PHENOTYPIC AND GENETIC PERFORMANCE OF TSWANA CATTLE SELECTED FOR EARLY GROWTH TRAITS IN BOTSWANA

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Preface

This study was conducted to evaluate the performance of indigenous Tswana cattle breed in Botswana mass selected for early growth traits, and to suggest the possible alternative breeding program for the future performance improvement of the breed. Four studies were conducted to come up with recommendations for the Tswana cattle national herd in Botswana. The document is made up of seven chapters. The first chapter is the general introduction providing synopsis of the beef production sector in Botswana, a brief description of the breed and outlining the Tswana cattle selection project as a source of data for the studies conducted. A review of literature in all aspects comprising the entire study was incorporated in chapter 2. Chapter 3 comprised of the study focusing on the non-genetic effects influencing early growth traits of the breed, while the genetic variance-covariance components for these traits are presented and discussed in chapter 4. Chapter 5 covers the important environmental and genetic effects on both calf survival to weaning and reproductive traits of the breed. Chapter 6 presents the discussion of the identified environmental and genetic effects on mature cow weight trait of the breed. Based on the results obtained in the current study, some general conclusions and recommendations to the Botswana beef production industry particularly with reference to Tswana cattle breeding are outlined in chapter 7.

It is my wish that the recommendations of this thesis serve as a source of information to provide guidance to Tswana cattle farmers and breeders for the development of effective future breeding program aimed at genetic improvement of the Tswana cattle national herd.

Declaration

I, **Mogomotsi Innocent Keoletile**, declare herewith that the thesis entitled**, Phenotypic and Genetic Performance of Tswana Cattle Selected for Early Growth Traits in Botswana,** which I herewith submit to the North West University as fulfillment of the requirements set for the **Doctor of Philosophy** degree in **Animal Science**, is my own work and has not already been submitted to any other university. I understand and accept that the copies that are submitted for examination are the property of the University.

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Date 24-04-2018

Abstract

The objective of this study was to evaluate the phenotypic and genetic performance of Tswana cattle mass selected for early growth traits. The approach will help optimize genetic selection in Tswana cattle through identification of important genetic and none genetic factors influencing growth, reproductive and calf survival traits and ultimately aid in redesigning active breeding program for this breed. Non-genetic effects on growth, average daily gains (ADGs), mature cow weight (MCW), reproductive and calf survival to weaning traits were identified so that they can be adjusted during the genetic analyses of these traits. Phenotypic and genetic analyses for ADGs and growth traits were conducted using 7223 records of animals which were born between 1996 and 2013 from 1662 dams and 188 sires in 54 contemporaries using both univariate and bivariate animal models. Analyses of environmental and genetic effects for calf survival traits were done using 7223 records of animals which were born between 1996 and 2013 from 1659 dams and 188 sires in 54 contemporaries. Analyses of environmental and genetic effects for age at first calving were done using 818 records of animals born between 1998 and 2013 from 611 dams and 136 sires in 49 contemporaries, while calving interval analyses were done using 1804 records of cows born between 1999 and 2013 from 496 dams and 121 sires in 45 contemporaries. Analyses of environmental and genetic effects for mature cow weight trait were done using 19301 records of cows born between 1996 and 2010 from 610 dams and 137 sires in 54 contemporaries.

Growth traits and average daily gains were analysed using mixed animal models that include and exclude maternal genetic effects fitted using the Restricted Maximum Likelihood (REML) procedures in Animal and Sire Restricted Maximum Likelihood (ASREML) program. The best model for each trait analysis was selected based on a log likelihood ratio test (LRT). Growth traits analysed were birth weight (BWT), weaning weight (WWT), yearling weight (YWT), eighteen months weight (EWT), pre-weaning average daily gain (ADG1) and post weaning average daily gain (ADG2). Reproductive traits analysed were age at first calving (AFC) and calving interval (CI). Age at first calving was analysed using univariate animal model while calving interval was analysed using repeatability model. Mature cow weight trait was also analysed using repeatability model. Calf survival to weaning was analysed as binomial trait using generalised mixed linear logistic model with logit link function in the ASREML program.

The identified significant environmental effects for growth traits and ADGs were sex of the animal, dam age, selection line and contemporary group while for reproductive traits the significant effects were selection line, calving year and season. Calf survival to weaning was significantly influenced by calf sex, selection line, calf-birth weight and dam age while the significant environmental effects for mature cow weight were selection line, cow age and contemporary group.

Heritability estimates for growth traits ranged from 0.12±0.03 for BWT to 0.45±0.03 for EWT while the estimates obtained for ADGs were 0.24±0.03 and 0.31±0.04 for ADG1 and ADG2, respectively. The estimated heritability values for reproductive traits were 0.07±0.02 for CI and 0.10±0.07 for AFC. The respective heritability estimates for calf survival to weaning and mature cow weight traits were 0.07±0.05 and 0.26±0.03. Permanent maternal environmental effects were significant for WWT and ADG1. Substantial maternal genetic effects were observed in BWT, WWT and ADG1. Genetic correlations among growth traits and ADGs ranged from 0.19±0.07 between BWT and ADG1 to 0.99±0.02 between WWT and ADG1. Phenotypic correlations among growth traits and ADGs ranged from 0.19±0.01 between BWT and ADG1 to 0.94±0.01 between WWT and ADG1. Genetic correlations between growth traits and MCW ranged from 0.15±0.17 between BWT and MCW to 0.84±0.19 between YWT and MCW. Phenotypic correlations between growth traits and MCW ranged from 0.15±0.04 between BWT and MCW to 0.31±0.03 between EWT and MCW.

