THE GENETIC PROPERTIES OF MATURE WEIGHT AND ITS RELATIONSHIP WITH EARLY GROWTH TRAITS IN BONSMARA BREED

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PREFACE

This research was conducted to provide information on the effect of selection practices on mature weight for South African Bonsmara cattle breed over the past two decades. This dissertation is divided into four chapters. The first chapter comprises of an introduction summarizing the general background of the Bonsmara breed in South Africa, the problem statement as well as the objectives of this research. The second chapter entails the literature review on genetic parameters of mature weight and early growth traits for Bonsmara and other beef breeds. The third chapter is dedicated to the methodology and statistical analysis employed in this study. Lastly, the fourth chapter presents the results and discussions of genetic parameters of early growth traits and mature weight; genetic trend of mature weight and the correlated responses to selection for mature weight.

DECLARATION

I, Sibusiso Alfred Hadebe, hereby declare that the research dissertation entitled "The genetic properties of mature weight and its relationship with early growth traits in Bonsmara breed" submitted to the North–West University in fulfilment of the requirement for Master degree in Agriculture in Animal Science, is my original work and is not submitted to any other university.

Student signature______________ Supervisor signature______________

Date_________________________ Date______________________

ABSTRACT

This study was conducted to evaluate genetic parameters for mature weight and its relationship with early growth traits, to determine whether the recent breeding programs which are directed at improving early growth traits have resulted in an undesirable correlated response in mature weight for the Bonsmara cattle in South Africa. Traits studied were birth weight (BWT), weaning weight (WWT-205days), yearling weight (YWT-365days), 18 month's weight (EWT-550days) and mature weight (MWT). MWT was estimated from cow weight using the Brody's growth curve and also from repeated weight measurements taken between the ages of 3 to 10 years. Contemporary groups for all traits were formed based on the herd, year and season of birth. Only contemporary groups comprising of a minimum of 8 sires were kept. Animals born as a single and reared on suckling of their own dams were considered.

The final dataset consisted of a total of 105 520 pedigree identities and performance records with 69 514 progenies born between the year of 1982 and 2006 over 6 generations. The (co)variance components for all traits were estimated by ASREML, using a single and multi-trait animal models; and in addition, the repeatedly measured MWT was analyzed using a repeatability model. The log likelihood ratio test indicated that accounting for maternal effects provided a good fit for all pre-weaning traits. Therefore, random effects fitted were; additive genetic for all traits, maternal genetic for all pre-weaning traits, direct-maternal genetic covariance for BWT, and permanent maternal environment for WWT. For analysis of MWT using the repeatability model, the direct genetic and permanent environmental effects were fitted as random effects. Direct heritability estimates from the univariate analysis for BWT, WWT, YWT, EWT and asymptotic MWT were 0.49±0.018, 0.43±0.013, 0.51±0.017, 0.55±0.02 and 0.51±0.064, respectively. Maternal heritability estimates were 0.11±0.012 and 0.06±0.011 for BWT and WWT, respectively. The direct heritability estimates obtained from the multi-trait model were slightly higher than the estimates obtained from the univariate analyses. The heritability estimate for MWT from the repeatability model was 0.40±0.04. The repeatability coefficient estimated for

MWT was 0.54±0.01. The direct genetic correlation estimates between MWT with BWT, WWT, YWT and EWT were 0.60±0.047, 0.54±0.051, 0.60±0.055 and 0.66±0.053, respectively. The realized genetic trends for BWT, WWT, YWT, EWT and MWT were -0.002±0.003, 0.15±0.02, 0.051±0.025, 0.094±0.026 and -0.095±0.094 kg per year, respectively. All trends were positive and significant except for BWT and MWT.

Using the estimated genetic correlations between early growth traits and MWT with the realized genetic trend in early growth traits, the expected correlated response in MWT was 0.22, 0.06, 0.1 kg/year for the selection emphasis given to WWT, YWT and EWT, respectively. In practical terms, these values are not far from the non-genetic trend observed for MWT. On the other hand, if the selection intensity on early growth traits would have been higher, say retaining top 5% or 10%, the predicted correlated response in MWT indicate that there would be a change ranging from 5.3 to 7.8 kg per generation. These results indicate that there is a potential to cause a significant change if intensive selection is applied on individual early growth trait without taking into consideration correlated response. Therefore, future genetic improvement programs of the Bonsmara cattle should consider a multi-trait index selection that prioritizes breeding objectives with constraints on traits that have a negative impact on production efficiencies, such as BWT and MWT.

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LIST OF ACRONYMS AND ABBREVIATIONS

BCS : body condition score

BLUP : best linear unbiased prediction

BWT : birth weight

E(CR) : estimated correlated response

EBV : estimated breeding value

EWT : eighteen-month weight

HH : hip height

HYS : herd year season

LRT : loglikelihood ratio test

MWT : mature weight

SAS : statistical analysis system

SRM : simple repeatability model

RRM : random regression model

WWT : weaning weight

YWT : yearling weight

CHAPTER 1

1. General Introduction

1.1 Background

Beef production system consists of a variety of breeds with different biological characteristics. In South Africa, there are about 39 breeds suitable for beef production. The Bonsmara breed is considered as the most popular among those participating in the South African national beef cattle improvement scheme (Bergh, 2013). The Bonsmara is also identified as a composite breed, which is based on the Sanga (Afrikaner) and British (Short horn and Hereford) breeds (Mostert & Exley, 2000). This breed showed the potential to thrive in subtropical conditions and it is also resistant to tick-borne diseases (Maiwashe *et al.*, 2002; Muchenje *et al.*, 2008). Due to its desirable characteristics, this breed is the best to keep under a wide variety of conditions ranging from highly intensive feeding to nearly desert conditions (Neser *et al.*, 1996). Traditionally, beef production industry has always been concerned with the genetic progress of early growth traits, placing more emphasis on selecting fast growing animals. The emphasis on early growth rate is to produce more animal protein for the projected human population growth in the coming decade (FAO, 2009).

One of the ways of improving livestock production is through genetic means. This, in general view, involves the selection of genetically superior animals to produce livestock that is genetically predisposed to high productivity. With regards to that, the establishment of effective breeding programs is one of the best tools that can be utilized to meet the anticipated growth in demand for meat. When designing a breeding program for beef cattle, it is important to understand the genetic relationship between the early growth traits and the mature weight

(Meyer, 1995; Burrow, 2001). These traits are easy to improve with their heritability estimates ranging from medium to high, therefore, responding fast to selection (Kars *et al.*, 1994; Schoeman *et al.*, 2000; Maiwashe *et al.*, 2002; Corbet *et al.*, 2006; Neser *et al.*, 2012). Several researchers have recognized and reported a positive genetic association between early growth traits and mature cow weight (Bullock *et al.*, 1993; Meyer, 1995; Costa *et al.*, 2011). With respect to that, if selection directed to increase the rate of gain was successful, then the mature weight of the breeding cows would be expected to increase as a result of the correlated response (Urick *et al.*, 1971). High mature weight is not desirable, especially in the breeding cows, because animals with large body size require more energy for maintenance. As evidence shows that large females may even be less efficient in terms of their reproductive and physiological performance under fluctuating nutritional conditions of tropical and sub-tropical regions (Hawkins *et al.*, 1965; Arango *et al.*, 2002; Scasta *et al.*, 2015).

1.2 Problem statement

The breeding objectives of most beef breeding programs aim to increase the growth rate. As a consequence, mature weight is expected to increase due to a correlated response. Animals with heavy mature weight require more energy for maintenance compared to animals with low mature weight. Particularly for animals grazing in the tropical and subtropical veld, increased mature weight is undesirable because the available nutrients might not meet their requirement for maintenance and production. The first step in understanding and dealing with this problem is through obtaining reliable estimates of genetic parameters associated with mature weight and early growth traits. Thus, knowledge of the genetic association between early growth traits and mature weight allows manipulation of mature weight change to the desired direction through its inclusion in a well-planned selection index. Regarding the genetic parameters, there is no known published report that addresses (1) the genetic variance and co-variance between mature and other growth traits for the Bonsmara breed, (2) the influence of selection of other growth traits on genetic trend of mature weight in this breed and (3) the expected correlated response to selection for mature weight as a result for early growth traits.

1.3 Research objectives were:

- To estimate the phenotypic and genetic variance-covariances for early growth traits and mature weight of the Bonsmara.
- To evaluate the correlated response to selection for mature weight as a result of selection based on early growth traits.
- To examine the genetic trend of mature weight of the Bonsmara cattle.

1.4 Hypothesis

- There is no phenotypic and genetic variances for early growth traits and mature weight in the Bonsmara breed.
- There is no phenotypic and genetic correlation between the early growth traits and mature weight.
- There is no genetic trend on mature weight for the Bonsmara breed.
- There is no correlated response to selection for mature weight as a result of selection based on early growth traits.

CHAPTER 2

2 Literature Review

2.1 Description of the breed

The Bonsmara is a crossbreed 5/8 Afrikaner and 3/8 (Hereford or Shorthorn) that was developed under the guidance of Professor Jan Bonsma at the Mara and Messina research station. Basically, it is a combination of 5/8 sanga and 3/8 *Bos Taurus*. It is one of the most common breeds in South Africa with its genetic material exported to other countries such as America, Brazil, Argentina and Australia (Mostert & Exley, 2000; Santana *et al.*, 2012; Bignardi *et al.*, 2014). The beef herd is largely found in the tropic and sub-tropical regions. These regions are associated with high temperatures, humidity and parasites, which are factors that limit production. However, due to a long period of natural selection, local breeds such as the Afrikaner and many other Nguni breeds have adapted to these conditions. On the other hand, European breeds such as the Hereford and Simmental are large in size and were developed under temperate environment, but as pure breeds, they do not perform to their full potential under veld conditions.

By combining the growth potential of the *Bos Taurus* (Hereford and Shorthorn) and adaptability of the *Bos Indicus* (Afrikaner), the Bonsmara cattle breed excels well in a wide variety of production systems. As reported in the literature, the Bonsmara's superiorities are in terms of meat quality, reproduction and its ability to thrive even under ticks and tick-borne disease conditions (Spickett *et al.*, 1989; Muchenje *et al.*, 2008). Some of the physical attributes that make the Bonsmara to standout are; its reddish to brown coat colour with a frame type that is classically of an efficient easy calving subtropical animal, a strong heterosis, an outstanding mothering ability and a good temperament (Bergh, 2013).

2.2 Growth traits in beef cattle

In South Africa, the Bonsmara cattle breed is involved in various production systems depending on the age the breed is marketed. Animals are expected to gain weight over time and this process is called growth. In beef production, animal`s live weight is taken at regular intervals to assess growth. These age intervals normally are weight at birth, weaning (205 days), yearling (365 days), 18 month's weight (550 days) and beyond. The aforementioned weights are broadly categorized into (1) pre-weaning growth, (2) post-weaning growth and (3) mature size (Arango. 2000). These traits are also referred to as production traits and are identified as important traits that influence profit margins in beef cattle production systems (Dickerson, 1970; Newman & Coffey, 1999; Nephawe *et al.*, 2004b). Production traits are included in most genetic improvement programs because they are easy to measure, are measured early in life and their data is readily available at various breeder associations in South Africa and elsewhere.

2.2.1 Birth weight

Birth weight is a live weight of calf taken within 3 days of birth (Vermaak, 2006). This trait is very important because of its association with calving difficulties and early survival. That is, calves that are born with very light birth weights are more susceptible to environmental stresses, including cold and diseases, requiring intense animal husbandry. On the other hand, extremely high birth weights result in mortality of calves and cows due to dystocia (Holland & Odde, 1992; Dzama *et al.*, 2001). Birth weight of calves is dependent on the frame size of the breed. For different beef breeds, the reported average birth weight ranges from 15 to 51 kg (Collins-Lusweti, 2000; Maiwashe *et al.*, 2002; Raphaka, 2008; Neser *et al.*, 2012; Bignardi *et al.*, 2014).

