1). WA365 had strong genetic correlations with ADG205-365 (0.67±0.04) and ADG365-550 (0.45±0.13). On the other hand, WA550 had a low, positive (0.17±0.09) and negative (-0.30±0.08) genetic correlation with ADG205-365 and ADG365-550, respectively. The association between KI365 and RGR365 was strong and positive (0.78±0.04) while the genetic correlations between KI365 and RGR550 (-0.35±0.13) and between RGR365 and KI550 (0.02±0.08) and RGR550 (-0.34±0.03) were low. Genetic correlations between growth rate and feed efficiency traits were low at all ages hence little or no effect on daily gain due to selection for increased KI or RGR. This study has provided genetic parameters for feed efficiency as measured by KI and RGR and genetic correlations with growth traits which can be used to design a selection programme aimed at improving feed efficiency and growth in beef cattle.

4.1 Introduction

Breeding programmes for beef cattle traditionally focus on selection for growth and fertility traits and carcass traits. This has resulted in enormous improvements in quantity and quality of products. Heavier animals or those with higher rate of daily gain are usually associated with larger appetite and therefore higher feed intake (Moore *et al.,* 2009). The consequence is greater cost of a unit product. In beef cattle feed costs account for close to 70% of production in beef cattle enterprises (Archer *et al.,* 1999) and favouring of animals with higher appetite may lead to further increase in production costs. From a genetic improvement perspective, feed efficiency can be improved by selecting genetically superior parents for these traits.

Measures of feed efficiency such as residual feed intake (RFI) (Callum *et al.,* 2019; Freetly *et al.,* 2020; Steyn *et al.,* 2014), feed conversion efficiency (FCE) (Hendriks *et al.,* 2021) and feed intake (FI) (McNeil *et al.,* 2013) have been suggested as a means of improving profitability of beef cattle enterprises by reducing cost of production. Cattle with high RFI consume more feed while those with low RFI less feed by up to 18% (Lancaster *et al.,* 2009) and Cattle produced 28% less methane (Nkrumah *et al.,* 2007). As a trait RFI is independent of growth rate and body size and is moderately heritable (0.30 – 0.43) and is therefore preferred as measure of feed efficiency. RFI is favourably correlated with growth and carcass traits (Shinoda *et al.,* 2022) but unfavourably correlated with fertility traits such as days to calving (Basarab *et al.*, 2011; Mu *et al.,* 2016; Shaffer *et al.*, 2011). However, some studies have reported lack of negative effects of selection for RFI on fertility (Basarab *et al.*, 2007; Callum *et al.*, 2019; Donoghue *et al.*, 2011). It is therefore essential to evaluate growth and fertility traits alongside measures of feed efficiency.

Most the feed efficiency indices (FI, RFI, FCE) require individual animal measurement of feed intake (Elolimy *et al.,* 2018; Kelly *et al.*, 2020). Performance recording of additional traits in the context of a breeding programmes is expected to result in an increase in cost of operations (Wasike *et al.,* 2011). This is important for breeding programmes in the tropics where breeding programmes are constrained by limited data recording (Wasike *et al.,* 2011) and the need to minimize costs (Kariuki *et al.,* 2014). Kleiber Index (KI) defined as the rate of gain per kilogram metabolic body weight (Matos *et al.,* 2019) and relative growth rate (RGR) which is the logarithm of rate of daily gain (Mehrban *et al.*, 2021) are derived from routine body weight records (Moore *et al.,* 2009). The heritability estimates for KI and RGR range from 0.28 to 0.32 and 0.40 to 0.44, respectively ((Matos, *et al.,* 2019; Mehrban *et al.,* 2021; Rezende *et al.*, 2022). These two traits can therefore be improved through selection to High values of KI or RGR indicate better feed efficiency (Ghafouri-Kesbi *et al.,* 2011). However, inclusion of KI and or RGR in selection programmes require information on their extend of genetic correlations with other traits of economic importance in beef production

Genetic correlations between KI and RGR and growth and carcass traits beef cattle populations are range from 0.21 to 0.65 (Mehrban *et al.,* 2021; Rezende *et al.*, 2022). This implies that inclusion of KI and or RGR in beef cattle breeding programmes could improve feed efficiency without negatively affecting growth traits (Kasahun *et al.*, 2022; Rezende *et al.,* 2022) and carcass traits (Mehrban *et al.,* 2021). However, the genetic correlations between feed efficiency traits (KI and RGR) with growth and are lacking and the consequences of selection for these traits have not been quantified. Therefore, the objective of this study was to estimate the genetic correlations between measures of feed efficiency with growth and fertility traits.

4.2 Materials and Methods

Data were obtained on weaning weight (WWT) yearling weight (YWT) and weight at 550 days, date of birth, date of weaning and date at 18 months of age were extracted from herd registers at each farm and entered into a MS excel database for further editing. After cleaning, growth rate and efficiency related traits were calculated from the dates and weights collected.

Average daily gain, in kg/day from weaning to yearling (ADG205-365) and from yearling to 550 days of age (ADG365-550) was calculated as: $ADG = (final\ weight - initial\ weight)/age$ where age is the age at yearling or 550 days. Kleiber index at 365 (KI365) days and at 550 (KI550) was calculated as $\frac{ADG}{BW^{0.75}}$ (Kleiber, 1947). Relative growth rate at 365 (RGR365) and 550 days (RGR550) was calculated as $RGR = \frac{Log(initial\ weight) - Log(final\ weight)}{interval, days}$ (Ghafouri-Kesbi & Eskandarinasab, 2018; Ghafouri-Kesbi & Gholizadeh, 2017).

4.3 Data analysis

Phenotypic records of the traits (WA205, ADGB-205, WA365, ADG205-365, KI365, RGR365, ADG365-550, KI550 and RGR550) were analysed using the general linear model (GLM) of the statistical analysis system (SAS, 2004) to determine the fixed effects to be included in the final analysis. The fixed effects included in the genetic analysis are given in Table 4.1.

Table 4.1: Fixed effects included in the respective models for genetic analysis of the growth and feed efficiency traits of Boran cattle

Trait	**Fixed factor**	
	Sex	HYS
WA205, kg	*	**
WA365, kg	**	*
WA550, kg		
ADG205-365, kg/day	**	*
ADG365-550, kg/day	*	*
KI365, kg/kg$^{0.5}$	*	*
KI365, kg/kg$^{0.5}$	**	ns
RGR365, kg	*	*
RGR550, kg	ns	*

HYSB=herd-year-season of birth; *=significant at P<0.05, **P<0.01; WA205=weaning weight adjusted to 205 days; WA365=weight at 1 year adjusted to 365 days; ADG205-365=average daily gain from weaning to yearling; KI365=Kleiber index at 365 days; RGR365=relative growth rate at 365 days; WA550=adjusted weight at 550 days; ADG365-550=average daily gain from yearling to 550 days; KI550=Kleiber index at 550 days; RGR550=relative growth rate at 550 days

The model used for the analysis of variance of fixed effects was:

$$y_{ijkl} = \mu + Sex_i + HYS_j + age_k + e_{ijkl}$$

where y_{ijkl}=the ith observation; μ=overall mean Sex_i=ith sex, i=1,2; HYS_j=jth herd-year-season of birth class, j=1…152; age_k=linear covariate of age at weaning and e_{ijkl}=residual associated with each observation.

Genetic correlations were estimated using unequal design bivariate animal model using the AI-REML of BLUPF90 software (Aguilar *et al.*, 2018). The statistical model for estimating genetic correlations was:

$$\mathbf{y} = \mathbf{X\beta} + \mathbf{Za} + \mathbf{Mmg} + \mathbf{Wmpe} + \mathbf{e}$$

where $\mathbf{y}$ was a vector of observations; β was a vector of fixed effects; $\mathbf{a}$ was a vector of direct genetic effects; $\mathbf{mg}$ was a vector of maternal genetic effects; $\mathbf{mpe}$ was vector of permanent environment effects associated with the dam; and $\mathbf{e}$ was the random residual. $\mathbf{X}$, $\mathbf{Z}$, $\mathbf{M}$ and $\mathbf{W}$ were incidence matrices linking, fixed, direct genetic, maternal genetic and permanent environment effects to the observations.

Maternal genetic effects were included for only W205. Assumptions for the model where applicable were:
E(y)=$\mathbf{X}\boldsymbol{\beta}$=0; E(mg)=0 and E(pe)=0. The respective variances were: Var(a)=$\boldsymbol{A}\sigma_a^2$; Var(mg)=$\boldsymbol{A}\sigma_{mg}^2$; cov(a,mg)= $\boldsymbol{A}\sigma_{a,mg}$; Var(mpe)=$\boldsymbol{I}_{nv}\sigma_{mpe}^2$; and Var(e)=$\boldsymbol{I}_{nb}\sigma_e^2$.

where $\mathbf{A}$ was the additive genetic relationship matrix; $\boldsymbol{I}_{nv}$ was the identity matrix of number of dams (nv); $\boldsymbol{I}_{nb}$ were the identity matrix of the number of total observations (nb); σ_a^2 was the direct genetic variance; σ_{mg}^2 was the maternal genetic variance; $\sigma_{mpe}^2$was the permanent environment variance; $\sigma_{a,mg}$was the genetic covariance between direct and maternal genetic effects; and $\sigma_e^2$was the residual variance.

4.4 Results

Estimates of genetic parameters from multiple trait animal model are given in Table 4.2. Heritability estimate for WA205 (0.08±0.02) was similar to that of WA365 (0.06±0.02) but higher than 0.12±0.03 for WA550. Genetic variation for KI and RGR was higher at yearling than at 550 days, registering a decline of 31.8% and 25.9%, respectively. However, while the heritability estimates for KI followed a similar trend, the estimate for RGR at 550 days increased by 29.2% on account of a smaller residual variance.