Substantial genetic variations were observed in all growth traits and ADGs suggesting that genetic improvement can be attained through selection for growth rate. High genetic correlations between growth traits and ADGs indicated that selection for one of these traits may result in indirect correlated response on the other traits. Low genetic variability obtained in reproductive traits and calf survival to weaning trait indicates that improvement of these traits through genetic selection may be slow. The existence of significant genetic variability and moderate repeatability in mature cow weight trait coupled with high genetic correlation between this trait and early growth traits suggest that caution should be exercised when selecting for growth traits to avoid undesirable resultant change in mature cow weight.

Improved performance in Tswana cattle breed can be attained through selection based on breeding values estimated from multi-trait analysis. Economic values should be established for growth and reproductive traits of this breed and selection indices consisting of these traits should be considered in future breeding efforts.

Keywords: Tswana cattle, selection, growth traits, genetic parameters

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Chapter 1

General Introduction

1.1. Brief account of beef production in Botswana

Beef production is the major source of export income in Botswana, comprising about 20% to 25% of the country's total export. In its effort to develop the beef industry while on the other hand preserving biological diversity, the government of Botswana through Department of Agricultural Research (D.A.R.) under the then Animal Production Research Unit (A.P.R.U.) now Animal Production and Range Research Division (A.P.R.R.D.) decided to emphasize on the need for advanced indigenous livestock research and development, especially commercially orientated beef production systems (APRU, 1992). However, due to the more favourable price of beef in European markets, local beef producers tend to concentrate on keeping heavy exotic beef breeds in order to maximize profit despite high maintenance costs and low survival under stressful climatic conditions found in the country. This has practically led to the gradual replacement of cattle breeds native to the country, especially Tswana breed. The breed reduced in proportion from almost 80% in 1970s to roughly 50% of the national herd in 1990s with the National Beef Recording Scheme recording few Tswana cattle in commercial ranches which clearly indicated that the breed is unpopular with commercial beef producers (APRU, 1993).

1.2. Tswana cattle breed characteristics and its role in beef production

Tswana cattle, which are of the Sanga type, are generally multi-coloured i.e. red pied, black or black pied and are long-horned. The breed is well built, showing good fleshing with moderately long legs. On average, the mature female and male weigh approximately 400kg and 580kg respectively (APRU, 1992). Figures 1.1 to 1.3 below show multi-coloured mature cows with their calves while Figures 1.4 and 1.5 show five year old and six year old mature bulls respectively. The breed has the ability to perform well under hot and dry environments and has high levels of tick and heat tolerance even though it suffers reduced recognition from beef producers as they prefer large framed exotic breeds that can deposit more beef. However, due to the breed's ability to perform better under harsh conditions and limited feed resources, it is preferred by newly established and small scale beef producers as they are usually resource limited. Furthermore, a lack of utilization plan for similar breeds all over the world tends to decrease the diversity of animal genetic resources available for future generations.

Figure 1.1: Red coloured mature Tswana cow with her four months old calf

Figure 1.2: Example of a black and white mature Tswana cow with her four months old calf

Figure 1.3: Example of red and white coloured mature Tswana cow with her five months old calf

Picture 1.4: Example of a five year old red and white coloured mature Tswana bull

Figure 1.5 Example of a six year old black pied coloured mature Tswana bull

Although the breed has been overlooked by commercial farmers, the majority of subsistence farmers have always given their preference to it. However, the most limiting factor to the improvement of Tswana cattle has always been a lack of proper research carried out on strategies that can be employed as well as parameters associated with their production performance. It is only in the early-1990s that Animal Production and Range Research Division (APRU, 1993) under the Department of Agricultural Research (DAR) started investing its considerable efforts in the improvement of this breed. A number of projects were established in different government ranches distributed throughout the production areas in the country to improve both growth and reproduction potential of the breed.

As one of the projects set to improve the production potential of the Tswana cattle breed and to promote the breed to local commercial cattle producers, a two line selection project was set in 1995 in one of the department's government ranches.

1.3. Description of Tswana cattle selection project as a source of data for the current study

In 1995 the Tswana Cattle selection project was initiated by the Botswana Department of Agricultural Research (APRU, 1999). In this project Tswana cattle were mass selected for two growth traits being weaning weight at seven months (selection line 1), and mature weight at eighteen months (selection line 2) with a population randomly selected at eighteen months as a control (selection line 3) kept concurrently with the two selected populations. A one stage selection was performed annually after which line 2 and control replacement heifers were allowed to join the breeding herds immediately while the line 1 replacement heifers were allowed to join the breeding herd in the following year after reaching eighteen months of age. Figures 1.6 and 1.7 show eighteen months old male calves from weaning weight selection line and eighteen months selection line respectively.

Figure 1.6: An eighteen months old Tswana male calf selected for weaning weight.