2.2.2 Weaning, yearling and 18 month's weights

Weaning weight (WWT), yearling weight (YWT) and 18-month weight (EWT) are weights taken in the following interval: 151-270, 271-450 and 451-634 days respectively (Vermaak, 2006). The goal of any beef producer is to produce high-quality meat with minimum input for maximum efficiency. As for weaning, yearling and 18-month weight trait, the heavier the animals are at these points, the more money the producer makes. For economic reasons, numerous studies in the tropic and subtropical regions have studied these traits extensively. The Bonsmara cattle breed remains one of best breeds that excel even under drought conditions occurring in those regions. Collins-Lusweti (2002) studied the performance of Bonsmara and two other indigenous breeds (Nguni and Afrikaner) under arid conditions in one of the driest provinces of South Africa. The findings were that, the Bonsmara performed better than the Nguni in terms of WWT. The average WWT of 150.6 kg and 213 kg reported by Collins-Lusweti (2000) and du Plessis *et al.* (2006) respectively are within the range of 124-335 kg reported for the Bonsmara by Maiwashe *et al.* (2002). For the different strains of Bonsmara, the 18-month's weight has been reported to range between 282-585 kg (Maiwashe *et al.*, 2002; Bignardi *et al.*, 2014). The weaning, yearling and 18 month's weights for the Bonsmara compare very well with other beef breeds (Archer *et al.*, 1998; Collins-Lusweti, 2000; Burrow, 2001; Neser *et al.*, 2012)

2.2.3 Mature weight

Animals that are not sold at 18 months of age are those kept as replacement breeding cows and bulls. Because of the reproductive limitations, the majority of the retained animals are females. Therefore, in most instances, mature weight is measured from cow herd. Mature weight has been shown to be a determinant of the nutrient requirement for beef cattle (McMorris & Wilton, 1986;

Montaño-Bermudez *et al.*, 1990; Williams *et al.*, 2009; Rump *et al.*, 2004a). According to the study done in the US, selection strategies over the past 40 years have resulted in over 30% increase in the cow weight (McMurry, 2008; Beck *et al.*, 2016a). This 30% increase is accompanied by a 22 to 28% more forage dry-matter requirement increase for maintenance (NRC, 1996). The impact of the increase in cow weight goes beyond the increase in maintenance requirements. Kress *et al.* (1969) reported an unfavourable correlation between energy efficiency and cow weight. Scasta *et al.* (2015) found that smaller cows were more efficient than large cows in terms of cow-calf weight ratio in the driest years. In agreement, Beck *et al.* (2016b) discovered that increasing cow weight reduces calf weaning weight. Furthermore, Hawkins *et al.* (1965) reported that light cows weaned more calves in their lifetimes than large cows. These reports (Hawkins *et al.*, 1965; Kress *et al.*, 1969; Scasta *et al.*, 2015; Beck *et al.*, 2016b) outline the benefits of using lighter cows, thus putting pressure on current breeding programs to evolve and select against high cow weight.

In beef production system, forage is deemed as the cheapest source of feed. However, the available nutrients may not meet the requirements for maintenance and production for high mature weight. Failure to meet the animal requirements will result in the following: (1) animals will be emaciated, (2) the body condition score will drop and subsequently, (3) the reproductive performance will be reduced (Dunn & Kaltenbach, 1980; Lalman *et al.*, 2013). In the past four to five decades, beef animals were selected with emphasis on feedlot performance, as result optimal cow size, however, has remained a great concern. A good question is, what is an ideal mature weight? An ideal mature weight solely depends upon the breeding objectives of the farmer. For example, the commercial beef producer may either select to increase mature weight to maximize returns from the selling of culled animals or select to exploit progeny growth while maintaining moderate levels of mature weight to minimize the feed cost of maintaining the breeding cows.

Beef animals are expected to reach maturity between the ages 4-5 years and that is where the growth curve starts to level off (Boligon *et al.*, 2009). Unlike the other traits with a definite age of measurement (BWT, WWT, YWT and EWT), knowing the exact age at which the cow matures is not easy. The simplest method might be to use an average of the weight taken after 5 years of age. However, very few animals are kept beyond 5 years and this procedure does not show whether the animal has finished growing (Bullock *et al.*, 1993). Most beef breed associations keep records of the cow's weight at calving and weaning of the calves. Using these repeated weight records, picking a particular weight as mature weight is difficult. To overcome such a problem, mature weight can be estimated by using a growth function such as the Brody's (1945). The implementation of growth function on weight records taken starting from early in life to maturity can reduce these records to a few parameters. As an example, the Brody's function with the limited number of parameters to be estimated is shown below.

$$\mathbf{W = A(1-Be^{-kt})}$$

Where: "W[t]" is the weight of an individual at time [t], "A" is a curve parameter that predicts the asymptotic limit of weight (mature weight) when "age[t]" approaches infinity.

This does not mean "A" is the heaviest weight attained by the animal, but is simply the average weight of a mature cow independent of the temporal fluctuations. "B" represents the integrated constant. "K" is a curve parameter that represents the ratio of maximum growth rate to mature size and also known as the maturing rate index. These functions assume that the point of inflation and the plateau resemble maturity. Of all growth functions, the Brody's (1945) function is the most commonly used to estimate mature weight because of its computational ease and its goodness of fit (Bullock *et al.*, 1993; Kaps *et al.*, 1999). However, other studies have claimed that the Richards growth curve fits the actual data points better than the Brody's curve (Denise & Brinks, 1985). The downside of Richard's curve as reported by Denise & Brinks (1985) and Brown *et al.* (1976) is computational complexity, whereby it requires more iteration for it to converge. The Gompertz growth curve that was developed in 1932, the von Bertalanffy of 1957 and the logistic of 1961 tend to over or underestimate mature weight (Brown *et al.*, 1976).

Using the asymptotic mature weight obtained from any of these functions, mature weight can be fitted in a univariate and also in a multivariate analysis to establish any genetic association it has with other traits of interest. Alternatively, repeatedly measured weights can be analyzed using either; the repeatability or random regression models. The repeatability model is simple and each observation is thought of as an expression of the same trait recorded at different time period. Theoretically, the genetic correlation between successive measurements is supposed to be 1. However, few studies discovered that this was not the case with field data (Arango *et al.*, 2000; Albuquerque & Meyer, 2001). This deviation can be attributed to minute statistical noises as a result of errors during data collection. The repeatability model is often preferred because of its simplicity and most importantly, it requires less computational costs. With the random regression model, growth measurements taken at different stages are considered as functions of age (Meyer, 1999; Nephawe, 2004a; Schaeffer, 2004; Boligon *et al.*, 2009). A thorough review on the abilities and shortcomings of these models has been documented in a review paper by Speidel (2010).

Recent studies on mature cow size reported mature weight that is adjusted according to the body condition score (BCS) and alongside with other traits such as hip height (Northcutt & Wilson, 1992; Meyer, 1995; Arango *et al.*, 2002). At maturity, animals are still subjected to numerous environmental conditions that some are impossible to account for (Bullock *et al.*, 1993). The impact of environmental influence on grazing beef cows is easily reflected on the body condition status of the cows. Hence, body condition score is known to be one of the best indicators of an animal's nutritional status.

2.3 Environmental factors affecting growth traits

The field measurement of production traits (phenotypic measurement) can be attributed to genetic and non-genetic components. The prediction of breeding values and other genetic parameters greatly rely on a breeder's capacity to accurately partition and eliminate the non-genetic effects from the field data. The performance records provided by the breed associations should provide details of the circumstances under which each measurement was taken. Through advanced statistical techniques, these effects are quantifiable and their influence on phenotypic record can be accounted for. Almost all studies on genetic parameters for growths traits have established that environmental factors significantly contribute to the variation in performance measurement (Archer *et al.*, 1998; Maiwashe *et al.*, 2002; Pico, 2004; Smith, 2010). Therefore, making adjustments for these factors from the phenotype is essential in establishing reliable genetic parameter estimates. Furthermore, understanding the influence of these non-genetic factors is not only to facilitate genetic evaluation but also used to evaluate the management action required to improve animal husbandry and profitability (Bwire, 2006; Raphaka, 2008).

Literature on genetic evaluation of production traits in beef cattle has identified a number of environmental effects that are important. These are factors such as herd-year-season, dam age, sex etc. The herd-year-season effect represents contemporary group effects, which consist of calves that were born in the same herd, in the same year and during the same calving season. This effect accounts for the environment and managerial practices that may vary from one contemporary group to the other. It also takes into consideration the changes that may take place within the same herd over a period of time.

Dam age is a continuous source of variation and its influence has been highlighted by several researchers, mostly who were studying both the pre and post weaning traits (Archer *et al.*, 1998; Smith, 2002; Pico *et al.*, 2004; Neser *et al.*, 2012). Calves born from a young and from an older cow are expected to be light in weight (Burris & Blunn, 1952; Krupa *et al.*, 2005). This can be attributed to the fact that young dams are still growing, therefore, their nutrition is not only directed to maintenance but is also partitioned for supporting lactation and early foetal growth and development. Elzo *et al.* (1987) and Rump & van Vleck (2004b) stated that beef cows are expected to reach their peak production at 5 to 8 years. During this period, the dams are considered matured and have a greater capacity to provide a conducive uterine environment for the development of the foetus than they did when they were still young. This capacity is, however, expected to decrease as the animals grow old, particularly in grazing beef cows because of reduced nutrient intake due to broken mouths.

The influence of sex in animal growth performance trait has been well documented (Archer *et al.*, 1998; Mwanza *et al.*, 1998; Smith, 2002; Pico *et al.*, 2004; Menendez-Buxadera *et al.*, 2008; Raphaka & Dzama, 2008; Neser *et al.*, 2012). Several studies have indicated that males are heavier than their female counter-parts at all ages provided that they are raised under the same environment (Pico *et al.*, 2004; Raphaka, 2008; Raphaka & Dzama, 2010; Smith, 2010; Riley *et al.*, 2016). For example, the South African Brahman and Simbra composite breeds reported birth weight differences of 1.77 and 1.33 kg between the male and female calves respectively (Pico *et al.*, 2004; Smith, 2010). Bulls weigh more than females at all ages because they are more muscular. This muscularity is as a result of testosterone exerting a direct anabolic effect on protein synthesis in the body tissue (Smith, 2010). This shows that the influence of sex is important and should always be accounted in any genetic evaluation including both the pre and post-weaning weight traits. However, a relatively large number of studies concerning mature weight disregard the influence of sex. The reason behind this is that, most animals that are kept beyond 18 months of age are female and few are male. Therefore, the logical decision is to remove all males and remain with a data set only consisting of female records.

2.4 Genetic parameters for early growth traits and mature weight

The aspect of evaluating and selecting animals based on genetic merit is old and has been instinctively practised (Todd, 2013). This practice involved the selection of animals based on their own phenotypic performance or that of their parents. During this period, no one understood the constituency of a phenotypic value hence it was referred to as a "black box". With regards to that, through the years, intense studies in the field of animal breeding have led to a considerable understanding of the concept of genetic inheritance. Today, prior to the implementation of selection, reliable genetic parameter estimates are needed for the practical application of selection in the breeding programs (Burrow, 2001; Neser *et al*., 2012). The method of estimating these parameters involves equating the function of phenotypic observations, the genetic relationship between relatives, the expectation of the model terms and then fitting of these terms by maximum likelihood (Henderson, 1953, 1975). Heritability, phenotypic and genetic (co)variances among economically important traits are the most important population genetic parameters required for the establishment of an effective breeding program.