Genetic and phenotypic correlations among growth and feed efficiency traits are presented in Table 4.3. WA365 had a strong and positive correlation with WA205 (0.98±0.06) and negative correlation with WA550 (-0.68±0.1). The phenotypic correlations were equally high (WA205=0.75 and WA550=0.64). The genetic correlations between WA365 and ADG205-365 and ADG365-550 were 0.67±0.04 and 0.45±0.13,

Table 4.2: additive ($\boldsymbol{\sigma_a^2}$), maternal ($\boldsymbol{\sigma_m^2}$), maternal permanent environment ($\boldsymbol{\sigma_{pe}^2}$), and residual ($\boldsymbol{\sigma_e^2}$) variances, direct ($\boldsymbol{h_a^2}$) and maternal heritability ($\boldsymbol{h_m^2}$), maternal repeatability ($\boldsymbol{r_m^2}$) of multivariate analyses of weight to 205 (WA205), 365 days (W365) and 550 days (WA550), Keiber index at 365 (KI365)and 550 days (KI550) and relative growth rate at 365 (RGR365) and 550 days (RGR550) for improved Boran cattle in Kenya

	σ_a^2	σ_m^2	σ_{pe}^2	σ_e^2	h_a^2	h_m^2	r_m^2
WA205, kg	34.61	18.32	46.78	-9.45	0.08±0.01	0.04±0.03	-0.4
WA365, kg	45.24			651.02	0.06±0.02		
KI365, kg/kg$^{0.5}$	2.74x10^{-3}			6.83x10^{-3}	0.29±0.02		
ADG205-365, kg/day	2.41x10^{-3}			9.70x10^{-3}	0.20±0.03		
RGR365, kg	2.94x10^{-4}			9.44x10^{-4}	0.24±0.01		
KI550, kg/kg$^{0.5}$	1.87x10^{-3}			6.30x10^{-3}	0.23±0.01		
WA550, kg	75.43			575.75	0.12±0.03		
ADG365-550, kg/day	2.06x10^{-3}			7.46x10^{-3}	0.22±0.02		
RGR550, kg	2.18x10^{-4}			4.92x10^{-4}	0.31±0.02		

respectively. On the other hand, WA550 had a low, positive (0.17±0.09) and negative (-0.30±0.08) genetic correlation with ADG205-365 and ADG365-550, respectively. The association between KI365 and RGR365 was strong and positive (0.78±0.04) while the genetic correlations between KI365 and RGR550 (-0.35±0.13) and between RGR365 and KI550 (0.02±0.08) and RGR550 (-0.34±0.03) were low.

Table 4.3: genetic (above diagonal) and phenotypic (below diagonal) among feed efficiency and growth traits for Boran cattle in Kenya

	WA205	WA365	KI365	ADG205-365	RGR365	KI550	WA550	ADG365-550	RGR550
WA205	1.00	0.98	-0.73	-0.39	-0.45	-0.09	0.78	0.53	0.21
WA365	0.65	1.00	-0.52	0.67	-0.82	-0.24	-0.68	0.45	0.52
KI365	0.12	-0.52	1.00	0.31	0.78	-0.17	-0.27	-0.01	-0.35
ADG205-365	0.78	-0.15	0.31	1.00	-0.15	-0.56	0.17	0.72	0.18
RGR365	0.09	-0.82	0.48	-0.15	1.00	0.02	0.08	-0.15	-0.34
KI550	0.21	-0.24	-0.17	-0.56	0.02	1.00	0.47	-0.90	-0.24
WA550	0.46	-0.33	-0.27	0.17	0.08	0.47	1.00	-0.30	0.41
ADG365-550	0.39	0.15	-0.01	0.72	-0.15	-0.90	-0.30	1.00	0.10
RGR550	-0.21	0.52	-0.35	0.18	-0.34	-0.24	0.41	0.10	1.00

WA205=weaning weight adjusted to 205 days; WA365=weight at 1 year adjusted to 365 days; ADG205-365=average daily gain from weaning to yearling; KI365=Kleiber index at 365 days; RGR365=relative growth rate at 365 days; WA550=adjusted weight at 550 days; ADG365-550=average daily gain from yearling to 550 days; KI550=Kleiber index at 550 days; RGR550=relative growth rate at 550 days

4.5 Discussion

There is increasing need to for strategies that improve efficiency of utilization of pastures under natural grazing (Rojas-Downing *et al.,* 2017). Selecting animals that require less feed to achieve the same production potential (Moore *et al.,* 2009) can improve the efficiency of feed utilization hence lowering cost of production as well as reduction of greenhouse gas emissions from pasture based grazing systems (Velaszo *et al*., 2017). The declining trend of KI and RGR as animals become older is consistent to finding by Rezende *et al.* (2022) for Chalorais and Limousin cattle in the United States. This confirms finding by Figueiredo *et al.* (2019) that animals with larger body structure are associated with lower KI. This could be due to high maintenance requirements in older larger bodied animals. Heritability estimates of previous studies of 0.24 in zebu breeds (Grion *et al.,* 2014), 0.12 to 0.28 in Brahman cattle (Matos *et al.,* 2019), 0.28 in Hanwoo beef cattle (Mehrban *et al.,* 2021), were similar to those found in the current study. Kasahun *et al.* (2022) reported higher heritability estimates (0.55) for KI and RGR at weaning for Fogera cattle. The heritability values found for Boran cattle in Kenya indicate that KI and RGR can be selected and genetic gains achieved through direct selection. For body weight, heritability estimates at 205 days and at 365 days from the current study were lower than 0.59 and 0.42 for Charolais and 0.22 and 0.22 for Limousin, respectively (Rezende *et al.,* 2022). Other higher heritability estimates for weaning weight include 0.26 for Fogera cattle (Kasahun *et al.,* 2022), 0.24 in Brahman cattle (Matos *et al.,* 2019).

The moderate direct-maternal genetic correlation (-0.40) in the Boran cattle indicate the need to consider maternal genetic effects when selecting dams. The maternal effect is due to the genes transmitted to the calves and the environment the dam provides for the calf (Romé *et al.,* 2023). Therefore, dams with poor maternal ability and low milk production are unable to adequately nurture the calf, leading to low weaning weights. on the other hand, dams with high growth potential transmit genes for high growth potential to their progeny and provide a superior maternal environment for fast growth up to weaning (Bignardi *et al.,* 2024). The influence of maternal effects has been shown to persist beyond weaning and yearling (Bignardi *et al.,* 2024), emphasising the importance of such effects. In beef cattle selection programmes, maternal effects should be included in genetic evaluations when performed at weaning. For weight at 550 days, Matos *et al.* (2019) reported a value of 0.24 for Brahman cattle. Similar to the study by Matos *et* *al.* (2019), maternal effects for yearling weight and weight at 550 days were absent for Boran cattle in Kenya.

The positive genetic correlation between ADG205-365 and KI365 mean that weaners that grew fast from weaning at about 7 months of age were also associated with better feed conversion efficiency. However, the high and negative genetic correlation between ADG365-550 and KI550 (-0.99) depict the exact opposite, meaning that selection of cows for greater ADG365-550 would result in cows with low values of KI, meaning that they would require more feed per unit of body weight gain. This would mean that the cows have higher feed requirements hence increasing the cost production. The genetic correlations between RGR365 and KI365 (0.48) was similar to that of 0.4 reported for Hanwoo cattle in Japan (Mehrban *et al.,* 2021). However, the correlation between RGR365 and ADG205-365 (-0.15) was lower than 0.70 reported in the same study. Mehrban *et al.* (2021) found low and negative genetic correlations between yearling weight and KI (-0.05) and RGR (-0.30) at yearling, values which were lower than those reported for improved Boran cattle in the present study between adjusted yearling weight and KI365 (-0.52) and RGR365 (-0.82), respectively. This implies that selection for greater KI365 would result in females with heavier yearling weight with similar consequences as selection for KI550. The genetic relationship between KI and ADG at 365 days and 550 days were similar, meaning that the category of animals selected would be similar. This means the animals would grow faster and be heavier at 365 days and 550 days of age. When selecting for KI365 i.e. increased feed efficiency at yearling, the result would be animals with low yearling weight given medium and negative genetic correlation (-0.52). Other studies which reported high genetic correlations between the feed efficiency traits and growth traits include Crowley *et al.* (2010) and Grion *et al.* (2014).

The results of the present study show that selection of animals for KI or RGR would improve ADG205-365 and WA365. The strong genetic and phenotypic correlations between KI and RGR at yearling (0.78) is consistent with estimates from other studies (Crowley *et al.,* 2010; Hoque *et al.,* 2009; Kelly *et al.,* 2010; Merhban *et al.,* 2020). Therefore, either of the traits can be used to weight an index of selection that aims at improving body weight without increasing maintenance costs. However, the genetic correlations between KI and RGR at 365 and 550 days were divergent, ranging from positive to negative and low, implying that the maintenance requirements of animal would increase between yearling and 550 days of age. From a genetic improvement perspective, selecting heifers for weaning weight will lead to heavy animals at yearling as well as 550 days of age, since the latter is highly correlated with WA205 and WA550. Moreover, the genetic correlation between WA365 and KI550 is low and negative (-0.24). Selection of dams would therefore be beneficial if selection for feed efficiency was carried out at one year with a selection index that aims at high values of feed efficiency and moderate values of WA550. The low genetic correlation between WA365 and KI550 (-0.23) could enable selecting of animals with high feed efficiency and moderate body weight at 550 days, which is closer to adult age. The results of the present study provide valuable information on the genetic parameters for measures of feed efficiency and their relationship with growth traits. However, the results should be applied with caution since the data was obtained sourced for a single beef herd.

The differences between genetic correlations found in the present study and those reported elsewhere could be due to the model of analysis, amount of data and fixed factors fitted. For instance, Matos *et al.* (2019) fitted breeder in addition to sex, farm (herd) and season and year of birth. Merhban *et al.* (2020) implemented a model that included batch-test and sex and year of birth. Genetic parameters are also influenced by the population of livestock studied and the history of selection of that population. Nilforooshan and Ruíz (2022) demonstrated that genetic variances are a function of quality of the pedigree and the additive genetic relationship within a population as well as the extent linkage disequilibrium. Selection within a population leads to changes in additive genetic covariance between traits by up to 120% (Gathura, 2021) causing a decline in genetic correlations over time (Careau *et al.*, 2015).