Figure 1.7: Eighteen months old Tswana male calves selected for eighteen months weight.

Replacement animals were selected on their own growth performance from both lines and young bulls were allowed to mate after three years of age. In the selection lines, mass selection was practiced based on the animal's weight index. The indices were derived as the difference between the animal's own weight for a trait and the average weight of the contemporary group for a trait. Animals born within the same month were weaned together as a contemporary group. Therefore, before the indices were calculated for both weaning weight and eighteen months selection lines, the weights of calves were adjusted to 205 days and 540 days respectively for the two sexes separately to eliminate the differences in individual age due to birth date differences.

1.4. The need for Tswana cattle breed evaluation

Since the goal of production for most beef cattle producers is sustainable profitability combined with the appropriate level of economic risk (Enns & Nicoll, 2008), the optimal use of expected progeny difference and breeding values together with the determination of the ultimate economic importance of each trait is very vital (Garrick & Golden, 2009). Although the concept of relating genetic evaluation with the economics of production has long been in existence (Enns & Nicoll, 2008), it is yet to be effectively utilized in the beef production industry outside the research settings in most countries, Botswana included. This is primarily due to unavailability of information on both genetic parameters and genetic response to selection for utilization in an amalgamated seed-stock-commecial beef production system, where selection decisions are based on indexes comprising two or more traits for a long term genetic change in commercial beef breeding program. However, since the implementation of Tswana cattle selection, APRRD has generated a reasonable amount of baseline data on productivity of indigenous Tswana cattle. As a result, there is a need for the evaluation of selection response achieved on different traits of economic importance as a result of the two selection strategies implemented, compared to the control population. There is also a need to generate genetic parameters for various traits that can be used in the development of future economic breeding objective for Tswana cattle in Botswana. Therefore, the current study attempted to utilize some of the data generated from Tswana cattle selection project to advise the future breeding objective for this breed.

The main purpose of the current study was therefore to investigate if the two selection strategies yielded any genetic changes in growth, reproductive and calf survival traits of the Tswana cattle breed when compared to the non-selected line. The specific objectives were:

i. To compare the phenotypic growth performance in the three groups of Tswana cattle (selected at weaning, eighteen months of age and the randomly selected control).

ii. To estimate variance-covariance components and genetic parameters for growth traits in Tswana cattle breed.

iii. To determine the environmental and genetic factors affecting reproductive traits and calf survival to weaning in Tswana cattle breed.

iv. To determine the environmental and genetic factors influencing mature cow weight trait in Tswana cattle breed.

Chapter 2

General literature review

2.1. Introduction

The aim of the beef production industry is to maintain profitability with the appropriate levels of economic risk. Therefore, it is important to evaluate and quantify the genetic progress that can be achieved through long term selection for economically based multi-trait breeding objective (Enns & Nicoll, 2008). On the other hand, very few studies on the selection for economic traits have been reported despite the opportunity that selections afford in changing the gene frequency in a population and hence altering the population's performance (Irgang et al., 1985). As a consequence, many studies have been conducted in recent years, across the world, with the aim of evaluating and quantifying the phenotypic and genetic response to selection by traits of economic importance in different beef cattle breeds (Chevraux and Bailey, 1977; Davis, 1987; Mercadante et al., 2003; Koch et al., 2004; Yilmaz et al., 2004; Enns and Nicoll, 2008; Boligon et al., 2010; Cervantes et al., 2010; Boligon et al., 2013; Shumbusho et al., 2013). This has led to validation of theoretically predicted direct and correlated responses, to estimate genetic parameters and to define more efficient breeding programs.

Besides, the productivity of a cow over her entire herd life is determined principally by her fertility, maternal ability, health, survival of herself and her calves (Martinez et al., 2004). Calf survival has a major influence on the profitability of cow-calf beef production systems (Phocas et al., 1998). The mortality of calves reduces beef income and adds significantly to beef production costs (Cervantes et al., 2010). Dystocia negatively affects calf survival via multiple mechanisms including prolonged hypoxia and potential traumas (Lombard et al., 2006). In dairy cattle, a calving ability index including calf survival and calving ease for sire selection has been proposed (Cole et al., 2007). In tropical regions where zebu cattle are predominant, calf mortality prior to weaning is reported to be high, accounting for close to 33% of calf crop losses (Magalhaes Silva et al., 2017). Despite the negative impact of calf mortality on the profitability of beef cattle farms, few studies have evaluated the genetic and environmental influence on preweaning calf mortality in zebu breeds (Schmidek et al., 2013). This has been confirmed by Magalhaes Silva et al. (2017) who also stated that few studies focused on calf mortality which is reported to be ranging from 8% to 10% in Brazilian beef herds. Genetic studies on calf survival in beef cattle are also generally scarce (Goyache et al., 2003; Tarres et al., 2005; Guerra et al., 2006). However, there is information on the genetic relationships between calving ease and calf survival basically being found in dairy cattle (Eriksson et al., 2004; Hansen et al., 2004; Cole et al., 2007). Therefore, more studies on genetic and environmental factors influencing calf mortality in different beef cattle breeds are essential.