The renowned importance of genetic variation is its role in determining the scope selection. Furthermore, genetic variation allows animals to meet production requirements at various environments (Clay, 1998). However, the implication of reduced genetic variation goes beyond the impact it has on improving productivity but threatens the fitness of the animals to adapt to new environments (Amos & Harwood, 1998). Santana *et al.* (2012) asserted that the practice of selecting a small group of animals based on their genetic superiority is expected to reduce genetic diversity. Furthermore, most herds of the population violate the four conditions stated by Hardy-Weinberg principle and because of that, changes in the variances are expected. Genetic selection for economically important traits is practised continuously, and as a result, the genetic variances of these traits are anticipated to change with time (Matjuda *et al.*, 2014). This shows the need for frequent updating of genetic parameters.

2.4.1 Heritability of growth traits

Heritability can be defined as the proportion of phenotypic variance in a population that is due to genetic causes. There are, however, two distinct meanings of heritability depending on whether they refer to genotypic or breeding value as defined by Falconer & Mackay (1996). Heritability in a broad sense is determined by the genotype and its ratio is calculated as $h^2 = V_g/ V_p$. On the other hand, in a narrow sense, heritability can be calculated as the ratio of breeding value or additive genetic value variance out of the total phenotypic variance: $h^2 =V_a/ V_p$, where V_g and V_a are genotypic and additive genetic variances respectively, and V_p = phenotypic variance (Bourdon, 2000). Heritability in a narrower sense measures the strength of resemblance between genetically related animals. In genetic selection, obtaining the most accurate breeding values for the traits of interest in a population is very important. Heritability has a huge influence on the accuracy of the estimated breeding value. The higher the heritability of a trait is, a limited number and sources of phenotypic information are required to achieve high accuracy in estimated breeding value, while a trait with low heritability requires a large number and diverse sources of information to increase the accuracy of the estimated breeding value. With accurately estimated breeding values, rapid genetic improvements can be achieved.

The estimation of heritability relies greatly on the ability to partition the observed phenotypic variation among animals into the components of genetic and environmental effects. The early growth traits are reported to be influenced by direct and maternal genetic effects (Brown & Lalman, 2008). The direct additive genetic value indicates the genetic potential of the individual to grow and it is estimated for each of the traits under consideration and for all the individuals in the population. The maternal effect influencing early growth trait of calves has two components, maternal genetic and maternal environmental effects. The maternal genetic effect arises from the mothering ability genes that the dam carries, while the maternal environmental effect arises from environmental effects influencing the mothering ability of the dam. However, due to the antagonistic relationship between the additive genetic and maternal genetic effects, predicting heritability for maternally influenced traits is a challenge. The importance of a maternal effect is studied by many researchers and is currently included in almost all genetic analysis because of the influence it has on pre-weaning growth trait (Neser *et al.*, 1996). Meyer (1992) reported a considerable inflation on direct additive genetic effect as a result of the exclusion of maternal effect. The expression of the maternal effect is limited to female animals and it ascends from the ability of the dam to produce enough milk for the young calf and many other maternal behaviours and also, accounting for the maternal effects increases the level of accuracy on selection (Robinson, 1996). The maternal effect is important on pre-weaning traits and its influence declines at post-weaning growth (Falconer & Mackay, 1996).

There is a negative association between direct and maternal genetic effects, particularly for early growth traits, where maternal effect is present (Meyer, 1992). Maiwashe *et al.* (2002) reported a correlation value of -0.44 and -0.54 between the direct and maternal genetic effects for birth and weaning weights respectively on the Bonsmara cattle. Likewise, several other researchers also reported a negative correlation between the direct and maternal genetic effects for other breeds (Meyer, 1992; Plasse *et al.*, 2002; Pico *et al.*, 2004). This negative relationship between these effects might be partly due to unaccounted environmental factors. Neser *et al.* (1996) reported that the exclusion of herd-year by sire interaction in the model could cause an overestimation of the direct additive component. He also reported that the exclusion of the permanent maternal effect might result to an overestimation of the maternal genetic component of weaning weight in the Bonsmara cattle. Similarly, Robinson (1996) and Lee & Pollak (1997), from a simulated study, presented a proof on the negative correlation not to be solely due to antagonism, but an unaccounted additional sire by year interactions. These reports outline the importance of accounting for sire by environmental effects and also to fit the direct-maternal interaction into the analysis models where appropriate, for reliable variance component estimation. These genetic parameter estimates are carried out using the best linear unbiased prediction (BLUP) method, which allows the evaluation across herd and across year, provided that there is a genetic connection between the herd and year (Crump *et al.*, 1997; Pico *et al.*, 2004)

2.4.1.1. Heritability estimates for early growth traits

The literature on Bonsmara and other beef breeds indicate that genetic improvement in production traits (weight from birth till 18 months old) can be rapidly achieved due to medium to high heritability values. The heritability estimate reported in the literature for birth weight of beef cattle ranges from moderate 0.32 to as high as 0.49 (Bullock *et al.*, 1993; Maiwashe *et al.*, 2002; Plasse *et al.*, 2002; Pico *et al.*, 2004, Raphaka, 2008). Through multivariate analysis, Maiwashe *et al.* (2002) reported moderate heritability values of 0.29 and 0.30 for weaning and 18 month's weights respectively for the South African Bonsmara. Likewise, using a multivariate model, Meyer *et al.* (1993) reported heritability values of 0.22 and 0.34 for weaning and 18 months weight respectively, for the Hereford breed. Comparable heritability estimates of 0.22 and 0.29 for weaning and 18 month's weights respectively were also reported for the Brangus by Neser *et al.* (2012) from a multivariate analysis that included other weight traits. Like the other traits, heritability estimate reported for the yearling weight of different beef breeds ranged from 0.25 to 0.47 (Bishop, 1992; Meyer, 1992; Bennett & Gregory, 1996; Dodenhoff *et al.*, 1998).

2.4.1.2. Heritability estimate for mature weight

In literature, estimates of heritability for mature weight is reported from mature weight predicted as a function of growth curve using a simple univariate model or from the repeated weight records, the complex multivariate and/or random regression models (Bullock *et al.*, 1993; Kaps *et al.*, 1999; Nephawe, 2004a; Crook *et al.*, 2010). Various published articles reported moderate to high heritability values for mature weight (Bullock *et al.*, 1993; Kaps *et al.*, 1999; Costa *et al.*, 2011). Kaps *et al.* (1999) reported heritability estimates for mature weight of the Angus cattle ranging from 0.44 to 0.53 from the univariate and bivariate models. According to these authors, fitting weaning weight as a second trait improved the heritability estimate for mature weight. The discrepancy in heritability estimates obtained from the univariate and multivariate models can be attributed to the culling effect being compensated for in the multivariate models. Thus, the use of multivariate model improves the accuracy of estimated heritability for the traits involved. Likewise, Bullock *et al.* (1993) reported a heritability value of 0.52, obtained from averaging seven heritability values from seven bivariate analyses with other weight traits for polled Hereford. However, Boligon *et al.* (2009) reported a slightly lower heritability value (0.35) from a multivariate animal model. Even though they used a similar approach, the possible cause of this difference is that, different breeds at different regions exhibit different genetic variation. Using a repeatability model, the literature reported a direct heritability of mature weight ranging from 0.28 to 0.47 for different beef breeds (Nephawe, 2004a; Crook *et al.*, 2010; Neser *et al.*, 2012). Nephawe (2004a) evaluated mature weight for the Bonsmara using the simple repeatability and random regression models, and reported heritability estimates ranging from 0.39 to 0.47. The overall heritability estimate as established by several authors using various approaches indicates that a significant genetic progress can be achieved through genetic selection for mature weight into the desired direction of change.

2.4.2. Genetic Correlations

The profitability of the beef enterprise is affected by several traits. For that reason, all the traits that are of economic benefit are needed to be included as part of the breeding objectives. The main objective of simultaneous selection is to improve the aggregate breeding value of the animals towards the desired direction (Kluyts *et al.*, 2003). Therefore, understanding the existing relationship among these traits is very important in ensuring that the breeding goals are met (Liu *et al.*, 1991). Several researchers reported a positive strong correlation between mature weight and early growth traits (Northcutt &Wilson, 1993; Bullock *et al.*, 1993; Bignardi *et al.*, 2014). Bignardi *et al.* (2014) reported the direct genetic correlations between mature weight with the birth, weaning, yearling and 18-month weights to be 0.67, 0.60, 0.59 and 0.75 respectively, for the Brazilian Bonsmara cattle. For the polled Hereford, Bullock *et al.* (1993) reported the direct genetic correlations between mature weight with the birth, weaning and yearling weights to be 0.64, 0.80 and 0.89, respectively. In view of that, selection focusing on other correlated traits might increase mature weight to the extreme. As expected, the genetic co-variances between close measurements were the highest and decreased as the age gap between the weight measurements increases.

The genetic correlation between traits can arise from two genetic causes: (1) pleiotropic effect and (2) gene linkage (Falconer & Mackay, 1996). These authors defined pleiotropy as the property of gene(s) influencing more than two traits. The pleiotropic gene segregation causes parallel variation in the traits it controls and the genetic correlation from this effect is permanent. On the other hand, gene linkage is defined as a set of closely linked genes located in one chromosome that are influencing more than two traits. These genes are transmitted together and cause temporary genetic correlations between traits until these genes are broken by meiotic recombination. The strong genetic correlation among traits implies that changes can occur in any of the traits including mature weight as a result of indirect selection. Therefore, breeding objectives needs to match the cow size to the environmental conditions and feeding practices while maintaining a saleable weight at the weaning and yearling stages (Baldi *et al.*, 2006). Considering the high heritability of mature weight and its positive association with the early growth traits, excluding mature weight in any genetic selection can potentially have a negative consequence in beef production, especially on the efficiency of the breeding cows.

2.4.3. Genetic trends and correlated response in mature weight

The basic goal of an animal breeder is to look for the best blend of gene effects to obtain an advantageous change in the trait of interest. Knowledge of these genetic changes taking place with time is important in order to make proper adjustments wherever necessary in the program. In simple terms, the genetic trend can be defined as average EBV change per unit time in a given population. It is one of the best tools commonly used to verify genetic progress and the effectiveness of breeding programs (Parra-Bracamonte *et al.*, 2016). With more emphasis directed at improving early growth traits, genetic trend can also be used to track the correlated behaviour of mature weight as a result of changes made on early growth traits (Abin *et al.*, 2016). Few studies on beef animals have investigated the influence of current breeding programs on mature weight, particularly in South Africa. Boligon *et al.* (2013) examined the trend of mature weight from a Nelore cattle herd selected for weaning and yearling indices, and surprisingly, the trend was not significant. Similarly, Rumph *et al.* (2004b) also reported a relatively low genetic trend for the Hereford when animals were selected to increase the yearling weight and decrease birth weight. This behavior of mature weight was not expected regarding the established genetic association it has with early growth traits.

With regard to the common selection indices in beef production, mature weight is expected to increase as well. However, this shows that genetic correlation alone does not provide sufficient information about the response of mature weight as an indirectly selected trait. Boligon *et al.* (2013) estimated the correlated response in mature weight of the Nelore cattle as a result of selection based on early growth trait indices. They calculated the correlated response as a function of genetic correlation between traits, genetic standard deviation for the traits and genetic trend for the trait selected for. This method of regressing mature weight on the genetic progress achieved on early growth traits, assists in monitoring the potential change in mature weight.

CHAPTER 3

3 Materials and Methods

3.1 Data description and editing

This study was based on performance data collected from the Bonsmara cattle breed. Data were extracted from the Integrated Registration and Genetic Information System (INTERGIS). The pedigree file consisted of 1,260,332 animals born between 1955 and 2014. The pedigree and performance data files were edited as follows: for each trait, incomplete records and records outside 4 standard deviations from the mean were eliminated. Sex was added as a fixed effect for weights that included both the male and female records. Only animals or their dams (for weaning weight) that were supplemented with either Ca/P lick, protein/energy lick or no licks at all in addition to grazing were kept. Animals that were reared on anything other than suckling their own dam were excluded.