4.6 Conclusion

The genetic correlations between KI and RGR with WA and ADG at 205 days, 365 days and 550 days were negative and low (-0.01) to high (-0.90). RGR365, RGR550 and KI550 had positive genetic correlations with WA550 (0.47, 0.08 and 0.41, respectively), while RGR550 had positive genetic correlations with WA205 (0.21), WA365 (0.52), ADG205-365 (0.18) and ADG365-550 (0.10). The positive and medium genetic correlations between RGR and all growth traits mean that an increase in feed efficiency would lead to a moderate increase in body weight thus lowering feed costs thereby increasing profitability of beef production.

CHAPTER FIVE

IMPACT OF MATERNAL GENETIC EFFECT ON BEEF CATTLE GENETIC EVALUATION WHEN THE DIRECT-MATERNAL GENETIC CORRELATION IS STRONG AND NEGATIVE

Abstract

Most traits of economic importance in beef cattle that are expressed during the early stages of growth such as growth are influenced by maternal effects. The direct-maternal genetic correlation (r_{dm})is usually negative and ranges from low to high. When the r_{dm} is small there is little or no effect animal ranking based on total breeding value and can be ignored in genetic evaluations. It is however expected that significant re-ranking should occur if the r_{dm} is medium to strong. An animal model was fitted to weaning weight either ignoring maternal genetic effects or fitting maternal genetic effects but assuming $r_{dm}=0$ or $r_{dm}\neq0$. The three linear models also included fixed effects of sex and herd-year-season of birth. A total of 15,431 records of weaning weight of improved Boran weaners progeny of 329 sires and 4405 dams from 3 herds which record with the Kenya Stud Book were available for analysis. The pedigree consisted of 18,600 animals born between 1974 and 2018 with a maximum pedigree depth of 8 generations. Preliminary analsyses were performed to identify factors influencing weaning weight. A univariate animal model was fitted to the data to estimate genetic and phenotypic variances and heritability estimates for weaning weight. Apart from fixed effects, the model included random effects of direct and maternal genetic effects, maternal permanent and permanent environmental effect due to animal as well as the covariance between direct and maternal genetic effects. Direct and maternal heritability estimates and common environment effects were 0.54±0.03, 0.2±0.02 and 0.07±0.01, respectively. The direct-maternal genetic correlation was strong and negative (-0.82±0.11). Ignoring direct-maternal genetic correlation led to significant re-ranking of animals based on direct (r_{rank}=0.827 to 0.875) and maternal breeding values (r_{rank}=0.221) and resulted in few top sires in common across models (5 to 7 sires). Ignoring r_{dm} reduced accuracy of direct and maternal breeding values by 21% and 14% and led to under- dispersion of estimated breeding values. The trend of weaning weight for improved calves increased significantly ($P<0.05$) by 0.5kg/ year while that of sires and dams remained constant over the study period (b = -0.58 kg/year to +0.26 kg/year). Inclusion of maternal genetic effects led to identification of the right superior individuals and also led to higher accuracy of estimated breeding values. Therefore, maternal genetic effects should be included in beef cattle evaluation when the direct-maternal genetic correlation is negative and strong.

5.1 Introduction

In beef cattle many traits of economic importance are influence by both direct and maternal genetic effects (Falconer & MacKay, 1996). Most of these traits are those expressed during the early stages of growth such as growth (weaning weight, pre-weaning daily gain) and pre-weaning survival (Eaglen & Bijma, 2009). Maternal effects are important since they reflect the mother's ability to provide a conducive environment for the offspring's survival and growth prenatal and post-natal until weaning (Eaglen & Bijma, 2009). Genetic evaluation models therefore account for direct and maternal genetic, maternal permanent environment and common environment effects (Mrode, 2014; Schaeffer, 2019). Such models are able to estimate breeding values for direct genetic and maternal genetic effects for selection decisions (Mrode, 2014). In most cases, maternal effects are included in the total merit for beef cattle to reflect the dam's abilities (ICBF, 2020; Institut de l'Elevage, 2020).

The relationship between direct and maternal genetic effects has been the subject of numerous studies. The two effects have been found to have negative and non-zero genetic correlations ranging from -0.02 to -0.31 (Panesa *et al.,* 2012), -0.53 to -0.62 (Lengyel *et al.,* 2004; Szabo *et al.*, 2012). Other studies reported values ranging from -0.59 to -0.76 (Martinez *et al.,* 2016) to -0.92 (Tilki *et al.,* 2008). The negative association between direct and maternal genetic effects is therefore expected to affect the relationship between direct and maternal breeding values as well as the genetic trend arising from selection on direct and maternal breeding values. Accurate estimation of the covariance and genetic correlation between direct genetic and maternal genetic effects require a large dataset (Meyer, 1992) with a pedigree depth of at least 3 generations of female data (Schaeffer, 2019).

Some studies ignore maternal genetic effects due to failure to approximate standard errors arising from overparameterization due to a small sample size (Khorshidi *et al.,* 2020; Meyer, 2018). When the covariance between direct and maternal genetic effects is small and the genetic correlation is not different from zero (-0.14 to +0.14) there is little or no effect sire ranking based on total breeding value (Bonifazi *et al.,* 2021a,b; David *et al.,* 2015) and can be ignored in genetic evaluations. However, the scenario should be different considering the medium to strong genetic r_{dm} ranging from -0.53 to -0.97 reported for various beef cattle populations (Martinez *et al.,* 2016; Szabo *et al.,* 2012; Tilki *et al.,* 2008). Ignoring strong direct-maternal correlation can lead to re-ranking of animals and reduction in accuracy of breeding values (Bonifazi *et al.,* 2021a). other studies found little or no effect on accuracy and magnitude of estimated breeding values when the direct-maternal genetic correlation is ignored (Bonifazi *et al.,* 2021b; David *et al.,* 2015). The present study therefore fitted a full model that included direct animal and maternal genetic and the covariance between direct and maternal genetic effects to weaning weight records in order to estimate the $r_{d,m}$. Breeding values were then estimated from the full models as well as from those which fitted either only the direct genetic effect or both the direct and maternal genetic effects but ignored the $r_{d,m}$. Rank correlations for sire, dam and calf for direct, and maternal EBVs for weaning weight. Therefore, the objective of this study was to evaluate the impact of direct-maternal genetic correlation on beef cattle genetic evaluation.

5.2 Materials and Methods

Weaning weight records, date of birth and weaning and pedigree data were obtained from the Livestock Recording Centre of the State Department of Livestock Production, Kenya, being performance of beef cattle from three beef ranches. The herds are Beef research herd at Lanet, Ol Pajeta beef ranch in Laikipia and Mugwoon beef ranch in Nanyuki, Kenya. The National Beef Research station is situated 150 km North West of Nairobi, while Ol Pajeta and Mugwoon ranches are situated Laikipia and Nanyuki Counties, respectively. These ranches maintain improved Boran cattle stud herds which are registered with the Kenya Stud Book and are members of the Kenya Boran cattle Breeders Society (KBCBS). The commercial ranches are located in agro-ecological zone (AEZ) IV, which is classified as arid and semi-arid land (ASAL). The National Beef Research Station is located in the transition zone of AEZ III to IV and receives an average annual rainfall of 800 mm. However, the animals are reared in AEZ IV in which all the grazing land is located. The rainfall pattern for the three herds is bimodal, with the long rains falling in March to June and the short rains occurring in September to October. The two rain seasons are separated by dry seasons. The hottest and the driest month in all the herds are January and February (Wasike *et al.,* 2006). Ol Pejeta ranch covers 90,000 acres (360km^2), it lies between Mt. Kenya and the Aberdare Mountains (0°7.288'N, 36°42.384'E and 0°8.634'N, 37°0.605'E) (0°1.831'S, 36°46.578'E and 0°5.7025'S 37°2.492'E), at an average altitude of 1810m, mean annual rainfall of 739mm, mean maximum and minimum temperatures of 28°C and 12°C respectively (Kavwele *et al.,* 2017). Mugwoon Ranch, lies between longitude 360 4’ West and 370 27’ East and between latitude 00 17’ South and 00 45’ North. The annual rainfall ranged from 600 to 900mm. The vegetation is predominantly Savannah with scattered acacia and shrubs (Njiru *et al.,* 2001).

An animal was included in the database if it had a record of weaning weight. In addition, the animal was required to have information on herd of birth, sex, date of birth and weaning and at least one of its parents known. After data cleaning and editing, a total of 15,259 animals with records of weaning weight being progeny of 4,404 and 375 sires from 3 herds which record with the Kenya Stud Book were available. Pedigree data were available for 18,600 animals born between 1974 and 2018 with a maximum pedigree depth of 8 generations. The data structure is given in Table 5.1.