Furthermore, the application of genetic philosophies in selective breeding of farm animals has steered major enhancements and enormous financial returns to the beef cattle production sector. However, in general early growth traits (e.g. weaning and other market or slaughter weights) augmented over the years, both breeders and scientists have argued whether mature cow sizes and or weights have also been amplified to extremes. The circumstance that the nutrients required to reach and maintain mature weight is a major cost in the beef cattle production system (Nephawe, 2004) is of pronounced concern. Therefore, selection to maintain or constrain mature cow weight while increasing marketable weights of calves at weaning and at slaughter is an essential process that entails good estimates of genetic parameters and correlations amongst weights at different ages or growth stages (Kaps et al., 1999; Nephawe, 2004; Crook et al., 2010; Boligon et al., 2013). The growth of an animal to a mature age is a longitudinal course in which an animal undergoes a continuous increase in size or weight over time until reaching an optimum point (plateau) at maturity (Nephawe, 2004). Such a course can be expressed using a set of size-age points describing a distinctive curve hence resulting in a set of several, extremely associated measures (Meyer, 1998; Nephawe, 2004; Randel and Welsh Jr., 2013).

2.2. Effects of selection for growth traits on reproductive traits

In a study conducted to evaluate and quantify the genetic progress achieved in New Zealand Angus herd through long term selection, Enns & Nicoll (2008) reported annual genetic change in both direct and maternal breeding values for weaning, yearling, and mature weights. They also stated the existence of annual change in the total number of calves weaned per cow's entire lifespan and further concluded that selection based on indexes developed to predict an economically based multi-trait breeding objective would yield the desired genetic changes. Likewise, Koch et al. (2004) also reported genetic response to selection in growth traits of Hereford cattle in the United States of America.

While some studies have indicated negatively correlated responses on reproduction of cows due to selection for growth rate (Albera et al., 2004; Luna-Nevarez et al., 2010; Berry & Evans, 2014), there are several other studies involving both field and experimental selection data that have refuted this negative correlation (Knights et al., 1984; Aaron et al., 1986; Fiss & Wilton, 1989; Smith et al., 1989; Gregory et al., 1995; Bennett et al., 2008; Boligon et al., 2010), indicating that selection of young animals for increased body weights did not have any significant opposing effect on the reproductive performance of the cow. However, a lot of these recent studies were carried out in less restrictive environments than tropical ones and the effects of selection for greater body weights on reproductive performance of cows have not been well proven and documented in populations of *Bos indicus* as Mercadante et al. (2003) confirmed. Consequently, other research findings have suggested that economically important reproductive traits be taken aboard when designing selection programs for enhanced growth traits (Niebel & Van Vleck, 1982; Smith et al., 1989; Gutiérrez et al., 2007; Santana et al., 2013).

Furthermore, it has been stated that the economic importance of reproductive traits may surpass that of production traits with number of calves weaned per cow mated and calving interval being of significant economic importance and a decrease in age of heifer at first calving increasing the cow's lifetime productivity (Yilmaz et al., 2004). In a study where selection was based on breeding values estimated from multi-trait model (i.e. two-year calving difficulty scores, birth weight, weaning weight and post-weaning gain) breeding objective, it was reported that two-year old heifer's calving difficulty was effectively reduced while on the other hand yearling weight was significantly increased (Bennett et al., 2008). The same authors also revealed that during selection, some changes were caused by typical genetic correlations resulting from common physiological pathways or chromosomal associations while others resulted from directly selecting for an indicator trait like in the case where selection for birth weight caused associated changes attained in calving difficulty. These findings indicate that both additive genetic variances and genetic correlations should be taken into consideration when designing a breeding objective especially where there is strong association between the traits of interest and the others that are not intended to be negatively influenced (Bennett & Gregory, 2001), which is consistent with the findings reported on the association between body weights and scrotal circumference of Nellore cattle by Boligon et al. (2010).

2.3. Importance of genetic effects on reproductive traits of beef cattle

Reproduction is considered the key component influencing the production competence of beef cattle (Dickerson, 1970; Dziuk and Bellows, 1983; Koch and Algeo, 1983). An outstanding reproductive ability is principal to any commercial and maintainable national beef cattle herd (Melton, 1995). Regardless of the low heritability estimates generally presented for most of reproductive traits in beef cattle (Koots et al., 1994; Martínez-Velázquez et al., 2003; Donoghue et al., 2004) and dairy cattle (Pryce and Veerkamp, 2001; Berry et al., 2013) the existent genetic variation in these traits has been described to be adequately large enough (Gutiérrez et al., 2002; Berry et al., 2003; Goyache et al., 2005) to warrant effective breeding programs for the improvement of reproductive performance. Although many studies have endeavored to quantify the ratio of phenotypic variances that is due to additive genetic effects in reproductive performance of beef animals, these studies have generally been limited by the number of animals or herds used in the analysis (Evans et al., 1999; Phocas and Sapa, 2004; Urioste et al., 2007). Furthermore, few studies were conducted (Gregory et al., 1995; Roughsedge et al., 2005; Gutiérrez et al., 2007) to evaluate the impact triggered by genetic selection for other economically important traits on reproduction performance; these studies were mainly limited in size and hence lack precision in the estimated parameters, particularly the genetic correlations.

Information on these genetic elements forms a crucial part in assessing the possibility to genetically improve reproductive performance in beef cattle herds (Berry and Evans, 2014).