3.1.1. Contemporary groups

The contemporary groups (fixed effect) were formed by concatenating herd, birth year and season, and only single born calves were considered. Prior to the formation of contemporary groups, the birth season was grouped into 2 categories following the climatic pattern prevailing in the country and these were hot-wet (October to March) and cold-dry season (April to September). Contemporary groups represented by less than 8 sires were discarded to avoid confounding of the genetic effect with the contemporary effect.

3.1.2. Growth traits, weight adjustments and mature weight prediction

The traits studied were: birth weight (BWT), weaning weight (WWT), yearling weight (YWT), 18-month's weight (EWT), and the asymptotic mature weight (MWT). The WWT, YWT and

EWT were pre-adjusted to 205, 365 and 550 days prior to the analysis, respectively. The pre-adjustments for these traits were calculated using the following formulae:

1. **WWT= ((unadjusted WWT-BWT)/weaning age)*205+BWT**
2. **YWT= ((unadjusted yearling weight -WWT)/(yearling age-205))*160 +WWT**
3. **EWT = ((unadjusted EWT-YWT)/(EWT age-365)*185 +YWT**

Mature weight (MWT) was predicted using the Brody growth curve (Brody, 1945). Since there were few males kept in the breeding herd after 18-month of age, they were removed from the dataset. Therefore, mature weight was predicted from the female's weight record. Cows with at least 7 records including the BWT, WWT and YWT, were included for estimation of the asymptotic mature weight. Using this information, the asymptotic mature weight of each animal was calculated using the following equation;

$$\mathbf{W[t] = A\ (1-Be^{-kt})}$$

Where: "W[t]" is weight of an individual at time [t], "A" is a curve parameter that predicts the asymptotic limit of weight (MWT) when age[t] approaches infinity.

This does not mean "A" is the heaviest weight attained by the animal but it indicates the mean weight of a mature cow independent of the temporal fluctuations. "B" represents the integrated constant. "K" is a curve parameter that represents the ratio of maximum growth rate to mature size and also known as the maturing rate index. The asymptotic mature weight for each animal was estimated using the non-linear procedure in SAS (SAS, 2010).

In addition, for estimation of mature weight through repeatability analysis, cow weights measured at weaning of their calves were considered. Cow weight records under the age of 3 years and over the age of 10 years were discarded. The dam's age (in years) was rounded off to the nearest whole number to determine the age class it falls. Cow weight contemporary groups were formed through a concatenation of the herd, weighing year and season (HYS). Contemporary groups with less than 8 animals were deleted. Only animals with a minimum of 2 records were kept.

3.2 Statistical analysis

3.2.1. The fixed effects

Preliminary analysis to identify important fixed effects to be fitted in genetic models was conducted using the SAS GLM model (SAS, 2010). Summary of factors and factor interactions that were fitted for the analysis of each trait are shown in Table 1. Factors and factor interactions that had a significant influence on each trait are marked with an asterisk (*). Factors were regarded significant using the statistical threshold level of $p<0.05$.

Table 1: Fixed factors and their interactions significantly influenced weight at different ages.

FACTORS	LEVELS	BWT	WWT	YWT	EWT	MWT
CALF SEX	1	*	*	*	*	-
HYS	243	*	*	*	*	*
DAMAGE (COVARIATE)	1	*	*	*	-	-
FEED[A]	2	-	*	*	*	-
DAMAGE*DAMAGE	1	*	*	*	-	-
DAMAGE*SEX	1	*	-	-	-	-

[a] Feed reference to a lick supplement given to calves at different ages. BWT-birth weight, WWT-weaning weight, YWT-yearling weight, EWT-18 month's weight and MWT-asymptotic mature weight

3.2.2 Estimation of the variance components

Variance component for the random effects was estimated using an ASREML software (Gilmore *et al.*, 2006). Various univariate models and a reduced multivariate animal model were fitted by combining the fixed effects selected from the preliminary analysis with random effects.

3.2.3 The univariate analysis

All traits were analysed on a series of univariate models with the various random effects fitted. A total of 5 models with the varying random effects that were fitted for each trait are presented below:

Model 1: $Y = X\beta + Z_{1a} + e$.

Model 2: $Y = X\beta + Z_{1a} + Z_{2mi} + e$, **{without cov(a,m)}.**

Model 3: $Y = X\beta + Z_{1a} + Z_{3pe} + e$.

Model 4: $Y = X\beta + Z_{1a} + Z_{2m} + e$, **{with cov(a,m)}.**

Model 5: $Y = X\beta + Z_{1a} + Z_{2m} + Z_{3pe} + e$, **{with cov(a,m)}.**

Where: y = a vector of observations (BW, WW, YW, AW or MW)

β = a vector of fixed effects

a = a vector of direct additive genetic effects

m = a vector of maternal additive genetic effects

pe= permanent maternal environmental effects

e = a vector of residuals

X, Z_1, Z_2 and Z_3= are the incidence matrices that relate the observations to their respective fixed and random effects.

Given the models above, the expectations of the random effects are all null and the expectation of y-vector is presented below:

$$\mathbf{E[Y] = X}\boldsymbol{\beta}$$

The (co)variance structure for the full single trait model is presented below:

$$\mathbf{Var}\begin{bmatrix} a \\ m \\ pe \\ e \end{bmatrix} = \begin{bmatrix} G_{0a} \otimes A & G_{0am} \otimes A & 0 & 0 \\ G_{0am} \otimes A & G_{0m} \otimes A & 0 & 0 \\ 0 & 0 & G_{0pe} \otimes I_C & 0 \\ 0 & 0 & 0 & R_0 \otimes I_n \end{bmatrix} \otimes$$

Where,

G_{0a} = direct genetic variance.

G_{0am}= Genetic covariance between direct additive and maternal effects.

G_{0m}= Genetic variance for maternal effect.

G_{0pe}= Variance for random maternal permanent environmental effect.

R_0= Variance for random residual effect.

A= additive genetic relationship matrix.

I_C= identity matrix whose order is equal to the number of dams.

I_n= identity matrix whose order is equal to the number of animals with record.

The following variance components were estimated by model 1-5:

1. **σ_a^2 = additive genetic variance;**
2. **σ_m^2 = maternal genetic variance;**

3. **σ_{am} =genetic covariance between direct and maternal effect;**
4. **σ^2_{pe} = permanent environmental variance,**
5. **σ^2_e = the error variance.**

These components were subsequently used to derive the following parameters:

1. **Additive genetic heritability, $h^2_a = \sigma^2_a/\sigma^2_P$**
2. **Additive maternal heritability, $h^2_m = \sigma^2_m/\sigma^2_P$**
3. **Genetic correlation between the direct and maternal effects $R_{am} = \sigma_{am}/\sqrt{\sigma^2_a \times \sigma^2_m}$**
4. **Ratio of permanent environmental variance over phenotypic variance $C^2 = \sigma^2_{pe}/\sigma^2_P$**

Where, σ^2_P represents phenotypic variance

3.2.3.1. Model comparison

The best models in the univariate analyses were identified in terms of the goodness of fit, using the log-likelihood ratio test. The difference in the log-likelihood values between 2 models was multiplied by 2 and then compared with the *chi*-square value obtained with the degrees of freedom equal the difference in the number of parameters between the two models under comparison. The model fit was considered significant at $P < 0.05$.

3.2.4 The multivariate analysis

The variance-covariance for BWT, WWT, YWT, EWT and MWT was estimated using a multi-trait animal model. Estimates obtained from the univariate analysis were used as starting values for the multi-trait analysis. The multivariate model is presented below:

$$\mathbf{Y}_i = \mathbf{X}_i\beta_i + \mathbf{Z}_{1\ a\ i} + \mathbf{e}_i$$

Where: Y_i= vector of observations corresponding to BWT, WWT, YWT, EWT and MWT, respectively.

β_i = vector of fixed effects corresponding to BWT, WWT, YWT, EWT and MW, respectively.

u = vector of direct and maternal additive effects

a = vector of direct genetic effects

e = vector of residuals

X_i and Z_i = are the incidence matrices that relate the observations to their respective fixed and random effects.

The (co)variance structure for the reduced multi-trait model is presented below:

$$\mathbf{Var}\begin{bmatrix} a \\ e \end{bmatrix} = \begin{bmatrix} \mathbf{G_{0a}} \otimes \mathbf{A} & \mathbf{0} \\ \mathbf{0} & \mathbf{R_0 I_n} \end{bmatrix}$$

Where, a = vector of direct genetic effects.

e = vector of residuals

G_{0a} = Direct genetic variance-covariance matrix.

R_0 = Variance-covariance matrix for random residual effects.

A = additive genetic relationship matrix.

I_n = identity matrix whose order is equal to the number of animals with record.

The package could not run the 5 traits simultaneously, and for that reason, a series of 3 multivariate analysis was run to estimate the correlations between the traits. Therefore, traits included in each analysis are shown below:

Analysis 1: BWT, WWT, YWT and MWT.

Analysis 2: WWT, YWT, EWT and MWT.

Analysis 3: BWT and EWT

3.3 The genetic trend for mature weight

The genetic trend of mature weight and early growth traits were analyzed by weighted least squares regression of the arithmetic means of additive genetic values of animals grouped according to their birth years (Boligon *et al*., 2012; Canaza-Cayo *et al*., 2015).

$$Y_i = b_0 + b_1 X_i + e$$

Where, Y_i is the mean of breeding values of the animals in the i-th birth year.

b_0 is an intercept.

b_1 is a slope.

X_i is the i-th birth year.

e_i is a random error.

3.4 The correlated response in mature weight

The expected genetic correlated response between trait-1 (indices) and trait-2 (mature weight as an indirectly selected trait) was calculated based on the genetic trend achieved in early growth traits using the following equation (Boligon *et al*., 2009);

$$\Delta G_{2,1} = r_g\left(\frac{\sigma_{g2}}{\sigma_{g1}}\right)\Delta G_1$$

Where i is the trait (growth trait) under selection.

r_g is the genetic correlation between the trait under selection and mature weight.

σ_{g2} is the genetic standard deviation of mature weight.

σ_{g1} is the genetic standard deviation for the trait under selection.

ΔG_1 is the annual genetic change of the trait under selection.

In addition, the correlated predicted response in MWT to the phenotypic selection of early growth traits (trait in selection index) with two selection intensities (retaining top 5% and 10%) was predicted using the following formula (Bourdon, 2000):

$$\Delta G_{2|1} = rg(\frac{h_1 h_2 i_1 \sigma_{p2}}{n})$$

Where, $\Delta G_{2|1}$ = genetic change in trait 2(mature weight) due to phenotypic selection for trait 1 (in index).

rg = genetic correlation between trait y and x.

h_1 = square root of heritability for trait 1.

h_2 = square root of heritability for trait 2.

i_1 = selection intensity

σ_{p2} = phenotypic variation for trait 2.

n = number of generations

CHAPTER 4

4. Results and Discussion

4.1. Descriptive statistics for growth traits

A summary of the descriptive statistics for growth traits is presented in Table 2. The overall mean values for BWT, WWT, YWT, EWT and MWT were 35.7, 218.9, 250.3, 341.5 and 524 kg respectively. The current mean values of the live weight from birth till 18 months of age are comparable to the values previously reported for the Bonsmara cattle in South Africa (Maiwashe *et al.*, 2002), Brazil (Santana *et al.*, 2012) and Botswana (Rakwadi *et al.*, 2016). The observed pre-weaning weight is also comparable to the Brahman cattle as has been reported by Pico (2004) and Neser *et al.* (2012). The literature, however, reveals that breeds that are comparable at pre-weaning in terms of growth performance may not be as comparable at post weaning (Bullock *et al.*, 1993; Pico, 2004; Neser *et al.*, 2012; Boligon *et al.*, 2013). The accompanying coefficient of variation showed an increase as the animals grow old until yearling and then started to decline. A similar observation was also reported for the South African Brahman by Pico (2004), therefore, implying that the YWT and EWT are the most phenotypically variable weight traits in the dataset used. In general, the number of available weight records declined with age. This trend, particularly after weaning, can be ascribed to the selling of weaners, culling and selection practices. There are other several possible reasons, including mortality and stock theft that might have been the cause of this reduction.