Table 5.1: Summary of weaning weight data per herd

Herd	Male	Females	Total	Mean	Minimum	Maximum
Mogwooni Beef Ranch	5336	5308	10644	188.7	111	267
Ol Pajeta Ranch	1430	1341	2771	192.2	122	245
Beef Research Centre	936	908	1844	141.6	142	222
Total	**7702**	**7557**	**15259**	**179.6**		

The trend of weaning weight over the years and number of records per year of birth are shown in Figure 5.1

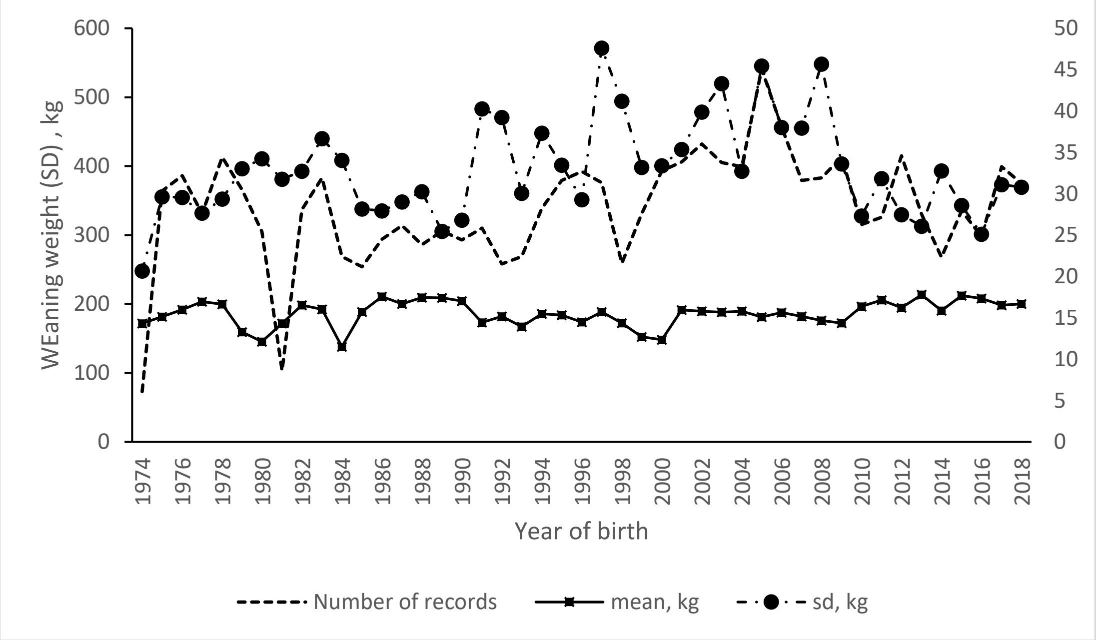

Figure 5.1: Trends of mean weight, standard deviation and number of records for weaning weight

5.3 Preliminary analysis

The Proc GLM of SAS version 9.4 (SAS, 2018) was used to identify effects that significantly influenced weaning weight. The effects in the final model were herd-year-season of birth, sex and dam weight at weaning. Age at weighing was fitted as covariate. The benefit of including maternal genetic effect and r_{dm} apart from direct genetic effect was evaluated using

Chi-square tests comparing the marginal change in the -2loglikelihood (-2LL) between adjacent models in order of complexity. For adjacent models the chi-square calculated was obtained as the different in the -2LL. This quantity was compared to the tabulated chi-square value at 95% level of confidence and degrees of freedom determined as the difference in the number of parameters. The model that resulted in the best fit of the data was the one that fitted maternal genetic and maternal permanent environmental effect as well as direct-maternal genetic correlation.

5.4 Estimation of genetic parameters for weaning weight

A univariate animal model was fitted to the data to estimate genetic and phenotypic variances and heritability estimates for weaning weight as:

$$\mathbf{y} = \mathbf{X\beta} + \mathbf{Za} + \mathbf{Mmg} + \mathbf{Wpe} + \mathbf{e}$$

where **y** is a vector of observations for weaning weight; $\boldsymbol{\beta}$ is a vector of fixed effects (sex=1,2; herd-year-season of birth= 1, 2 … 152), **a**, **mg**, and **pe** are vectors of random direct genetic, maternal genetic and permanent maternal environmental effects, respectively; **e** is a vector of random residual effects. **X**, **Z**, **M** and **W** are incidence matrices relating $\boldsymbol{\beta}$, **a**, **m**, and **pe**, respectively, to **y**. The assumptions of the model were:

$$\boldsymbol{E} = \begin{bmatrix} \boldsymbol{y} \\ \boldsymbol{a} \\ \boldsymbol{m} \\ \boldsymbol{c} \\ \boldsymbol{e} \end{bmatrix} = \begin{bmatrix} \boldsymbol{Xb} \\ \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \end{bmatrix};\ \boldsymbol{V}\begin{bmatrix} \boldsymbol{a} \\ \boldsymbol{m} \\ \boldsymbol{c} \\ \boldsymbol{e} \end{bmatrix} = \begin{bmatrix} \boldsymbol{G}\otimes\boldsymbol{A} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \boldsymbol{I_d}\otimes\boldsymbol{\sigma_c^2} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \boldsymbol{I_n}\otimes\boldsymbol{R} \end{bmatrix} \text{ and } \mathbf{G} = \begin{bmatrix} \sigma_{a}^{2} & \sigma_{a,mg} \\ \sigma_{mg,a} & \sigma_{mg}^{2} \end{bmatrix}$$

where **G**=matrix of genetic covariances between direct and maternal effects; **A** = the additive genetic relationship matrix; $\mathbf{I}_d$ and $\mathbf{I}_n$ = identity matrices of number of dams (d) and total number of observations (n); σ_a^2 =the direct additive genetic variance; σ_{mg}^2 = the maternal genetic variance; $\sigma_{a,mg}$ =the covariance between direct and maternal genetic effects; σ_{pe}^2 =the variance of maternal permanent environment; and σ_e^2 = the residual variance.

The variance-covariance for the direct and maternal genetic effects was:

$$\mathbf{var} = \begin{bmatrix} \mathbf{u} \\ \mathbf{m} \end{bmatrix} = \begin{bmatrix} \mathbf{G_{d,d}} & \mathbf{G_{d,m}} \\ \mathbf{G_{m,d}} & \mathbf{G_{m,m}} \end{bmatrix} \otimes \mathbf{A}$$

where u and m are vectors of random genetic and random maternal genetic effects, respectively. $\mathbf{G_{d,d}}$ and $\mathbf{G_{m,m}}$ are the direct genetic and maternal genetic covariances, respectively and $\mathbf{G_{d,m}}$($\mathbf{G_{m,d}}$) is additive genetic covariance matrix between direct and maternal genetic effects;

A is the numerator relationship matrix and ⊗is the Kronecker product. Breeding values were estimated using single trait animal model implemented in MTDFREML software (Boldman *et al.,* 2018).

To investigate the impact on breeding values of ignoring the direct-maternal genetic correlation, breeding values were estimated for the following scenarios:

i) The model fitted only direct genetic effects
ii) The direct-maternal genetic correlation was assumed to be zero i.e. $r_{d,m}=0$
iii) The direct-maternal genetic correlation was obtained from the data i.e. $r_{d,m}\neq 0$

Fitted this way, scenario 1 produced total breeding values while models 2 and 3 resulted in direct and maternal breeding values. For scenario 3, the breeding values were adjusted for $r_{d,m}$.

The effect of modelling $r_{d,m}$ on population accuracy ($\rho_{p,f}$) defined as the correlation between true breeding values (TBVs) and EBVs of individuals in a population was evaluated using the LR method of Legarra and Reverter (2018) as:

$$\rho_{p,f} = \frac{acc_p}{acc_f} = \frac{\left(\hat{\mathbf{u}}_\mathbf{p} - \bar{\hat{\mathbf{u}}}_\mathbf{p}\right)'\left(\hat{\mathbf{u}}_\mathbf{f} - \bar{\hat{\mathbf{u}}}_\mathbf{f}\right)}{\sqrt{\left(\hat{\mathbf{u}}_\mathbf{f} - \bar{\hat{\mathbf{u}}}_\mathbf{f}\right)'\left(\hat{\mathbf{u}}_\mathbf{f} - \bar{\hat{\mathbf{u}}}_\mathbf{f}\right)\left(\hat{\mathbf{u}}_\mathbf{p} - \bar{\hat{\mathbf{u}}}_\mathbf{p}\right)'\left(\hat{\mathbf{u}}_\mathbf{p} - \bar{\hat{\mathbf{u}}}_\mathbf{p}\right)}}$$

where $\hat{\mathbf{u}}_\mathbf{p}$ and $\hat{\mathbf{u}}_\mathbf{f}$ are vectors of animal's estimated breeding values obtained from partial and full model evaluations, respectively; acc_p is the population accuracy obtained with partial information and acc_f is the population accuracy with full information (Legarra & Reverter, 2018). The relative increase in accuracy when moving from partial to full model evaluation, $\Delta\rho$, was calculated as (Macedo *et al.,* 2020):

$$\Delta\rho_{ij} = \frac{acc_p}{acc_f} = \frac{1}{\rho_{p,f}}$$

where i=model with direct genetic effects only; j=model that fitted either maternal genetic effect and or direct-maternal genetic correlation.

The changes in the dispersion of EBVs between partial and full model evaluation, $\hat{\mathrm{b}}_{\mathrm{f,p}}$ was evaluated as the regression of $\hat{\mathrm{u}}_\mathrm{f}$ on $\hat{\mathrm{u}}_\mathrm{p}$ as:

$$\hat{\mathrm{b}}_{\mathrm{w,p}} = \frac{cov(\hat{\mathrm{u}}_{\mathrm{f,}}\hat{\mathrm{u}}_\mathrm{p})}{var(\hat{\mathrm{u}}_\mathrm{p})}$$

If $\hat{u}_w$ and $\hat{u}_p$ have the same dispersion the expectation of $\hat{b}_{w,p}$=1. $\hat{b}_{w,p}$>1 indicates less dispersion of $\hat{u}_p$ compared to $\hat{u}_w$, while a value <1 means that $\hat{u}_p$ has more dispersion compared to $\hat{u}_w$.

5.5 Results

The model fitting both direct and maternal genetic and their correlation resulted in the best fit (Table 5.2). Based on this full model, genetic parameters for weaning weight in Boran cattle in Kenya indicate that direct genetic variance accounted for 62% of the total variation, with maternal genetic effect being the second most importance cause of variation in Boran cattle in Kenya (Table 5.2).