2.4. Heritability estimates for calf survival in beef cattle

Heritability is essential in computing the anticipated responses to selection and to predict breeding values in traits of economic importance. Deese and Koger (1967) and Buddenberg et al. (1989) reported statistically higher estimates of heritability for calf survival when sire model binomial estimates were transformed to the probit scale. However, average weighted threshold model heritability estimates of 0.17 and 0.10 were presented by Koots et al. (1994) for calving rate and perinatal mortality, respectively. In addition to that Riley et al. (2004) reported heritability estimate of 0.06±0.05 for preweaning survival of Brahman calves. Guerra et al. (2006) also estimated corresponding preweaning heritabilities of 0.049±0.022, 0.160±0.058, and 0.190±0.078 for calf survival from linear, threshold, and logistic models in multibreed beef cattle population. Cervantes et al. (2010) also reported direct and maternal heritabilities of 0.024±0.007 and 0.034±0.011, respectively for Asturiana de los Valles beef cattle breed. In general, most estimates of heritability reported for calf survival are relatively very low. This may indicate that the trait is more affected by environmental factors than by genetic effects (Magalhaes Silva et al., 2017).

2.5. Effects of selection for economic growth traits on mature cow weight

Most beef cattle breeding programs are designed to considerably improve the production competence of the herd, with preference being given to selection based on data collected at the commencement of the growth or development phase such as birth weight and weaning weight or gains at certain ages. Mature cow weight is an important measurement used to assess and regulate mature cow size. The application of cow weight measurement is also useful in selection for efficiency where mature cow weight has a significant impact on the feed or nutrient requirements, reproduction and other physiological traits of the breeding cows (Garrick, 2006; Dickerson, 1970; McMorris and Wilton, 1986; Montaño-Bermudez et al., 1990; Miller and

Wilton, 1999; Shorten et al., 2015). The high maintenance costs associated with large mature cows makes this trait an indispensable component determining the efficiency of beef cows (Fiss and Wilton, 1992; López de Torre et al., 1992; Regatieri et al., 2012). However, selection of young animals for advanced early growth weight traits have been reported to result in animals being heavier at birth and at mature age due to correlated response (Boligon et al., 2010; Pedrosa et al., 2010; Shorten et al., 2015).

Archer et al. (1998) and Forni et al. (2007) reported an increase in mature weight due to an indirect response to selection for increased growth rates in Angus and Nellore cattle, respectively. Jenkins and Ferrell (1994) described mature cow weight as an essential trait in beef cattle breeding programs because of its strong association with the expenses for the maintenance of dams. In addition, large females have been reported to be less resourceful in relation to competence in reproductive and physiological performance (Montano-Bermudez et al., 1990; Owens et al., 1993; Silveira et al., 2004). Dams of heavier mature weights are said to be particularly undesirable in production systems based exclusively on pasture. Genetic evaluations for mature cow weight of most beef cattle have already been done (Boligon et al., 2013). However, studies conducted on correlations between traits commonly included in selection indices and the indices themselves with mature cow weights of beef cattle are limited (Boligon et al., 2010; 2011; Pedrosa et al., 2010). In view of the importance of mature cow size in beef cattle production system, mature cow weight should be evaluated, monitored and controlled to avoid excessive increase in cow size due to an indirect response to selection of animals with a superior early growth potential (Boligon et al., 2010).

2.6. Some approaches used in analysing mature cow weight trait

A number of approaches have been proposed for the analysis of mature cow weight data, the methods range from simple repeatability models to complex multivariate models. The simplest repeatability models consider several records taken at different stages (ages) as a realization of the same genetic trait with constant variance. However, in multivariate models approach all the recorded measurements of an individual animal are treated as different traits with heterogeneous variances. Recently, random regression models have been proposed for the analysis of longitudinal data (Kirkpatrick et al. 1990; 1994). In beef cattle the method was outlined by Varona et al. (1997) and was used by Meyer (1999; 2000; Nephawe, 2004) and Arango (2002). With the random regression models approach, models with unlimited dimensions are used with the phenotype of an individual represented by a continuous function of time. The core advantageous characteristic of random regression models is their capacity to express responses reliant on time as a linear function of a set of covariates (Schaeffer and Dekkers, 1994; Jamrozik et al., 2010; Ferreira et al., 2015). Of late, random regression models approach has rapidly become the most preferred approach in analyzing longitudinal data in the field of research in general. Crook et al (2010) fitted uni-trait and bi-variate animal models that made provision for up to four weights per cow when analyzing mature cow weight at calving and at weaning in South African Simmental cattle.