Table 2: Characteristics of the dataset for growth traits of the South African Bonsmara.

Trait	No. records	Mean (kg)	%CV	Min (kg)	Max (kg)
BWT	69514	35.66	12.37	19.00	50.00
WWT	69514	218.90	14.88	91.70	372.40
YWT	27079	250.30	17.6	102.50	523.2
EWT	17801	341.5	16.47	151.6	628.5
MWT	1788	524	12.38	365.5	703.2

BWT-birth weight, WWT-weaning weight, YWT-yearling weight, EWT-18 month's weight, MWT-asymptotic mature weight

4.2. Genetic parameters for early growth traits and mature weight

4.2.1. Variance component and heritability estimates for the birth weight

The variance component and heritability estimates for the BWT are presented in Table 3. The log likelihood ratio test (LRT) showed that besides direct genetic effect, the influence of maternal genetic effect and genetic correlation were significant ($p<0.05$) sources of variation for the BWT. The direct heritability estimates for BWT from the univariate and multivariate analysis were 0.49 and 0.44 respectively. The estimated direct heritability for the BWT from both models was moderate and comparable to values in the literature. Ahunu *et al.* (1997) reported a comparable direct heritability estimate of 0.45 for the Ndama and West African Shorthorn cattle breeds. In agreement with the current result, a direct heritability value of 0.41 was also reported by Kars *et al.* (1994) for the Nguni cattle using data collected from the Bartlow Combine breeding station. Mostert *et al.* (1998) and Meyer (1992) also reported comparable estimates of 0.45 and 0.41 for the Brahman and Hereford breeds respectively. Nevertheless, the direct heritability estimates from both models were generally higher than previous estimates in the literature (Eler *et al.*, 1995; Haile-Mariam & Kessa-Mersha, 1995; Maiwashe *et al.*, 2002). These authors reported heritability estimates ranging from 0.22 for the Nelore in Brazil (Eler *et al.*, 1995) to 0.38 for the Bonsmara in South Africa (Maiwashe *et al.*, 2002). Even though Maiwashe *et al.* (2002) focused on the same population as was this study, the possible reason for this discrepancy could be the sample size used and/or the types of models employed for the estimation.

The maternal heritability estimate obtained from this study (0.11± 0.012) was moderate and similar to the estimates reported in the literature (Waldron *et al.*, 1993; Meyer., 1994; Eler *et al.*, 1995; Gutierrez *et al.*, 1997). Maiwashe *et al.* (2002) reported a comparable maternal heritability value of 0.13 for the same breed. The literature on other breeds reported a maternal heritability value ranging from 10% for the Angus (Meyer, 1994) to 14% for the Hereford (Waldron *et al.*, 1993). The implication is that, for the birth weight, maternal effect exerts a significant influence and should never be ignored. Furthermore, this magnitude also indicates that a greater selection response for the maternal ability can be expected if the selection is based on birth weight because the maternal heritability is at maximum. On the other hand, the direct-maternal genetic correlation obtained in this study is unfavourable, indicating an antagonistic relationship between the direct and maternal genetic effects. This implies that a certain number of genes that favour maternal ability have an unfavourable influence on the growth genes for the calf. However, previous reports show that this correlation does not only reflect a conflicting relationship between the calf's growth and maternal performance but may also be the unaccounted sire by year and sire by herd-year interactions (Robinson, 1996; Meyer, 1997).

As a result, breeding programs selecting animals based on their high additive direct genetic values may result in a serious reduction of maternal performance over time. This result implies that animals with a high direct genetic value for the birth weight might lower their maternal genetic potential for this trait. Comparable estimates were also reported in the literature for the other beef breeds (Koots *et al.*, 1994; Mostert *et al.*, 1998; Schoeman *et al.*, 2000). These results provided a compelling reason to include the maternal genetic effect and its correlation with the direct genetic effect in breeding programs.

4.2.2. Variance component and heritability estimates for the weaning weight

The direct heritability estimate for the WWT obtained from a univariate maternal model (0.43±0.013) was 10% lower than the estimate from a multivariate analysis (0.53±0.012). The increase of the heritability estimate from the multivariate analysis seems related to the fitting of the reduced model containing only the direct genetic effect for the WWT because of the convergence problem associated with a full model for the WWT in the multi-trait analysis. An estimate of direct heritability for the WWT from the univariate analysis was higher than that reported for the Bonsmara in South Africa and Australia (Maiwashe *et al.*, 2002 & Corbet *et al.*, 2006) and also for the other breeds (Meyer, 1992, 1994; Norris *et al.*, 2004 & Mostert *et al.*, 1998). In agreement with the direct heritability estimates obtained in this study, Wasike *et al.* (2006) reported a direct heritability estimate of 0.40 for the WWT of the Boran cattle from a multi-trait model. Likewise, Costa *et al.* (2011) also reported a direct heritability estimate of 0.44 obtained from a multi-trait animal model that included maternal effect as a second random effect. The direct heritability estimate obtained from the multi-trait animal model (0.53) was in accord with the estimate of 0.53 reported by Schoeman *et al.* (2000) for the South African synthetic breeds consisting different levels of Simmentaler genes. Moreover, a comparable heritability estimate was also reported by Kaps *et al.* (1999) for the WWT of the Angus breed from a bivariate analysis with MWT. The high heritability estimate obtained in the current study indicates that a rapid genetic gain in the WWT can be achieved through the exploitation of existing genetic variation.

In addition to that, the maternal heritability estimate obtained (0.06±0.011) in this study was moderate and similar to estimates reported in other studies. Haile-Marriam & Kassa-Mersha (1995) and Mostert *et al.* (1998) reported a comparable maternal heritability of 0.06 and 0.08 for the Boran and Brahman respectively. A maternal genetic effect on the WWT decreased compared to its influence on the BWT, however, it still accounts for 6% of the total phenotypic variation for the WWT. The influence of dams in their calves have not been solely genetic, the current study indicated that 7% of the total phenotypic variation for the WWT was due to a permanent environment effect of the dam. A maternal environmental effect for the South African Bonsmara found in this study is relatively lower than for the other breeds as has been reported in the literature. Several studies reported maternal environmental effects ranging from 0.14 for the Nelore in Brazil (Eler *et al.*, 1995) and the Boran in Ethiopia (Hail-Mariam & Kassa-Mersha., 1995) to 0.23 for the Hereford in Australia (Meyer, 1992). However, these proportions indicated that the maternal effect is markedly important for the WWT. This implies that a calf is still dependant onto the environment provided by the dam. These results confirm the significance of including maternal effects in the evaluation breeding values for the WWT.

4.2.3. Variance component and heritability estimates for the yearling weight

The variance component and heritability estimates for the YWT from the univariate and multi-trait analysis are shown in Table 3. The heritability estimates obtained for the YWT were 0.51±0.017 and 0.53±0.015 form the single trait and multi-trait models respectively. Using the multi-trait model slightly increased the estimate. This improvement perhaps can be attributed to the additional information from the other traits incorporated in the analysis using the multi-trait model. The current heritability estimate for the YWT is somewhat higher than most of the previous estimates for the various breeds using different models. Costa *et al.* (2011) reported a direct heritability estimate of 0.43 for the Angus cattle using a multi-trait animal model, where they were studying the association between MWT measured at 2 to 5 years with WWT and YWT. Neser *et al.* (2012) reported a direct heritability of 0.22 for the Brangus cattle breed obtained from a univariate model. Koots *et al.* (1994), Eler *et al.* (1995), Diop & Van Vleck (1998) and Mostert *et al.* (1998) also reported direct heritability estimates ranging from 0.16 to 0.34 for the different beef breeds. This suggests that progress in terms of the direct genetic components of the South African Bonsmara can be faster than the projection for the Gobra, Nellore (Mostert et al., 1998; Diop & Van Vleck, 1998).

The maternal heritability estimates for the weight traits beyond WWT are rarely in the literature. The present study found that the maternal influence on the YWT for the South African Bonsmara was not a significant source of variation. This indicated that weight at 12 months seems mainly to be determined by the calf's own genes. Hence, this could be the reason why most of the genetic evaluation studies are ignoring maternal influence beyond the weaning age (van Niekerk & Neser, 2006; Bennett & Gregory, 1996). The high direct heritability estimate for the YWT obtained in this study suggests that there is a high genetic diversity and a potential to achieve a rapid genetic change through selection based on breeding values.

4.2.4. Variance component and heritability estimates for the 18 month's weight

The estimated genetic parameters for the 18 month's weight are presented in Table 3. From the LRT, maternal influence was not a significant ($p>0.05$) source of variation for the EWT. The absence of maternal influence signifies that the EWT for the South African Bonsmara is mainly determined by the animal's additive merit. The direct heritability estimates for the EWT obtained from a single and multi-trait analysis were 0.55 and 0.57 respectively. The heritability estimate obtained in this study is higher than most estimates reported for this trait in the literature (Diop &

van Vleck, 1998; Mostert *et al.*, 1998; Pico *et al.*, 2004; Rakwadi *et al.*, 2016). Authors reported estimates ranging from 0.14 for the Gobra in Senegal (Diop & van Vleck, 1998) to 0.22 for the Hereford in Australia (Meyer, 1992) and Brahman in South Africa (Mostert *et al.*, 1998).

The current heritability estimate indicates that a considerable portion of the phenotypic variation is as a result of the additive genetic effect, thus indicating a high genetic variability for the EWT in the Bonsmara population. The implication is that, EWT may respond efficiently to selection.

4.2.5. Variance component and heritability estimates for the mature weight

The variance components and genetic parameters of the MWT for the South African Bonsmara are shown in Table 3 and Table 4. The heritability estimates for the MWT from various models were ranged between 0.40±0.04 and 0.53±0.05. The repeatability value estimated for the MWT was 0.54±0.01. The spearman's sire rank correlation for the MWT based on estimated breeding values of the top 10% sires from the uni-trait and multi-trait models were 54%. This shows that differences in heritability as a result of different models fitted may result in a re-ranking of sires (Boligon *et al.*, 2009).

Analysing asymptotic mature weight in a multi-trait animal model improved heritability by 2% from the estimate obtained from the univariate animal model. In agreement with this result, Kaps *et al.* (1999) reported estimates of 0.44 and 0.52 for a single trait animal model with an asymptotic weight and a bivariate animal model with an asymptotic mature weight and weaning weight, respectively. This improvement in the estimates can be attributed to the fact that a multitrait model assumes that there is a correlation structure between growth traits. Using information from different traits, selection and culling effects are accounted for, subsequently providing better estimates or accuracy of the estimated parameters.

A direct heritability of estimates obtained from the multi-trait model agreed with the estimates in the literature (Bullock *et al.*, 1993; Kaps *et al.*, 1999; Costa *et al.*, 2011). Using a series of bivariate analysis of the MWT and other weight traits, a comparable average direct heritability of 0.53 was reported for the polled Hereford cattle (Bullock *et al.*, 1993). Using early weight traits and repeated mature weights taken yearly from 2 to 5 years of age in a multi-trait model, Costa *et al.* (2011) reported comparable heritability values ranging between 0.50 and 0.56 for the Angus. In contrast, using the multi-trait model on data of the Nellore cattle, Bolligon *et al.* (2009) reported a slightly low heritability estimate of 0.35. The possible reason for this discrepancy is that different breeds in different locations and also different population sizes exhibit different genetic variation.