Table 5.2: Estimates of genetic parameters of weaning weight for Boran cattle in Kenya

	Model		
Population parameter	**Model 1**	**Model 2**	**Model 3**
Direct genetic variance, σ_d^2	450.85±21.56	488.51±24.81	584.62±25.20
Maternal genetic variance, σ_m^2	-	9.6±9.80	42.12±32.77
Direct-maternal genetic covariance, $\sigma_{d,m}^2$	-	-	-129.22±43.93
Permanent environment variance, σ_{pe}^2	87.01	77.74±11.46	92.01±13.88
Residual variance, σ_e^2	621.04±16.09	448.82±16.72	349.42±39.92
Phenotypic variance, σ_p^2	984.38	984.67	938.95
Direct heritability, h_d^2	0.46±0.03	0.46±0.03	0.62±0.05
Maternal heritability h_m^2		0.01±0.01	0.04±0.02
Ratio of σ_{pe}^2 to σ_p^2	0.08±0.01	0.08±0.02	0.10±0.02
Direct-maternal genetic correlation, r	-	-	-0.82±0.11
-2LogLikelihood	118523.59	118522.88	118471.63

The direct heritability was high (0.62±0.05) and as such this trait could primarily be improved through selection on direct breeding values. The covariance between direct and maternal genetic effect was negative and the direct-maternal genetic correlation was strong and negative (-82±0.11).

From the results of breeding value of sires with a reliability ≥50%, large differences were exhibited between direct and maternal breeding values (Table 5.3). Due to the strong and negative direct-maternal genetic correlation, sires with positive direct genetic breeding values had negative maternal genetic breeding values and vice versa. The differences resulted in high and negative (-0.97) rank correlation coefficient between ranks of evaluated all animals with weaning weight records (-0.97) and sires (-0.99) on the basis of their direct and maternal breeding values.

Table 5.3: Direct and maternal breeding values and reliability of Improved Boran sires for weaning weight of their weaners

	Weaning weight, kg				
	Breeding value, kg			Reliability, %	
Sire ID	N	Direct	Maternal	Direct	Maternal
219	510	-32.62	15.79	74.6	38.2
279	345	-27.19	11.74	69.9	27.9
141	300	2.64	-0.35	68.1	36.5
157	258	-30.82	15.49	65.9	32.4
129	255	-12.42	8.32	65.3	25.9
254	232	-7.06	1.06	63.7	10.1
278	225	-4.03	3.04	62.7	2.4
294	223	-17.53	9.02	63.5	23.3
211	218	-16.83	7.55	62.7	16.7
169	210	-27.00	13.11	61.8	7.1
223	208	-14.58	6.48	62.4	20.5
82	188	-40.49	19.96	60.1	3.8
288	186	-1.93	0.80	60.2	10.0
48	166	-34.09	16.34	57.8	0.6
41	165	-24.45	11.80	58.1	11.3
153	165	31.35	-13.93	57.6	2.3
204	159	45.07	-21.07	58.1	18.7
271	159	-27.13	12.68	57.0	2.6

Genetic trends for sires and dams who were parents of the evaluated population and the population of animals with weaning weight records are shown in Figures 5.2 to 5.4. In Figure 5.2, the estimated breeding values for direct genetic and maternal EBVs did not change (P>0.05) during the study period.

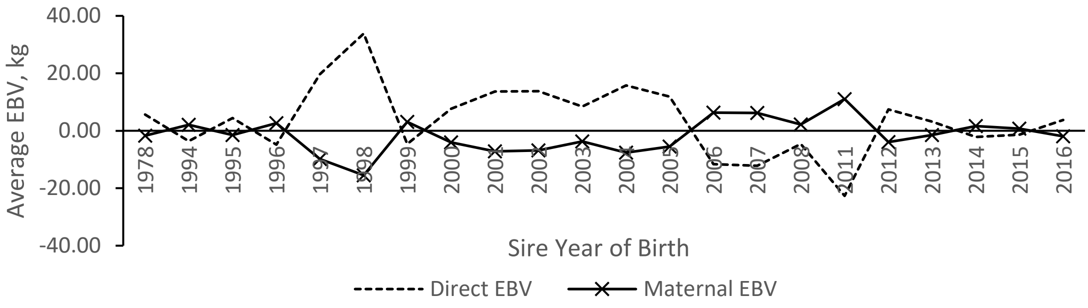

Figure 5.2: Genetic trend of weaning weight for direct and maternal breeding values of Boran Sires

The Figure 5.3 shows the trends for direct and maternal EBVs for dam. From this Figure, the dam's direct and maternal EBVs remained constant (P>0.05) over time.

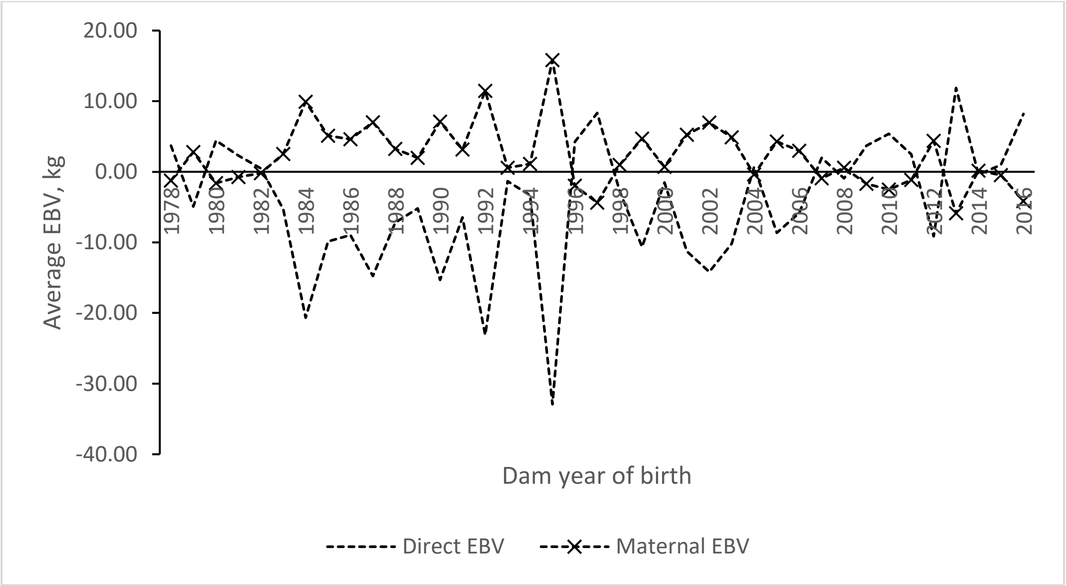

Figure 5.3: Genetic trend of weaning weight for direct and maternal breeding values of Boran Dams

The trends for direct and maternal EBVs of Boran calves are dislayed in Figure 5.4). Direct and maternal breeding values for the whole population displayed a significant (P<0.05) upward and downward trend, respectively (Table 5.4).

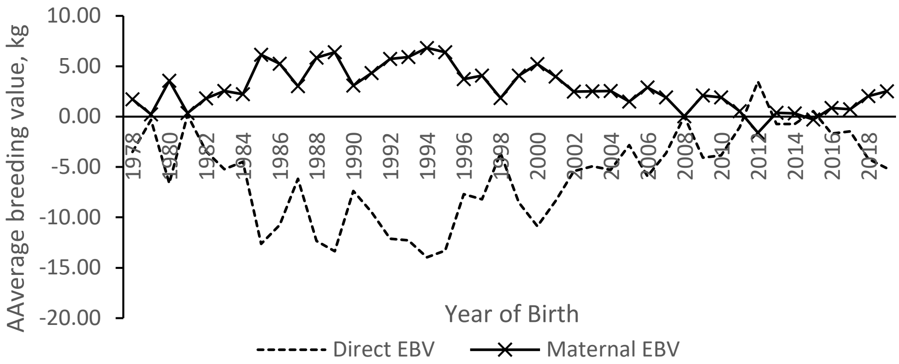

Figure 5.4: Genetic trend of weaning weight for direct and maternal breeding values of the whole population

Parameters obtained from linear regression show that the slope for direct and maternal breeding values for sires and dams was not different from zero, meaning that genetic progress was achieved in weaning for the period under study (Table 5.4). However, direct breeding values and maternal breeding values for evaluated animals significantly ($P<0.05$) increased and decreased, respectively (Table 5.4). This meant that while direct breeding values improved, maternal breeding values deteriorated in the study period.

Table 5.4: Genetic trends of sire, dams and the whole population for weaning weight in Boran cattle in Kenya

		Coefficient of slope		Y intercept		
		b	se	a	se	R^2
Sires	D_EBV	-0.58	0.24	+10.42	4.4	0.10
	M_EBV	+0.26	0.12	-4.58	2.9	0.08
Dams	D_EBV	+0.22	0.31	-8.99	1.9	0.08
	M_EBV	-0.11	0.15	+4.46	2.7	0.09
Whole population	D_EBV	+0.15*	0.05	-9.02	3.7	0.17
	M_EBV	-0.33*	0.12	4.40	1.3	0.19

*=Regression coefficient significant at $P<0.05$; D_EBV=direct estimated breeding value; M_EBV=maternal estimated breeding value; R^2=coefficient of determination

Using the full model as a point of reference (model fitting direct, maternal, and direct-maternal genetic correlation), significant re-ranking of animals based on direct breeding values occurred when maternal genetic and or the direct-maternal genetic correlation were ignored (Table 5.5). This was confirmed by the few numbers of common sires between scenarios

Table 5.5: Spearman's rank correlation of animal's direct (dir) and Maternal (Mat) estimated breeding values (EBV) between scenarios and number of top 10 sires selected in common between scenarios

	Between		**Top 10 sires**	
	Dir	Mat	Dir	Mat
Ref			0	0
None	0.827		6	-
Matg	0.875	0.221	7	5

The increase in population accuracy using was about 21% when moving from fitting direct genetic effects only to both direct and maternal genetic effects and their correlation (Table 6). The increase in population accuracy moving from g-mat to g-mat-cor resulted in an increase in accuracy of about 14% for maternal breeding values (Table 5.6).