2.7. Heritability estimates for mature cow weight

Nephawe (2004) estimated heritability values ranging from 0.39 to 0.47 for monthly weights of Bonsmara cows while Meyer (1999) estimated heritability values that ranged from 0.37 to 0.57 for Hereford cows, and from 0.42 to 0.49 for Wokalups using random regression models. The latter further reported the values of permanent environmental variances as a ratio of the total phenotypic variance ranging from 0.30 to 0.42. However, the two authors reported the respective heritability estimates of 0.41 and 0.31 for Bonsmara and Hereford using simple regression models. In their evaluation of maternal traits, Roughsedge et al. (2005) estimated heritability values of 0.21±0.10, 0.19±0.09, 0.40±0.14 and 0.39±0.16 for mature cow weight in Aberdeen Angus, South Devon, Limousin and Simmental, respectively. Croock et al. (2010) obtained heritability estimates of 0.29±0.04 and 0.37±0.04 for mature cow weight at calving and cow weight at weaning, respectively in South African Simmental cattle. The same authors further reported genetic correlation estimate between the two cow weight traits of 0.95±0.03, with a residual correlation value of 0.61±0.02. Boligon et al. (2013) reported heritability estimate of 0.44±0.018 for Nellore cattle. The same author further reported positive genetic correlations between mature cow weight and weaning and yearling indices of medium magnitude (0.30±0.01 and 0.31±0.01, respectively. An increase in mature cow weight as a result of correlated response to selection for superior growth rates in Angus and Nellore cattle, respectively has also been reported by Archer et al. (1998) and Forni et al. (2007).

2.8. Summary

Since most researchers emphasized the impact of selection for increased early growth traits on reproductive traits of beef cattle (Smith et al., 1989; Albera et al., 2004; Gutiérrez et al., 2007 Luna-Nevarez et al., 2010; Berry and Evans, 2014), it will be advisable to take the two traits and their associations into consideration when evaluating the performance of Tswana cattle breed. Therefore analyses of genetic parameters and correlations among growth and reproductive traits will be of great importance in an attempt to redesign the future multi-trait breeding objective for Tswana cattle breed.

It has also been revealed in the literature (Varona et al., 2009; Guerra et al., 2006; MacNeil, 2005) that calf survival has a huge impact on herd economic efficiency in beef cattle production, the trait is said to have a binomial phenotypic expression with anticipated fundamental continuous genetic and environmental influences (McCurley and McLaren, 1981; Bullock et al., 1993; MacNeil, 2005). Despite the trait's vitality on herd efficiency, relatively low estimates of heritability for calf survival have been reported (Koots et al. (1994; Riley et al., 2004; Guerra et al., 2006). Due to the crucial contribution of cow fertility and calf survival in beef cattle production systems and the relatively low number of heritability estimates presented in literature (Guerra et al., 2006; Cervantes et al., 2010; Koots et al. (1994; Riley et al., 2004) it will be of great importance to estimate heritability for calf survival in Tswana cattle breed mass selected for early growth traits so as to find out how this trait responds to selection for these growth traits.

Beef cattle breeding programs are mainly aimed at increasing the production efficiency of the herd. Therefore, priority is given to selection based on data collected at the beginning of the growth phase such as birth weight or gains at certain ages. As a result, selection of young animals for advanced growth traits may lead to heavier animals at birth and at adult age due to indirect correlated response (Boligon et al., 2010; Pedrosa et al., 2010). In addition, it has been reported that large females are less efficient in terms of both reproductive and physiological performance (Montano-Bermudez et al., 1990; Owens et al., 1993; Silveira et al., 2004). Therefore, considering the importance of mature cow size in natural pasture based beef cattle production systems, mature cow weight should constantly be evaluated and monitored to avert an unfavorable increase in cow size due to an indirect response to selection for superior growth potential (Boligon et al., 2010).

Chapter 3

Phenotypic response to mass selection for weaning weight and 18-month weight in Tswana cattle

3.1. Introduction

Although the Tswana cattle breed is highly adapted to the harsh environment of the Southern African region, profitability from Tswana cattle farming is limited by biological and socio-economic factors. The market weight of Tswana cattle weaners, yearlings and eighteen months is inferior to that of other local beef breeds, pure exotics and their crosses (APRU, 1993). As a result, the breed has been overlooked by commercial farmers although the majority of subsistence farmers have always given preference to it. The most limiting factor to the improvement of Tswana cattle has been a lack of proper research on strategies that can be employed as well as parameters associated with their production performance. It was on this basis that a two line mass selection project i.e. selection for weight at weaning and at eighteen-months of age using phenotypic index, was set in 1995 at the Department of Agricultural Research (DAR) in Botswana (APRRD, 1999). The project has since generated a reasonable amount of data and the current study attempted to utilize this data to provide guidance on the future breeding objective for Tswana breed.

Selection of animals for growth traits has proven to result in enhanced growth performance (Kahi and Hirooka, 2007; Bennett et al., 2008; Enns and Nicoll, 2008). In addition to that, McHugh et al. (2014) asserted that genetic evaluations provide information to aid in breeding decisions that increase long-term performance of animals and herds. Furthermore, growth traits of animals are determined by both genetic potential and environmental influence (Koch et al., 2004) described. As a result, accurate genetic evaluation can be achieved by adjusting animal records for known systematic environmental effects such as individual age differences at recording, sex, dam age, year, season etc. (Bohmanova et al., 2005).

The objectives of this study were: (1) to identify the significant environmental factors that influenced growth traits and; (2) to evaluate phenotypic response of growth traits to selection at weaning and 18-months of age in Tswana cattle.