A direct heritability estimate of 0.40 obtained from the repeatability model in this study was similar to previous reports in the literature. Northcutt and Wilson (1992) reported MWT heritability values of 0.45 and 0.48 with and without a body condition score (BCS). A comparable estimate of 0.47 obtained from a simple repeatability model was reported by Nephawe (2004a) for the South African Bonsmara. In agreement, Crook *et al.* (2010) also obtained the estimates of 0.29 and 0.37 when they were investigating whether cows must be weighed at the calving or weaning of their calves using a repeated model for the South African Simmental cattle. MWT was moderately repeatable (0.54). Nephawe (2004a) reported a slightly higher repeatability coefficient of 0.72. This discrepancy might be attributed to the population size and models used in each of these analyses. A moderate repeatability value for the MWT indicates that there is less variability between the successive measurements within the cow for this trait. The temporary environmental effect accounted for 46% of the total variation.

The estimate of direct heritability obtained from the repeatability model was also comparable to previous reports that used a random regression model. Nephawe (2004a) and Meyer (1999) reported estimates varying from 0.39-0.47, 0.37-0.57 and 0.42-0.49 for the Bonsmara, Hereford and Wokalups respectively. A high heritability estimate obtained for the MWT indicates that there is a high level of genetic variability among cows for this trait in the population. This further indicates that selection for MWT based on a predicted breeding value could yield a rapid genetic change in the direction desired. However, due to the fact that MWT is measured later in the individual's life and also the long generation interval involved, a slow genetic progress can be expected (Boligon *et al.*, 2009). In general, the upward change caused by a direct or indirect selection is not desirable because of increased maintenance cost associated with high cow MWT.

Table 3: Estimate of the variance components and genetic parameters from a univariate and multivariate analysis for growth traits of the South African Bonsmara

	Univariate model					multi-trait model				
Trait[a]	BWT	WWT	YWT	EWT	AMWT	BWT	WWT	YWT	EWT	AMWT
σ^2_a±SE	7.21±0.3	262.85±8.8	429.22±16.6	772.08±34.5	1878.53±262.0	6.31±0.2	295.9±8.4	504.69±17.2	814.35±30.9	2117.26±243.9
σ^2_m±SE	1.66±0.2	38.75±6.5	-	-	-	-	-	-	-	-
σ^2_{am}±SE	-1.11±0.2	-	-	-	-	-	-	-	-	-
R_{am}	-0.32	-	-	-	-	-	-	-	-	-
σ^2pe±SE	-	41.54±6.1	-	-	-	-	-	-	-	-
σ^2_e±SE	6.93±0.2	266.73±5.4	418.97±12.8	619.2±26.3	1808.34±222.2	8±0.1	264.84±5.4	454.55±13.1	618.98±23.4	1858.23±203.8
σ^2p±SE	14.69±0.1	609.87±4.0	848.2±8.3	1391.28±16.9	3686.9±106.7	14.31±0.1	560.74±5.0	959.24±9.3	1433.33±16.8	3975.49±115.5
h^2a±SE	0.49±0.018	0.43±0.013	0.51±0.017	0.55±0.02	0.51±0.064	0.44±0.012	0.53±0.012	0.53±0.015	0.57±0.017	0.53±0.05
h^2_m±SE	0.11±0.012	0.06±0.011	-	-	-	-	-	-	-	-
C^2 ±SE	-	0.07±0.01	-	-	-	-	-	-	-	-

BWT=birth weight: WWT=weaning weight. YWT: yearling weight: EWT=18 month's weight: AMWT= mature cow weight; σ^2_p = phenotypic variance:

σ^2_a=direct genetic variance: σ^2_m=maternal genetic variance: σ^2_{am}=direct-maternal genetic covariance; σ^2_{Pe}= permanent maternal environmental effect:

σ^2_e=residual variance: h_a^2 = direct heritability; C^2 = fraction of total variance due to the permanent environmental effect of the cow. SE=standard error.

Table 4: Estimates of variance components and genetic parameters for mature weight using repeatability model

Model	No. records	Mean±SD	σ_p^2	$h_a^2 \pm SE$	C^2±SE	e^2	R
Repeatability	13130	500.1 ±70.5	2904.5±57.4	0.40± 0.04	0.14 ±0.04	0.46±0.01	0.54± 0.01

No = number of records; Mean = adjusted mean; SD. = standard deviation; σ_p^2 = phenotypic variance; h_a^2 = direct heritability; SE-standard error; c^2 = fraction of total variance due to the permanent effect of the cow; e^2 = fraction of total variance due to temporary environmental effects. R- Repeatability coefficient.

4.3. Phenotypic and genetic correlations among growth traits

The estimates of a direct genetic correlation between the BWT, WWT, YWT, EWT and AMWT are presented in Table 5. A direct additive correlation between all growth traits ranged from medium to high (0.36 BWT & YWT to 0.73 WWT & EWT) and tended to be greater than their phenotypic counterparts. All correlation estimates were associated with lower standard errors, indicating that they are reliable and significantly ($p<0.05$) different from zero. As expected, adjacent traits exhibited a high genetic association and the magnitude decreases as the intervals between the traits widen. Results obtained in this study agree with the literature (Meyer., 1995; Maiwashe *et al.*, 2002; Costa *et al.*, 2011; Neser *et al.*, 2012; Rakwadi *et al.*, 2016). The genetic correlation between MWT and early growth traits was also high and ranged from 0.54±0.051 (with WWT) to 0.66±0.053 (with EWT).

A direct genetic correlation estimate between the MWT and BWT (0.60±0.047) was high. Bullock *et al.* (1993) and Meyer (1995) reported comparable genetic correlation estimates of 0.64 and 0.65, respectively for the polled Hereford. However, the current estimate is lower than the correlation value of 0.85 reported for the Wokalup by Meyer (1995). A direct additive genetic correlation between the MWT and WWT (0.54±0.051) is slightly lower than that of 0.63 and 0.66 reported for the Angus by Kaps *et al.* (1999) and Costa *et al.* (2011), respectively. In addition, an extremely high correlation between the MWT and WWT of 0.80 was also reported by Bullock *et al.* (1993) for the polled Hereford. Boligon *et al.* (2013) however, reported a lower genetic correlation value of 0.30 between the MWT and WWT for the Nelore cattle. A direct additive genetic correlation estimate between the MWT and YWT (0.60±0.055) is within the range of 0.31 to 0.89, reported for the different breeds of beef (Bullock *et al.*, 1993; Meyer, 1995; Costa *et al.*, 2011; Boligon *et al.*, 2013). A direct additive genetic correlation estimate between the MWT and EWT has been found to be 0.66±0.053 and was the highest, with respect to a genetic correlation between the MWT and other growth traits in the current study. This estimate is comparable to a genetic correlation value of 0.69 between the MWT and EWT reported for the Wokalup cattle by Meyer (1995).

The correlations obtained in this study in conjunction with estimates in the literature suggest that MWT may be regulated by the same sets of genes that control early growth traits. The implication of these correlation estimates is that any of the early growth traits can be a good indicator trait for MWT. The estimated high positive genetic correlations indicated that a heavy WWT is genetically associated with a high MWT in the breeding cows. This type of a relationship is not desirable particularly, for the MWT because of the economic losses associated with it. Conversely, even though genetic correlations between the MWT and other weight traits were high, they are far from unity. This shows a practical possibility of increasing or changing early weight traits while maintaining the MWT constant. According to the nature of the MWT trait, collecting its data is expensive and time-consuming and as a result, few animals are kept until mature age, except the breeding stock (Northcutt & Wilson, 1992). Using the knowledge of genetic correlations among growth traits from all animals weighed at early ages but with the missing records for MWT, a genetic evaluation of sires through multiple-trait analysis can be implemented to maintain or change the MWT to a desirable direction.

Table 5: A direct genetic and phenotypic correlation (±standard) for the growth traits of the South African Bonsmara[ab]

Trait[a]	BWT	WWT	YWT	EWT	AMWT
BWT	-	0.49±0.017	0.35±0.021	0.37	0.60±0.047
WWT	0.17±0.012	-	0.69±0.14	0.73±0.016	0.54±0.051
YWT	0.14±0.016	0.46±0.014	-	0.67±0.017	0.60±0.055
EWT	0.14±0.027	0.43±0.017	0.53±0.017	-	0.66±0.053
AMWT	0.08±0.051	0.24±0.054	0.22±0.058	0.24±0.06	-

[a] BWT-birth weight; WWT= weaning weight; YWT= yearling weight; EWT=18 month's weight; AMWT= Asymptotic mature cow weight.

[b] Genetic correlation above diagonal, phenotypic correlation below diagonal

4.4. Genetic trends for growth traits

The regression coefficients of the average predicted breeding values for growth traits on the birth year for the South African Bonsmara are presented in Table 9. The graphical representations of their genetic trends are displayed in figure 2 to 6. The genetic trends were generated from results obtained from the single trait analysis. For the genetic trends, the estimated regression coefficients varied among the growth traits. All traits exhibited a significant genetic change over the years of selection, except for the BWT and MWT. The non-significant trends observed for the BWT and MWT were desirable considering implications associated with the high BWT and MWT on production and reproduction efficiency. A higher BWT is associated with calving difficulties, which may result in mortalities of either or both the dam and the calf (Holland & Odde, 1992). With regard to a high MWT, this trait is directly proportional to nutrient requirement (Williams *et al.*, 2009). The nutrient requirement for a mature cow represents 70% of her expenses (Ferrel, 1988; MacNeil, 2005; Scholtz *et al.*, 2013). Therefore, the logical decision is to employ extensive production system to utilize the naturally occurring vegetation.

Forage is deemed as the cheapest source of feed for beef animals in South Africa and in other parts of the tropical and subtropical regions. However, it may not be enough to support the heavy breeding stock. Evidence from research indicates that failure to meet the nutrient requirements of cows may cause a reduction in body condition and subsequently, a reduction in the reproductive performance (Dunn & Kaltenbach, 1980; Lalman *et al*., 2013). In order to maintain the body condition of cows for optimum reproduction, the producer needs to provide supplementary feed, which directly affect the profit margins. Other studies in literature also showed that a large frame size at maturity is associated with a low reproductive efficiency in beef cattle (Van Niekerk *et al*., 1985; Collins-Lusweti, 2000; du Plessis *et al*., 2006).

The current study demonstrated that the overall breeding programs in South Africa involving the Bonsmara breed so far managed to keep BWT and MWT constant. In accord, Abin *et al.* (2016) reported a non-significant genetic trend of the BWT for the indigenous African breeds (Boran and Drakensberger). The lack of a significant change in the BWT and MWT was surprising, given the genetic correlations and progress observed on the other traits in this study. Perhaps the insignificant trend for the BWT might arise from the fact that animals were selected for a lighter BWT as a proxy for calving ease.

Traditional breeding objectives for beef cattle are based on producing fast-growing animals particularly, for the WWT because it reflects the animal's value in the market. Results in the current study indicate that selection has led to a significant increase in the WWT and EWT over the past decades. Consistent with this report, positive significant genetic trends for the WWT and EWT were registered for the Guadali and Wakwa cattle breeds from Cameroon (Ebangi *et al*., 2000). Likewise, Abin *et al.* (2016) also reported a significant genetic progress on WWT for the Afrikaner, Boran, Drakensberger, Nguni and Tuli breeds in South Africa.

The general pattern of genetic trends for the WWT, YWT and EWT shows that there has been a reasonable improvement in animal's live weight, thus indicating that the initial animals were lighter in weight. The possible reason for these trends is that, in early years, beef animals were primarily kept for draught purposes whilst beef was a secondary product in South Africa (van Marle, 1974). It was only in 1972 that the market changed from selection for other traits to putting more emphasis onto the growth traits, thus forcing breeders to adapt to the new market demand. This explains why the WWT was lower and only started increasing as time went. These results showed that beef producers were efficient in identifying animals with high growth rate and those that reached their MWT earlier. However, the random fluctuations observed in trends indicate a lack of consistency in the selection practice based on estimated breeding values.

Table 6: Genetic trends expressed as average annual weight increase per year (kg/year) accompanied by the relevant standard error.