Table 5.6: Accuracy ($\rho_{p,f}$), increase in accuracy ($\Delta\rho$) of moving from partial (p) to whole evaluation (f) and regression coefficients of EBVs of full (f) on partial evaluation (p)

	Effect	**p**	**f**	b	$\rho_{p,f}$	$\Delta\rho$
Increase in accuracy	Direct	None	g_mat		0.98	1.03
			G_mat_cor		0.83	1.21
		g_mat	G_mat_cor		0.88	1.14
	Maternal	g_mat	G_mat_cor		0	
Regression coefficient	Direct	None	g_mat	0.995		
		None	g_mat_cor	1.380		
		g_mat	G_mat_cor	1.384		
	Maternal		G_mat_cor	0.981		

None=model without maternal effects; g_mat=model with direct and maternal genetic effects; _mat_cor=model with direct and maternal genetic effects and direct-maternal genetic correlation

Regression coefficients of full model on partial evaluations for all animals are reported in Table 5.6. The regression coefficients $\hat{\boldsymbol{b}}_{\boldsymbol{f},\boldsymbol{p}}$ for direct EBVs of the model fitting direct genetic effects and that fitting direct and maternal genetic effects was about 1. Regression coefficients of the model fitting direct genetic effects and those with maternal-genetic correlation were >1, indicating that models that ignored $r_{d,m}$ resulted in direct EBVs with less dispersion compared to full evaluation. Maternal EBVs of the partial model had similar dispersion (b=1) as those from the full model.

5.6 Discussion

Direct and maternal heritability estimate for weaning weight for Boran cattle in this study are similar to those reported for Limousine cattle (Szabó *et al.,* 2021), Nellore (Chud *et al.,* 2014) and beef cattle (Koury Filho *et al.,* 2010). Lower estimates of direct heritability for weaning weight have been reported for Limousin and Limousin-Angus crossbred cattle (Lucaszewicz *et al.,* 2015) and crossbred beef cattle (Crews *et al.,* 1999), yearling cattle (Boligon *et al.,* 2018) and Brahman cattle (Martinez *et al.,* 2016). In conformity with previous studies, this study confirmed that genetic effect on weaning weight of beef calves is equally important as environmental effect. Maternal heritability value for Boran cattle of 0.04 was lower than that reported by Kaps *et al.* (2000) and Szabó *et al.* (2021) of 0.29. The high direct heritability estimate for weaning weight indicate the potential for genetic improvement through selection in the studied population

The direct-maternal genetic covariance in the present study is similar to those reported by Szabó *et al.* (2021). The resultant strong and negative genetic correlation coefficient between direct and maternal genetic effects was higher than the reports of Martinez *et al.* (2016), Penasa *et al.* (2012) and Szabo *et al.* (2021). This indicates a negative relationship between direct and maternal genetic effects. Ignoring direct-maternal genetic correlation resulted in limited re-ranking for direct breeding values and substantial re-ranking for maternal breeding values and caused a decline in accuracy of direct EBVs of up to 21%. For Interbeef beef cattle international evaluation in Europe, Bonifazi *et al.* (2021a) reported limited impact on accuracy from ignoring $r_{d,m}$. This study reported an increase in accuracy of between 0% to 8% which is lower than the 3% to 21% reported in the present study. This could be due to the higher $r_{d,m}$ reported in the present study (-0.82) that that of Bonifazi *et al.* (2021b) of -0.14. Similar re-ranking when considering impact of fitting or not fitting direct-maternal genetic correlation has been reported for European beef cattle (Bonifazi *et al.,* 2021a). The increase in accuracy for maternal EBVs of 14% was similar to that reported by David *et al.* (2015). This indicated that the direct-maternal genetic correlation has greater impact on maternal EBVs since they are obtained from offspring performance as compared to direct EBVs. Direct genetic variances are usually greater than maternal genetic variances (David *et al.,* 2015), contributing to direct-genetic correlation having a greater impact on maternal EBVs. Bonifazi *et al.,* (2021a) reported that ignoring direct maternal correlation had little impact on re-ranking for direct than for maternal EBVs, because for young sires, their weaning weight record is available early in life, while his progeny records are available later in life.

Early growth traits are influenced by maternal effects in beef cattle (Bignardi *et al.,* 2024; Bonifazi *et al.,* 2021b). A strong maternal influence as also been reported even in later life (Mandal *et al.,* 2006). The maternal effect is due to general fixed effects and animal-specific effects analysed as random effects. The fixed effects include the age of the dam, season of calving and dam's body weight which affect the all the offsprings of das in the same classification the same way (Romé *et al.,* 2023). Animal-specific effects include the genetic and permanent environmental maternal effects only affect the offspring of a given dam. Therefore, ignoring maternal effects in genetic evaluation of early growth traits leads to bias in estimation of breeding values by inflating the EBVs and a reduction in estimation accuracy (Bonifazi *et al.,* 2021b; Romé *et al.,* 2023). The Kenya Boran is raised under arid and semi-arid land (ASAL) conditions either under ranching or pastoral production systems (Rewe *et al*., 2006), in these conditions the calves are allowed to run with the dam until weaning. Inclusion of maternal effects in genetic evaluation of the Kenya Boran is therefore expected to have a positive impact on the breeding programme through improvement in accuracy of superior animals.

5.7 Conclusion

The goal of the breeding program of the Kenya Boran cattle is select heavy animals at maturity. Genetic effects were more important (h_d^2 =0.54±0.03 and h_m^2 =0.2±0.02) in determining weaning weight than environmental effects (c^2=0.07±0.01). The direct-maternal genetic correlation was strong and negative (-0.82±0.11). The spearman's rank correlation between direct and maternal breeding values was high and negative (r_{rank}=0.98; P< 0.01). Ignoring direct-maternal genetic correlation led to significant re-ranking of animals based on direct (r_{rank}=0.827) and maternal breeding values (r_{rank}=0.221) resulting in few top sires in common across models (5 to 7 sires). Ignoring r_{dm} led to loss of accuracy of breeding values by up to 21% and under- dispersion of estimated breeding values. The trend of weaning weight for improved calves increased significantly (P<0.05) by 0.5kg/ year indicating genetic improvement due to selection. The negative $r_{d,m}$ points to the importance of maternal genetic effect and should be considered when selecting for weaning weight in beef cattle

CHAPTER SIX

GENRAL DISCUSSION, CONCLUSIONS AND RECOMMENDATIONS

6.1 Aim of the study

A high proportion of input costs in beef production is associated with feeds and pasture hence improvement of feed efficiency can have a big impact on profitability (Kenny *et al.,* 2018; Larson, 2010). Animals with high Kleiber index or relative growth rate are more efficient (lower feed intake) and have similar growth as those with low KI and RGR (Basrab *et al.,* 2003). KI was defined as the ratio of average daily gain to metabolic body weight while RGR is the log of average daily gain multiplied by 100 (Matos *et al.,* 2019). For the feed efficiency measures to be used as selection criteria in commercial beef production, there should not exist antagonist effects on other traits of economic importance in beef cattle such as reproduction, carcass and growth traits. This is especially so because the profitability of cow-calf systems largely depends on carcass yield and the reproductive process (Dickerson, 1970). Juvenile growth traits such as weaning weight have a strong indication on subsequent growth and reproductive performance in beef cattle (Zeleke *et al.,* 2016) and have been used as selection criteria to improve meat production due to their strong genetic association with mature body weight (Pires *et al.,* 2016; Tesafa & Garikipati, 2014).

The Kenya Boran breed preferred beef producers and pastoralists because of its superior growth and fertility compared with other indigenous breeds and high adaptive performance compared with exotic beef breeds (Wasike *et al.,* 2009). The breed is therefore utilised in crossbreeding programmes many countries including Kenya, Ethiopia, Australia and South Africa (Haile *et al.,* 2011). In these programmes, The Kenya Boran has shown exemplary heterosis (Haile *et al.,* 2011). Additionally daughters of Boran sires rank highly compared to those sired by Brahman and Tuli breeds in terms of fertility and maternally influenced traits as well as longevity (Muntean, 2011).

Evaluation of growth performance is therefore essential in designing selection programmes for beef cattle. Heavy mature weights are usually associated with higher feed intake, this notwithstanding the fact that feeds comprise a significant proportion of the cost of production. Animals with high feed requirements are also associated with higher methane gas emissions, especially in extensive grazing systems. There is lack of knowledge of genetic parameters of feed efficiency traits and their genetic correlation with growth and other traits. This has hampered their inclusion in the selection criteria and breeding goal of beef cattle improvement programmes in the tropics. This study aimed at estimating the genetic parameters of feed efficiency traits and their correlation with growth traits. The study had three objectives namely: (i) to estimate genetic parameters for feed efficiency traits, (ii) to evaluate the effect of maternal genetic effect on selection for weaning weight when the direct-maternal genetic correlation is strong and negative and (iii) to estimate the genetic correlations between feed efficiency and growth traits. This study was conducted to answer three research questions namely: (i) what are the genetic parameters for feed efficiency traits in improved Boran cattle in Kenya? (ii) what is the effect of maternal genetic effect on selection for weaning weight when the direct-maternal genetic correlation is strong and negative? And finally (iii) what are the genetic correlations between growth and feed efficiency traits in improved Boran cattle in Kenya?

6.2 Study methodology

In the first objective, feed efficiency traits, Kleiber Index and relative growth rate as well as average daily gains at weaning, yearling and 50 days were derived from body weight records of beef cattle reared in three farms. In terms of derivation of the feed efficiency traits, Kleiber index is defined as the ratio of rate of gain to metabolic body weight, while RGR obtained as the logarithm of rate of daily gain multiplied by 100. Average daily gains were obtained by dividing the difference between consecutive body weights by the interval in days. For objective one, a univariate animal model fitting maternal genetic effect where necessary was fitted to each of the traits to obtain genetic variation and genetic parameters (direct heritability, maternal heritability and direct-maternal genetic correlation where applicable). For objective two a full animal model i.e. fitting direct, maternal genetic, direct maternal genetic covariance and permanent environment effect due to dam was fitted to estimate direct and maternal genetic breeding values. The failure to consider maternal breeding values on selection was considered in terms of change of accuracy of selection and ranking of selected animals. In objective three, genetic correlation between feed efficiency (Kleiber index and relative growth rate) and growth traits were estimated using a 7-trait animal model. All the parameters were estimated via Bayesian inference in THRGIBBSF90 Software. This software implements gibbs sampler for mixed threshold-linear models with multiple categorical and linear traits (Aguilar *et al.,* 2018).