3.2. Materials and methods

3.2.1. Data description

Data of selected Tswana cattle collected over a period of 18 years from 1995 to 2013, acquired from the Department of Agricultural Research (D.A.R.) in Botswana was used in this study. The data consisted of 2940 records for 7 months selection line (S1), 3034 for 18 months selection line (S2) and 1252 records for the unselected control line (S3). In both S1 and S2, mass selection was practiced based on the animal's weight index. The weight indices were derived as the difference between the animal's own weight record for a trait and the average weight of the contemporary group. Therefore, before the indices were calculated on both weaning and eighteen-month weights, the weight records were pre-adjusted to 205 and 540 respectively, to eliminate the differences in individual age within the contemporary group. The S1 and S2 replacement animals were then selected using 205 and 540 days weight indices respectively while S3 replacement animals were randomly chosen into the breeding herd at eighteen months of age without using any distinct selection procedure. All the animals were allowed to join the breeding herd at 18-months of age. The data comprised of the following: pedigree information i.e. calf identity number (CALFID), sire identity number (SIREID), dam identity number (DAMID) and associated important information such as birth date, sex of the calf, and selection line. The pedigree structure showing the number of animals, dams and sires for each line is presented in Table 3.1.

Table 3.1: Pedigree structure for the data used

Parameter	Selection line		
	1	2	3
Number of animals	2940	3034	1252
No of dams[a]	731	671	266
No of sires[a]	80	82	31

[a] sires and dams with progeny records, selection lines 1, 2 and 3 are selection for weaning weight, 18-moth weight and unselected control population respectively.

3.2.2. Traits recorded

Growth traits consisted of birth weight (BWT), weaning weight (WWT) recorded at seven months, yearling weight (YWT) recorded at twelve months, eighteen month weight (EWT), pre-weaning average daily gain (ADG1) and post-weaning average daily gain (ADG2). ADG1 was calculated by dividing the change in body mass from birth to weaning by the number of days in the interval while ADG2 was calculated as the change in body mass from weaning to eighteen months divided by number of days in the interval.

3.2.3. Data editing and Statistical analysis

In this study the dam age was fitted as a fixed categorical variable after grouping the dam age into three classes due to dam age distribution: those dams aged less than 5 years were grouped to form class 1, those aged greater than 5 to 9 years were grouped to form class 2, while those aged older than 9 years and above formed class 3. Weaning, Yearling and 18-month weights were pre-adjusted to 205, 365 and 550 days respectively, therefore individual age difference at recording was not fitted as an effect in the analysis model.

Since seasonal mating was practiced, all animals were born from late September to early January; hence there were few birth records in September and January than in other months. As a result the birth seasons were regrouped as follows: those born in September and October were grouped as season one, those born in November as season two and those born in December and January as birth season three. After regrouping the birth month, contemporary group was then formed by concatenating birth year and birth season, and it was fitted as random effect in a mixed model due to its large size.

Estimation of least square means for birth weight was carried out by fitting selection line, sex and age of dam as fixed class variables and contemporary groups as a random effect. The fixed and random effects fitted for weaning weight, post weaning weights, ADG1 and ADG2 were similar to those fitted for birth weight. For all traits, the significant interaction effects were sex by contemporary group and line by contemporary group.

Data for all the traits were analyzed using proc mixed procedures of Statistical Analysis System (SAS, 2012). The general form of the mixed models fitted for birth, weaning, yearling and 18-month weights as well as ADGs was as shown below;

$$Y_{ijklm} = s_i + d_j + l_k + c_l + (s*c)_{il} + (l*c)_{kl} + e_{ijklm}$$

Where;

Y_{ijklm} is the observation of the weight trait (BWT, WWT, YWT, EWT, ADG1 and ADG2),

s_i is the i^{th} sex of the calf effect fitted as fixed,

d_j is the j^{th} dam age class effect fitted as fixed,

c_k is the k^{th} contemporary group effect fitted as random effect,

l_l is the l^{th} selection line effect fitted as fixed,

$(s*c)_{il}$ is sex by contemporary group interaction fitted as random effect,

$(l*c)_{kl}$ is selection line by contemporary group interaction fitted as random effect,

and e_{ijklm} is random residual error distributed independently with mean zero and common variance, σ^2_e

3.3. Results and discussion

3.3.1. Sex effect

Least square means for all growth traits by sex are presented in Table 3.2. The sex of the calf was generally a significant source of variation in all weights and ADGs. The magnitude of the differences between the sexes in weight traits increased as the age of the animals advanced from birth (1.77±0.15 kg) to eighteen-months (13.06±1.69 kg). Mean differences between males and females were 0.05±0.003 kg and 0.02±0.002 kg for ADG1 and ADG2 respectively and were both significant.

The higher male ADGs imply that male calves grow faster than their female counterparts both prior to weaning and from weaning to eighteen months of age. The results of the current study are in agreement with the findings reported by both Irgang et al. (1985) for Hereford cattle and Casas et al. (2011) for British and indigenous tropical beef breeds. Contrary to the values obtained in current results for ADG1, Casas et al. (2011) reported higher ADG1 values ranging from 0.93±0.1 kg/day to 1.0±0.1 kg/day for crossbred calves sired by Tuli, Boran and Brahman bulls in temperate climate.