Trait	Regression coefficient ±SE (kg/year)	R^2	Level of significance
BWT	-0.002±0.003	0.0204	Ns
WWT	0.15±0.02	0.6771	****
YWT	0.051±0.025	0.1618	*
EWT	0.094±0.026	0.3795	***
AMWT	-0.095±0.094	0.0530	Ns

BWT = birth weight; WWT = weaning weight; YWT = yearling weight; EWT = 18month's weight; AMWT = asymptotic mature weight; R^2- coefficient of determination; ****- $P \leq 0.0001$; ***-$P \leq 0.001$; ns- $P > 0.05$. SE=standard error

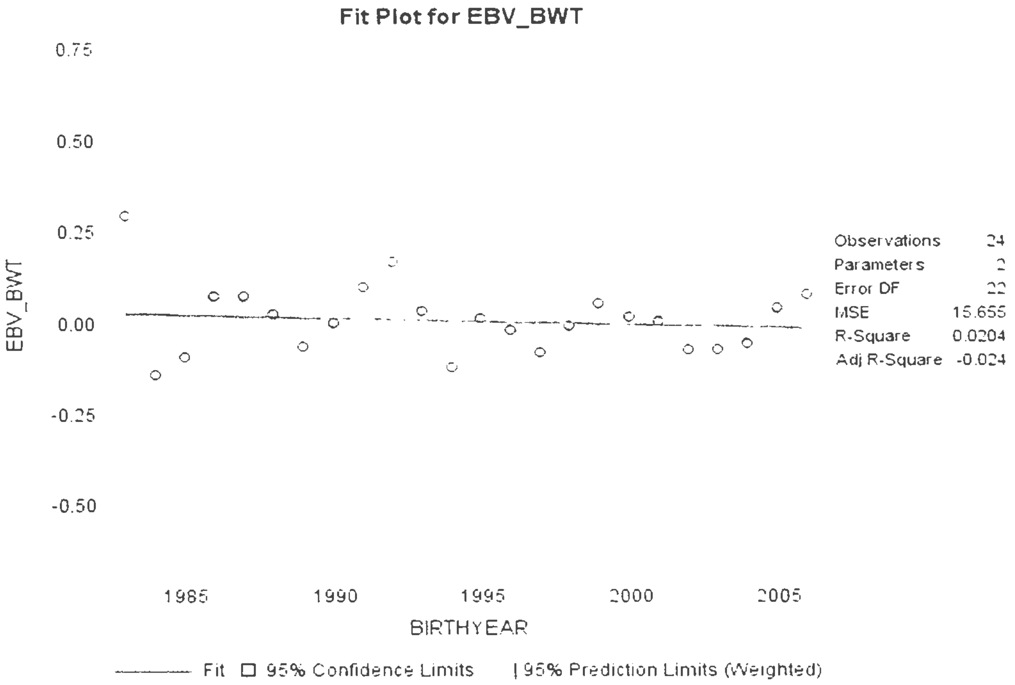

Figure 1: Genetic trend for the mean EBV by year of birth observed for the birth weight.

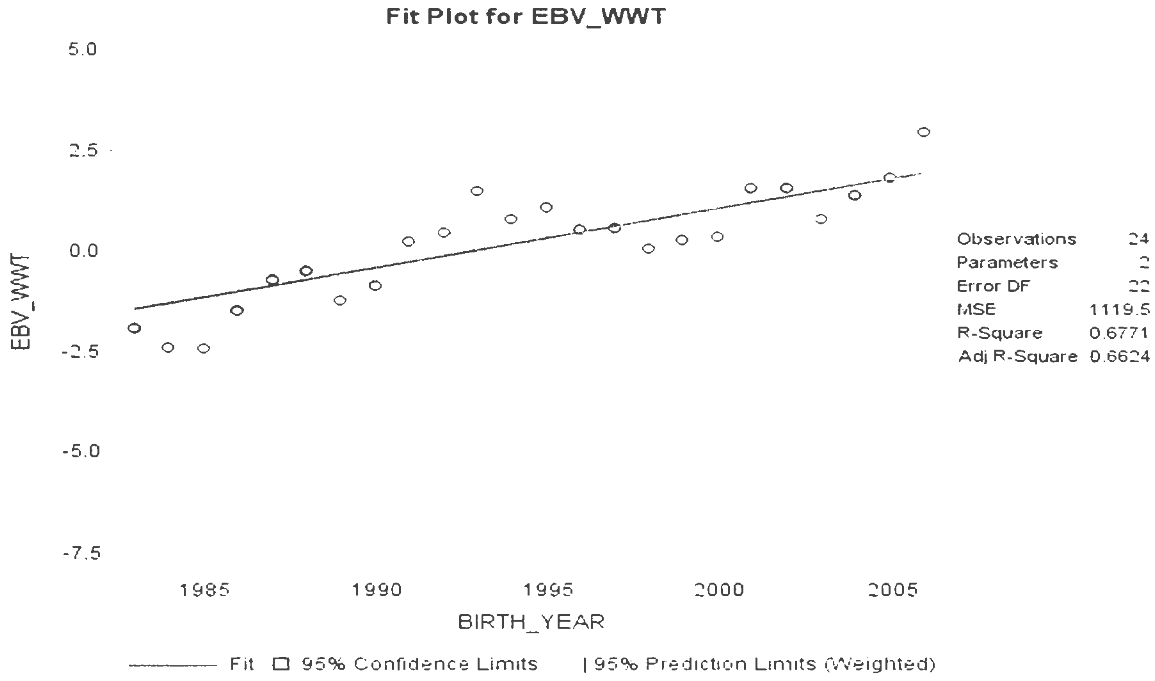

Figure 2: Genetic trend for the mean EBV by year of birth observed for the weaning weight.

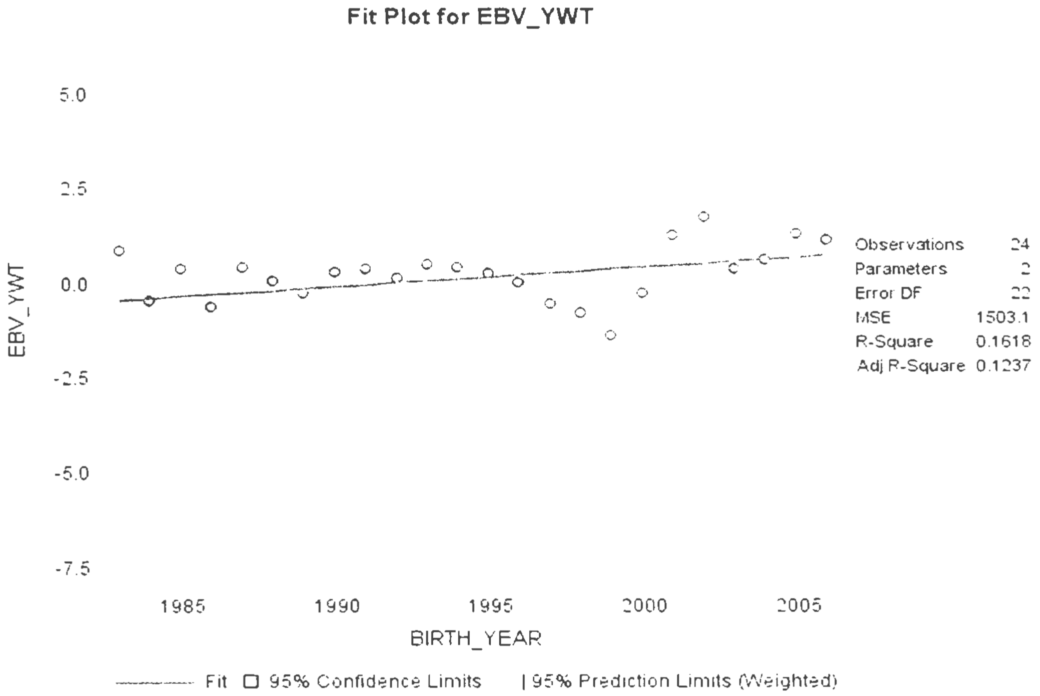

Figure 3: Genetic trend for the mean EBV by year of birth observed for the yearling weight.

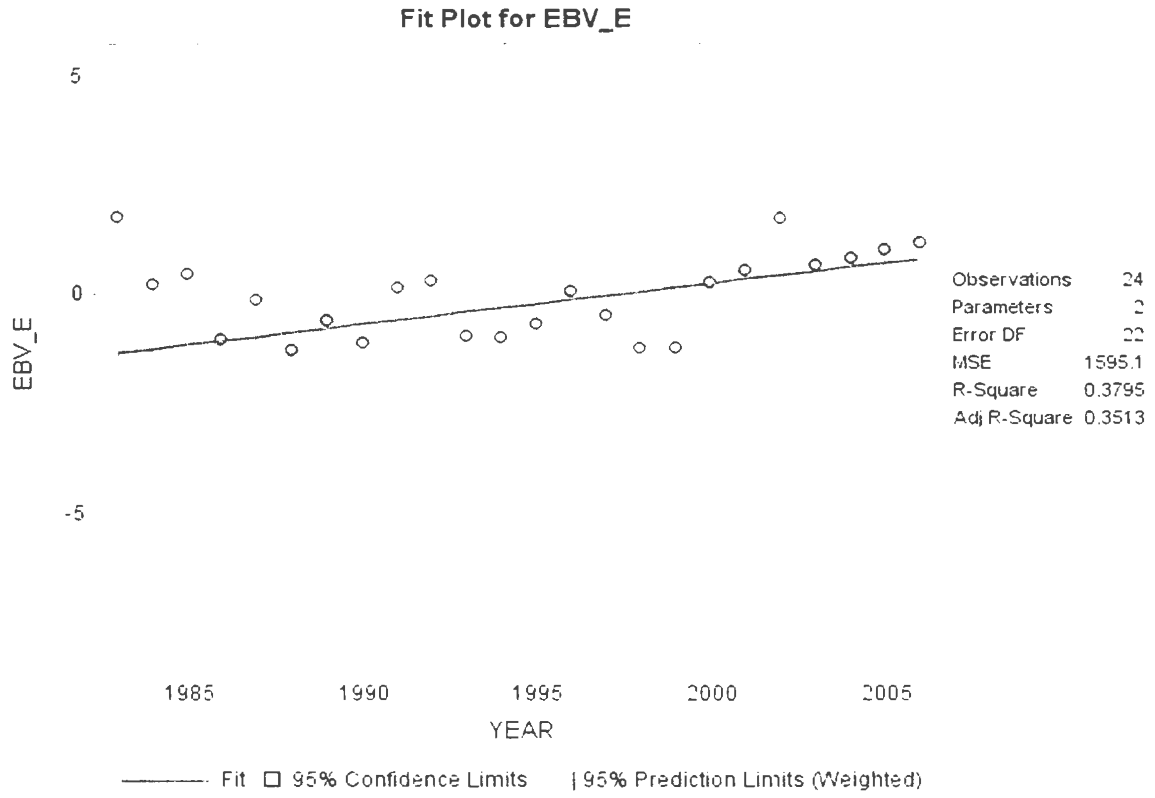

Figure 4: Genetic trend for the mean EBV by year of birth observed for the 18 months weight.