6.3 Direct response for feed efficiency and growth traits

In the present study, the heritability estimates for pre-weaning daily gain, yearling, 550-day weight and weaning weight of 0.05, 0.05, 0.10 and 0.45, respectively, were low to moderate, suggesting that growth traits in beef cattle can be improved through selection.

However, a significant outcome of selecting for growth traits is the undesirable correlated effect this has on other traits of economic importance such feed efficiency and reproductive traits. The results of genetic correlations between growth and feed efficiency traits reported in this study show that selecting for weight at weaning or yearling would lead to less efficient individuals at any stage of life considered in his study. This implies that the result is a population of heavy animals that have high feed intake. Considering the fact that feed cost is the single most important cost element in beef cattle enterprises (Kenny, *et al.,* 2018) there is need to consider strategies to bring it down. A selection index that utilises balanced selection for EBVs of multiple traits in a breeding objective should be implemented to ensure the antagonisms found in the current study do not limit genetic progress in growth and feed efficiency traits.

Residual feed intake (RFI) (Callum *et al.,* 2018), feed intake (FI) (McNeil *et al.,* 2013) and Feed conversion efficiency (FCE) (Hendriks *et al.,* 2021) have been used to measure feed efficiency in beef cattle because they are not directly related to growth rate and liveweight. However, these traits require records on individual animal feed intake, resulting in increased cost associated with feed intake recording (Robinson & Oddy, 2004). On the other hand, Kleiber Index and residual growth rate do not require additional recording since they utillize already existing information and also provide insights on animal energy metabolism (Kleiber, 1936). The heritability estimates for KI and RGR for the improved Boran cattle at weaning (0.12 and 0.21, respectively), at yearling (0.29 and 0.24, respectively) and at 550 days (0.21 and 0.31, respectively) were moderate. Similar low to moderate heritability estimates were reported in other beef cattle populations (Matos *et al.,* 2019; Mehrban *et al.,* 2021) and present an opportunity to improve feed efficiency in the improved Boran cattle through breeding. KI and RGR as measures of feed efficiency are derived from body weight measurements at specific ages. Therefore, the extend of genetic variation and magnitude of genetic parameters will be population or herd/environment specific. This may be explained by the range of heritability estimates for KI (0.12 to 0.55) and RGR (0.28 to 0.55) reported for different cattle populations (Kasahun *et al.,* 2022; Matos *et al.,* 2019; Merhban *et al.,* 2021; Rezende *et al.,* 2024). As such every breeding programme requires specific estimates derived from data obtained from within.

6.4 Consequences of selecting for feed efficiency on other traits of economic importance

In beef cattle breeding programmes, it is desirable to improve feed efficiency without adverse effects on other traits. The results of the current study showed that feed efficiency traits have sufficient genetic variation, indicating that selecting directly for these traits would lead to an improvement in feed efficiency. Based on the results, selection of KI365 would have a desirable effect on ADG205-365 since the genetic correlation between the two traits was moderate (0.31). The result is selecting dams with high feed efficiency and good weight gain, without increasing W365 and consequently W550 since it is important to avoid having heifers or cows with high genetic merit for adult weight. The strong negative correlation between KI365, RGR365 and W365 (-0.52 and -0.82) imply that selection for any of the feed efficiency traits would result in a decline in body weight in heifers and cows. Whereas, in beef cattle heavy mature weights among heifers and cows is not desirable, the other extreme is also not accepted. Low weights of cows and heifers would negatively affect the weight of the calf crop. Studies which quantified the effect of selecting for KI and or RGR include Matos *et al.* (2018) and Mehrban *et al.* (2021). The study by Matos *et al.* (2018) found that KI was not a viable selection criterion for bulls and cows for Brazilian Brahman cattle due to the antagonist genetic correlations between body weight and KI at different ages. On the other hand, Mehrban *et al.* (2021) reported that KI and or RGR could be included in the breeding programme without having adverse effects on carcass traits in in the Hanwoo cattle.

A number of studies have quantified the outcomes of selecting for feed efficiency on fertility traits. Improvement of RFI was shown to lead to a 5-day increase in age at first calving in cows and a delay in attainment of puberty (Artur *et al.*, 2005; Basarab *et al.*, 2007; Basarab *et al.*, 2011; Mu *et al.*, 2016). This is so because selection at weaning or yearling during pubertal growth the energy requirements of animals increase by 4% to 5% due to sexual development, and therefore late maturing individuals are favoured (Basarab *et al.*, 2011). In another study, Schaffer *et al.* (2011) showed that a unit increase in feed efficiency led to a delay in age at puberty by about 8 days, suggesting that animals with high feed efficiency were associated with late reproductive maturity. A remedy to this could be to delay selection to about 14 months of age or older to avoid the negative bias towards later maturing animals due to the increased energy requirements at puberty.

6.5 Implications for beef cattle breeding programmes

Beef cattle especially those reared under extensive grazing systems are not efficient converters of feed to meet, hence the current interest to improve feed conversion efficiency (Kenny *et al.*, 2018). The present study has shown that it is feasible to select for feed efficiency (KI or RGR) as indicated by the reported heritability estimates. Inclusion of feed efficiency traits has been shown to reduce feed intake by up to 18% (Lancaster *et al.*, 2009). As feed conversion efficiency improves the emission of methane gas is reduced by close to 30% (Nkruma *et al.,* 2007). This is an outcome that fits well with the current global agenda to combat the menace of climate change through reducing emissions of greenhouse gases of which methane is key. Hence inclusion of KI or RGR in beef cattle selection programmes can be considered as a mitigating strategy.

Kleiber index and relative growth rate a derived from growth records which are routinely kept in most beef cattle enterprises and as such makes their utilization attractive because there is no added cost. From a cost perspective, this is an important advantage compared to other feed efficiency traits such as FI, RFI, and FCR which require individual animal records on feed intake (Elolimy *et al.,* 2018; Kelly *et al.,* 2020). The addition of extra cost associated with individual animal feed measurements being undesirable, especially to breeding programmes in the tropics where even basic performance recording is greatly constrained (Wasike *et al.,* 2011). Despite being cheaper, more practical and easier to derive, selection for KI or RGR is expected to yield more or less similar results in terms of improving feed efficiency due to the relatively strong and negative (favourable) genetic correlations with for example FCR (Arthur *et al.,* 2001; Hoque *et al.,* 2009).

6.6 Construction of a selection index

Similar to the results of selecting for feed efficiency on body weight and weight gain found in the present study, other authors have reported conflicting and antagonistic results. For instance, the study by Matos *et al.* (2018) found high and positive genetic correlations between KI at 205 and 550 days and weights at 365 and 550 as well as most associated growth rates (0.43 to 0.99). This study therefore argues that selection for KI and body weight will essentially select the same animals. The selected animals will have high feed efficiency as well as heavy body weight at maturity, an aspect that is not desirable for beef heifers and cows. Merhban *et al.* (2020) outcome is than the selected argued that selection of dams would work well if done after one year of age. Mu *et al.* (2016), Basarab *et al.* (2011) and Shaffer *et al.* (2011) found that fertility traits such as days to calving were affected negatively by selecting feed-efficient animals whereas Callum *et al.* (2019), Donoghue *et al.* (2011) and Basarab *et al.* (2007) reported lack of negative effects on fertility. Overall, and especially for the improved Boran beef cattle, inclusion of feed efficiency in the breeding goal is possible due to the genetic parameters (heritability and correlations) provided by the current study. The adverse effect of growth traits on feed efficiency and vice versa can be dealt with by developing a selection index that weights each of the traits appropriately.

The negative direct-maternal genetic correlations indicate antagonistic pleiotrophy and can restrict response to selection and maintenance of genetic variation. Simulation studies have shown that a strong direct-maternal genetic correlation may also be as a result of data structure or failure to account for sire by herd interactions (Eler *et al.,* 2000). The estimate may also be biased if the dataset contains a high proportion of dams without records (Heydarpour *et al.,* 2008). However, assessing the r_{dm} in actual livestock populations is more complex due existence of data source bias (Bignardi *et al.,* 2024). The assessment of the r_{dm} requires large dataset on dams and grand dams. This encompasses the number of dams with records, progeny records per dam and data recorded across multiple generations (Boligon *et al.,* 2012; Maniatis & Pollot, 2003). Maternal genetic effects also need to be disentangled from maternal permanent environmental effects (Maniatis & Pollot, 2003). The data from the present study was obtained from three herds in Kenya. Thought the pedigree was deep at a maximum of 8 generations, the size of the number of animals with records of weaning (15,259) and dams with progeny record (4,404) may have contributed to the strong and negative rdm of -0.82±0.11

6.7 General conclusions

1. Feed efficiency traits have moderate heritability and therefore have potential for improvement through direct selection
2. Weaning weight has high heritability estimate and is the direct-maternal genetic correlation is high and negative
3. The genetic correlations between growth and feed efficiency traits were unfavourable and selection for growth traits would result in decline of feed efficiency

6.8 General recommendations

1. Feed efficiency traits should be included in the selection criteria of the improved Boran cattle
2. Selection of animals for weaning weight should be based on an index that include direct and maternal breeding values
3. A weighted selection index that comprises growth and feed efficiency should be developed to ensure balanced results of selection

6.9 Recommendations for further studies

Further studies are needed on the correlated response on feed efficiency due to selection on growth traits as well as derivation of economic values for feed efficiency traits

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APPENDICES

Appendix A: Genetic parameters for weaning weight from model 1

```
 Started 19:04:11.74 on 05/24/2022
+++++++++++++++++++++++++++++++++++++++++++++++++++++++++++++++++
++++++++++++++
        PROGRAM "MTDFRUN"  - Estimate Covariance Components for MT-IAM
                         Last revised          8/         31/          0
+++++++++++++++++++++++++++++++++++++++++++++++++++++++++++++++++
++++++++++++++
 Cold start, i.e., not a continuation of previous run
 Run option 1: iterate for variance components
 0 constraints imposed by user
 (Co)variances in model:
  No. in likelihood calculation              =       3
  No. to be held constant                    =       0
  No. to be maximized                        =       3
 Starting values for this run:
 G matrix:
  500.0
 C matrix:
  100.0
 R matrix:
  300.0
********** UNIVERSITY OF WATERLOO
    ********** SPARSE MATRIX PACKAGE
    **********  ( S P A R S P A K )
    **********      RELEASE   4
    **********      July 2000
  ** reordering called **
  ** reordering completed **
 The elapsed time was: 00:00:18.11

  ** solve5 called **
  ** solve5 completed **
 The elapsed time was: 00:00:01.66
      SPARSPAK-A statistics. .
        Time:
         Ordering       =    17.750 secs.    (    .296 mins.)
         Total/solution  =      .586 secs.    (    .010 mins.)
           Allocation    =      .258 secs.    (    .004 mins.)
           Factorization =      .320 secs.    (    .005 mins.)
           Solve         =      .008 secs.    (    .000 mins.)
        Storage:
         No. equations                  =     23044
         Non-zero hs elements in MME    =    336990
         Sparsity of MME                =      .118%
         Maximum storage required       =   532892.   (   4.066  MB  )
         Size of storage array (MAXSA)  =   6250000   (   8.526% used)
 *******  RESULTS FROM SIMPLEX *******
```

```
 OPTIONS SET FOR THIS RUN:
 MAXIMUM NO. OF SIMPLEX ITERATES ALLOWED        =    300
 MINIMUM VARIANCE OF FUNCTION VALUES IN SIMPLEX  =   .1000000000E-05
 RESULTS FOR THIS RUN:
 NO. OF SIMPLEX ITERATIONS CARRIED OUT          =     30
 NO. OF LIKELIHOODS EVALUATED                  =     59
 NO. OF NON-PERMISSABLE PARAMETER VECTORS       =      0
  No. of failed contractions                  =      0
  Variance of simplex function values           =   .5728301438E-06
    Convergence criterion attained
 Final Simplex: (++ best L; *** parameter held constant)
   1     118523.5926      451.4970   87.0954  446.4249
++ 2     118523.5908      450.8471   87.0105  446.5238
   3     118523.5914      450.9999   86.7820  446.7576
   4     118523.5915      449.3375   86.9641  448.0151
 -2 log L =   118523.5908418090   ( 2)      Var =        .0000005728
  Large Sample Variances of Variance Estimates
  Half-store elements of AI inverse
          1          1     1273.112304347534000
          1          2      -39.714711301943030
          1          3     -886.399037562902800
          2          2       61.060329391526010
          2          3  -9.995877931717487E-001
          3          3      720.877620788896100
          0 Constraints:
 Estimates:
 GENETIC VARIANCES AND COVARIANCES :
            a1
   a1 :   450.84712
 UNCORRELATED RANDOM VARIANCES AND COVARIANCES:
             T1 C2
 T1 C2 :    87.0105
 ENVIRONMENTAL VARIANCES AND COVARIANCES :
            e1
   e1 :   446.52384
 PHENOTYPIC VARIANCES AND COVARIANCES :
            p1
   p1 :   984.38149
HERITABILITIES AND GENETIC CORRELATIONS
            a1
   a1 :     .46
         ( .032)
 UNCORRELATED RANDOM EFFECTS
 PROPORTION OF TOTAL VARIANCE ON DIAGONALS, CORRELATIONS ON OFF
DIAGONALS
 T1 C2
 T1 C2 :   .88E-01
             ( .008)
ENVIRONMENTAL PROPORTION OF TOTAL VARIANCE  AND CORRELATIONS
            e1
```

```
  e1 :     .45
        ( .031)
Files written:
  MTDF4   (ascii): Parameter file (IUN5) for "cold" restart
  MTDF54  (ascii): Last simplex
  MTDF58 (binary): SPARSPAK reordering
  MTDF59  (ascii): Constraints imposed
  MTDF68  (ascii): Likelihoods by rounds
  MTDF67  (ascii): Sampling variances if requested
  MTDF72  (ascii): Predicted BVs and PEVs if requested
  MTDF76  (ascii): Program log file
  MTDF77  (ascii): Solutions for covariates and fixed effects if requested
  MTDF78  (ascii): Solutions for trait within animal if requested
  MTDF79  (ascii): Solutions for independent random effects if requested
  The current time is:  19:06:46.65
  Total time of analysis
The elapsed time was: 00:01:37.57
```

Appendix B: Abstract of conference presentation

Genetic parameters for feed efficiency and growth traits for boran cattle in Kenya

Majoya, A. A[1]., Khobondo, J.O[1], Tura, S[2] and Muasya, T.K[1]

[1]Department of Animal Sciences, Egerton University, P.O. Box 536-20115, Nakuru, Kenya

[2]Beef Research Centre, Kenya Agricultural and Livestock Research Organisation, Nakuru, Kenya

Abstract

The aim of this study was to evaluate the effect of fixed factors on measures of feed efficiency and estimate genetic parameters for measures of feed efficiency for the Boran cattle in Kenya. A total of 1348 records of birth weight and weaning weight were used to derive pre weaning measures of feed efficiency. the traits derived were pre-weaning daily gain (ADG), weaning weight adjusted to 205 days (WA205), Kleiber Index at 205 days (KI205), relative growth rate (RGR). The fixed effects model included effects of sex, parity, year-season of birth or weaning and dam weight at weaning. A maternal genetic effects model was fitted to estimate the genetic parameters for the traits. All fixed effects except parity and dam age at weaning significantly influenced the studied traits. Direct heritability estimates for W205, kg, ADG, kg/day, KI205, kg/kg$^{0.75}$, RGR were 0.05±0.02, 0.27±0.02, 0.13±0.02 and 0.21±0.02 while the maternal heritability estimates were 0.04±0.02, 0.29±0.02, 0.10±0.02 and 0.23±0.02, respectively. The genetic correlations between direct and maternal genetic effects for the traits were -0.18±0.05, -0.30±0.04, 0.9±0.05 and -0.72±0.04, respectively. This study has for the first time provided genetic parameters for measures of feed efficiency for the improved Boran cattle in Kenya. The parameters can be used to incorporate the traits in the selection programmes with an aim of reducing the cost of feed leading to improved profitability and sustainability of beef cattle enterprises and also as a mitigation strategy to the climate change.

Key words: climate change; greenhouse gases, kleiber index, relative growth rate

Appendix C: Research permit

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Appendix D: Abstract of published journal paper

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Majoya AM
Department of Animal Sciences, Egerton University, PO Box 536-20115, Nakuru, Kenya

Khobondo JO
Department of Animal Sciences, Egerton University, PO Box 536-20115, Nakuru, Kenya

Tura S
Beef Research Centre, Kenya Agricultural and Livestock Research Organisation, Nakuru, Kenya

Muasya TK
Department of Animal Sciences, Egerton University, PO Box 536-20115, Nakuru, Kenya

Genetic variation and parameters for growth and feed efficiency traits in Boran beef cattle in Kenya

Majoya AM, Khobondo JO, Tura S and Muasya TK

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Abstract
A major drawback of improving feed efficiency in beef cattle enterprises is to identify measures of feed efficiency which do not require feed intake information on an individual animal basis. Kleiber Index, (KI) and relative growth rate (RGR) are alternative measures which do not need individual measurement of intake and can be used select for improved feed and growth efficiency in relation to their body size. The aim of this study was to estimate genetic parameters for measures of feed efficiency and growth traits for the Boran beef cattle in Kenya. A total of 1348, 2209, 2183 and 2184 weight records were available for birth, weaning, yearling and 550-day weight records, respectively, were available for animals born between 1973 and 2019. The traits derived were growth rates (ADG), adjusted weights (WA), KI and RGR at weaning (205 days), yearling (365 days) and 550 days. Genetic parameters were estimated using a maternal genetic effects model. Direct heritability estimates for direct heritability estimates for ADG ranged from 0.12±0.04 for ADG205-365 to 0.27±0.02 for ADGB-205. Estimates for WA were in range of 0.05±0.05 at to 0.10±0.05 at 550 days. Estimates for KI were 0.13±0.05 at 205 to 0.29±0.05 at 550 days. For RGR estimate direct heritability at 205 was 0.21±0.05, 0.19±0.04 at 365 and 0.33±0.05 at 550 days. The direct-maternal genetic correlations for WA, ADG, KI and RGR at 205 days were -0.30±0.05, -0.30±0.04, 0.90±0.05 and -0.72±0.04, respectively. Alongside growth traits, Kleiber Index and residual growth rate had substantial heritability estimates, implying potential for improvement through selection.

Keywords: Climate change, greenhouse gases, kleiber index, relative growth rate

Introduction
Feed provision in beef cattle enterprises is a major economic factor influencing the profitability of beef enterprises since feeds account for up to three-quarters of total direct costs (Kenny *et al.*, 2018) [14]. A strategy that is increasingly being adopted to reduce feed cost is to improve feed efficiency through selection (Matos *et al.*, 2019) [17]. Generally, feed efficiency is defined as the ratio between product (product) and feed intake (costs) in the form of mass or energy value of product per kilogram of dry matter intake (DMI) (Lovendahll *et al.*, 2018) [16]. Feed efficiency related traits have been shown to have low to medium heritability, meaning that animals that can efficiently make use of feed resources for reducing feeding costs and improving feed efficiency can easily be identified (Mehrban *et al.*, 2021) [18].