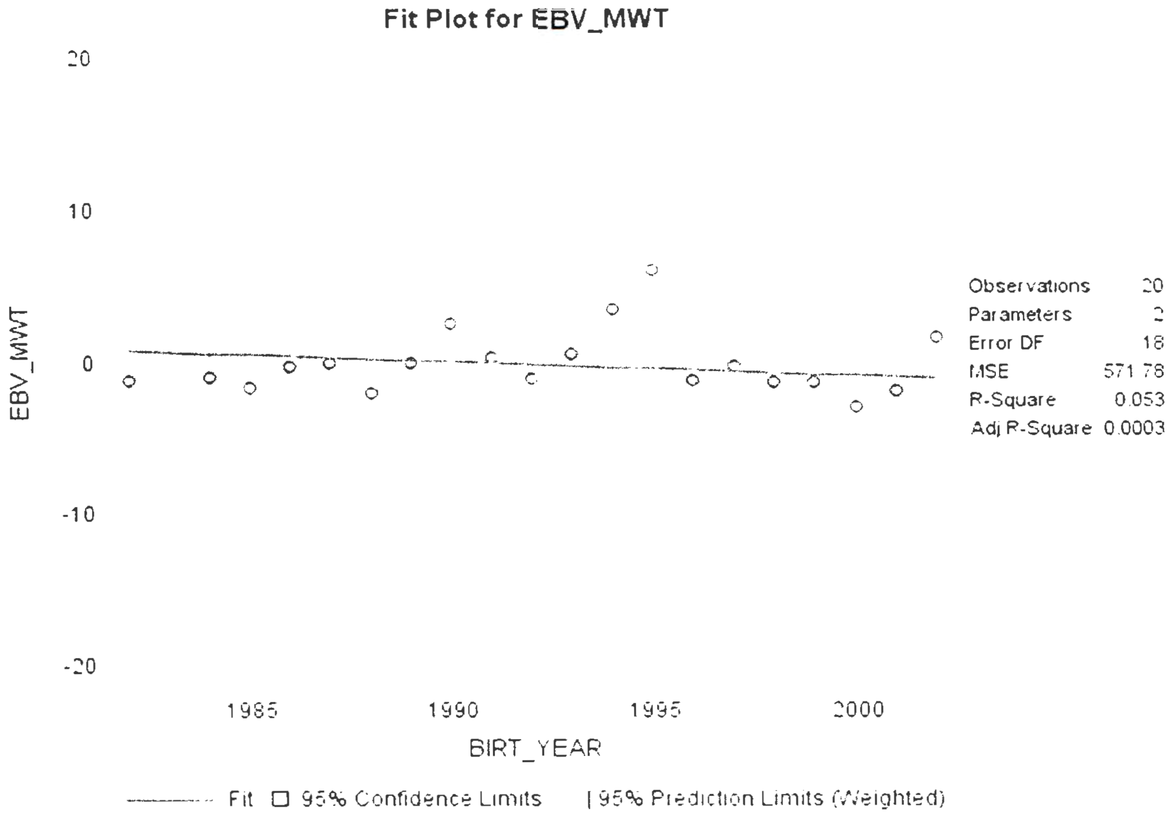

Figure 5: Genetic trend for the mean EBV by year of birth observed for the mature weight.

4.5. The predicted correlated response of the MWT as a consequence of selection based on early growth traits

Using the estimated genetic parameters and the rate of genetic change achieved in early growth traits in this study, the expected indirect genetic responses or changes in MWT are shown in Table 7. All predicted (expected) correlated responses of the annual genetic trends for MWT were all greater than the observed genetic trend presented in Table 6 and Figure 5. The correlated responses estimated for MWT as a function of the genetic correlations with direct responses of the YWT, EWT and WWT were 0.06, 0.10 and 0.22 kg/year respectively. These values indicate that MWT should have shown an increase in response or than the observed zero trend. The reason for the discrepancy could be that cows with heavy weight were probably culled for other production inefficiencies.

In animal breeding, one of the underlining challenges related to a genetic change for one trait is that it affects other traits (Bennett & William, 1994). With regard to that, Pico (2004) pointed out the importance of understanding the genetic relationship to ascertain an effective breeding program. Generally, WWT is of great concern in beef production as it directly affects profitability. However, focusing only on WWT may result in an undesirable correlated response in MWT. The expected response to the selection of MWT as a result of selection based solely on WWT was higher to the reported observed value of 0.01 kg/year for the Nelore breed as was reported by Boligon *et al.* (2013). However, both estimates were not significantly different from 0 ($p>0.05$). The correlated response is a function of the annual genetic change of the trait/s in the selection indices. Therefore, increase in the MWT was expected because of the genetic improvement that was achieved for the WWT and the other traits included in the selection criteria.

Results obtained in this study indicate that breeding programs with selection emphasis on early growth traits in their selection indices will propel MWT to the same direction but at different magnitudes. Single trait selection may result in an undesirable cost increase of the breeding stock in the form of nutritional maintenance (Kress *et al.*, 1969; McMorris & Wilton, 1986; Montaño-Bermudez *et al.*, 1990; Rump *et al.*, 2004; Boligon *et al.*, 2009). Some studies in the literature reported that in some breeds, cows with heavy weight produce lighter calves at weaning and also wean less number of calves in their lifetime compared to cows with lighter weight (Hawkins *et al.*, 1965; Beck *et al.*, 2016b). As for the discrepancy between the observed genetic trend and the expected correlated response based on selection for early growth traits, it can be attributed to the fact that not all farmers select their animals strictly on genetic merit.

Table 7: Expected correlated response in MWT based on genetic correlation and genetic trends achieved in early growth traits.

Traits in selection index	Correlated annual genetic Δ MWT in Kg/year
WWT	0.217 Kg per year
YWT	0.06 Kg per year
EWT	0.097 Kg per year

Correlated response was calculated as $\Delta G_{MWT,i} = r_g(\frac{\sigma_{gMWT}}{\sigma_{gi}})\Delta G_i$, Where, *i* = the trait (growth trait) under selection. r_g = the genetic correlation between the trait under selection and mature weight. σ_{gMWT} = the genetic standard deviation of mature weight. σ_{gi} = the genetic standard deviation for the trait under selection. ΔG_i is the annual genetic change of the trait under selection (Boligon *et al.* 2013).

In addition, the correlated response to selection of MWT as result of the direct selection of early growth traits was also tested under varying truncation points, to estimate the potential genetic change that could have been achieved, should farmers and breeders strictly select animals based on their genetic merits. This study assumed that only the top 5 and 10% were used in a single trait selection of the early growth traits. The correlated response of MWT was calculated based on the heritability of 0.53 (h^2_y) and the phenotypic standard deviation of 93.05 kg (σ_p) obtained from the multi-trait model for MWT in this study, and the prediction results are presented in Table 8.

The expected correlated responses for the different selection scenarios were expressed as an average genetic gain per generation. The expected correlated responses per generation to selection based on early growth traits ranged from 5.32 to 7.82 kg/generation. The corresponding expected correlated response per annum ranged from 1.39 to 2.01 kg. These figures are generally higher than the ones previously presented in Table 7. The reason for this increase is that, Table 8 values represent that potential increase that could be achieved if strict genetic selection was practiced. On the other hand, the values in Table 7 show what we could expect based on the genetic progress already achieved in early growth traits over the past decades.

Selection for EWT could lead to a highest correlated response of MWT compared to selection for any of the other growth traits. The reason for this behaviour is due to the fact that both traits (EWT & MWT) are highly heritable and also have a high degree of genetic association. WWT and YWT also exhibited high heritability (0.53), nevertheless their correlated response was lower as a result of their relative weaker genetic association with the MWT. Arthur *et al*. (1997) studied the correlated responses of growth traits as a result of a divergent selection on the YWT. The findings were that, all growth traits went to the same direction as to that of YWT that was selected for. Even though MWT was not considered in their study, the knowledge of the genetic correlation between MWT and other growth traits shows that it would have behaved in the same way.

According to the current prediction, selection based on WWT would result in a relatively slower correlated response in MWT compared to selection based on YWT or EWT. However, the expected correlated response due to a direct selection for WWT is significant and needs monitoring not to cause an undesirable change in MWT. In terms of the trait that causes the highest correlated response in MWT, the results in Table 8 contradict those in Table 7. The reason for this contradiction is that the correlated responses in Table 7 were regressed from the genetic change already achieved for the early growth traits. On the other hand, in Table 8, the correlated response was computed as a function of genetic correlations, heritabilities and selection intensity to estimate the potential genetic change that could be achieved if the strict genetic selection is practised. As seen from the results, this might not be a major issue when selection is practised with less intensity by many breeders in large-scale breeding programmes of the Bosmara population.

On the other hand, knowledge of genetic correlation between the early growth traits and mature weight is important when there is a desire to select for efficient cows that are able to produce heavy calves at weaning. The traditional approach of selecting cows based on the ratio of calf weight at weaning to cow weight might not yield results because of the theoretically undesirable properties of the ratio (Gunsett, 1986; Iwaisaki, 1989). However, in general, there is an optimum MWT for maximum efficiency within a breed at a given production environment, that provides sufficient energy and does not limit reproduction and milk production that was expressed in the form of calf weight (Jenkins & Ferrell, 1994).

Based on genetic correlations between traits and the expected correlated response of the MWT, early growth traits are good indicators of MWT. Performance records for early growth traits are easy to take and cost-effective. Therefore, an indirect selection for the optimum mature weight using early growth traits in combination with the other economically important traits in selection index may be beneficial to farmers. Even though, there is no change in the MWT of the Bonsmara cattle as result of the past selection on early growth traits; the predicted response in MWT for the indirect selection on early growth traits with strong selection intensities show that there is a potential to bring undesirable change in MWT.

Table 8: The expected correlated response [E(CR)] for mature cow weight from selection based on early growth traits.

Selection indices	Truncation point (%)	Ix	h_y	h_x	r_g	E(CR) kg per generation	E(CR) kg per annum
WWT	5	2.06	0.73	0.73	0.54	6.23	1.63
	10	1.76	0.73	0.73	0.54	5.32	1.39
YWT	5	2.06	0.73	0.73	0.6	6.92	1.81
	10	1.76	0.73	0.73	0.6	5.91	1.54
EWT	5	2.06	0.73	0.75	0.66	7.82	2.04
	10	1.76	0.73	0.75	0.66	6.68	1.74

Where Ix = selection intensity for trait x, h_y = the square root of heritability for trait y (MWT), h_x = the square root of heritability for trait x, r_g = genetic correlation between trait x and y, E(CR) kg per generation = the rate of genetic change in trait y per generation, E(CR) kg per annum = the rate of genetic change in trait y per annum.

4.6. Summary and Conclusion

Genetic parameters for the MWT and early growth traits were obtained in this study. These parameters were derived from both the univariate and multitrait animal models. In addition, MWT was analysed using a repeatability model. Heritability estimates for MWT and early growth traits across the models ranged from moderate to high. MWT as the trait of interest showed high genetic variability in terms of heritability estimates with values ranging from 0.40 to 0.53 across the models. These magnitudes were within the range reported for other beef breeds in the literature. Results obtained from the multivariate analysis verified the theory that a multi-trait model provides estimates with high accuracy than a univariate model. The log likelihood ratio test identified all pre-weaning traits to be influenced by the maternal effects. On the other hand, there were no maternal carryover effects observed beyond the WWT. The genetic correlations ranged from moderate to high. These correlations indicated that selecting to increase any one of the early growth traits may result in an undesirable increase in the MWT unless it correlated response is considered.

The breeding values of animals born in the past two decades were utilized to evaluate the genetic trends in weights from birth to mature age. Findings were that WWT, YWT and EWT exhibited a significant rate of increase per annum in the past 2 decades. As for MWT and BWT, the progress was not significantly different from zero. Relatively, the higher genetic trend observed for WWT indicates that more selection emphasis was given by farmers for this trait. This is not surprising given that WWT determines the animal's value in the market. However, the overall selection pressure seems not to be strong enough to cause a correlated indirect response in BWT and MWT. It is important to keep the BWT and MWT of the breed at optimum levels because of the economic losses associated with their increase. On the other hand, the predicted correlated indirect response in MWT indicates that theoretically, it is possible to cause a huge change if intensive selection is applied on an individual early growth trait without taking into consideration the correlated response. Therefore, future genetic improvement programme of the Bonsmara cattle should consider a multi-trait index selection that is based on prioritized economically important breeding objectives with constraints on traits that have a negative impact on production efficiencies, such as the BWT and MWT.

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