Table 3.2: Least square means (± S.E.) for BWT, WWT, YWT, EWT, ADG1 and ADG2 by calf sex

Sex	Trait					
	BWT (kg)	WWT (kg)	ADG1(kg/day)	YWT (kg)	EWT (kg)	ADG2(kg/day)
F	30.7±0.19^a	157.7±2.63^a	0.61±0.01^a	160.3±2.94^a	211.5±3.64^a	0.16±0.01^a
M	32.5±0.19^b	168.9±2.63^b	0.65±0.01^b	172.5±2.95^b	224.6±3.69^b	0.18±0.01^b

F=Female, M=Male, BWT= Birth weight, WWT=Weaning weight, YWT=Yearling weight, EWT= Eighteen month weight, ADG1=pre-weaning average daily gain and ADG2=post weaning average daily gain, means within a column showing the same superscript did not show significant difference.

It is well documented that male calves are heavier at all stages of growth than their female counterparts and the differences have been detected regardless of breed (Bellows et al., 1996; Cundiff et al., 1998; Chase et al., 2000; Holloway et al., 2002; Riley et al., 2007). Birth weight mean difference of 1.77±0.15 kg obtained in this study between the two sexes was consistent and within the range of values (1.4±0.5 kg, 1.72 kg and 2.4 kg) reported for indigenous tropical beef cattle breeds (Dillon et al., 2015; Robinson et al., 2013; Tubman et al., 2004). However, these values are lower than the range of values (2.74±0.11 kg to 3.73±0.14 kg) reported for the European beef breeds by Bennett et al. (2008). Likewise, Casas et al. (2011) also reported the differences ranging from 2.2 kg to 3.1 kg between female and male calves for the crossbred calves from Hereford, Angus, Tuli and Belgian Blue sires. The differences between the weights of male and female calves were also reported by Smith et al. (1976), Gregory et al. (1978), Gregory et al. (1979) and Cundiff et al. (1998), and may be attributed to physiological differences arising from sex linked secondary characters.

The mean weight differences obtained between male and female calves were 11.25±0.53 kg, 12.28±1.34 kg and 13.06±1.69 kg in WWT, YWT, and EWT respectively. Weaning weight differences obtained in this study were consistent with the findings by Chase Jr. et al. (2004) and Casas et al. (2011) who as well observed the persistence of sex effect from birth to weaning weight. In addition, Irgang et al. (1985) also reported sex effects at weaning and post weaning while evaluating lines selected for both weaning weight and post weaning gain. Furthermore the results obtained by Luna-Nevarez et al. (2010) in their study of associative relationship between growth characteristics and reproductive performance also revealed females to be lighter than males at weaning and yearling, and weight differences became large as the age of animals advances. This may be due to the development of secondary male sexual characteristic such as production of hormones such as testosterone which helps build the muscle hence increase body frame in males. However, this effect has not resulted in heterogeneous variance component (Mercadante et al., 2003; Casas et al., 2011). It is therefore necessary to adjust for sex effect whenever genetic evaluation of Tswana cattle for growth performance is carried out.

3.3.2. Dam age effect

The least square means for birth, weaning, yearling and eighteen-month weights and pre-and post-weaning average daily gains by dam age categories are presented in Table 3.3. The mean weight differences between calves born from young dams aged 5 years or less and to those born from mature dams aged above 5 years to 9 years were 0.84±0.14 kg, 10.96±0.64 kg, 7.61±0.82 kg and 8.83±1.04 kg for BWT, WWT, YWT and EWT respectively while the corresponding mean differences between calves born from young dams and older ones aged above 9 years were 0.85±0.15 kg, 9.29±0.68 kg, 6.40±0.89 kg, and 6.58±1.12 kg for BWT, WWT, YWT and EWT. All the differences were significant. However, the differences between calves born from dams older than 9 years and mature ones ranged from 0.01±0.15 kg for BWT to 2.25±1.10 kg for EWT and were not significant ($P<0.05$) except only for weaning weight which was significant. The results revealed ADG1 mean differences to be significant across dam age categories and were 0.04±0.003 kg/day between young and older dams, 0.05±0.003 kg/day between young and mature dams and 0.01±0.003 between mature and older dams. ADG2 mean differences were not significant ($P<0.05$) across dam age categories and ranged from 0.003±0.003 kg between young and mature dams to 0.006±0.003 kg between older and mature dams. The means for both ADG1 and ADG2 are presented in Table 3.3.

Table 3.3: Least square means (± S.E.) of BWT, WWT, YWT, EWT, ADG1 and ADG2 significance of within traits differences between dam ages

Trait	Dam age category (years)		
	≤5	>5 and ≤9	>9
BWT (kg)	31.0±0.19^{a}	32.9±0.19^{b}	31.9±0.20^{b}
WWT (kg)	156.7±2.64^{a}	167.3±2.64^{b}	165.9±2.66^{c}
ADG1(kg/day)	0.60±0.01^{a}	0.65±0.01^{b}	0.64±0.01^{c}
YWT (kg)	161.7±2.90^{a}	169.3±2.90^{b}	168.1±2.92^{b}
EWT (kg)	212.9±3.61^{a}	221.7±3.61^{b}	219.5±3.63^{b}
ADG2 (kg/day)	0.17±0.01^{a}	0.17±0.01^{a}	0.16±0.01^{a}

BWT=Birth weight, WWT=weaning weight YWT= Yearling weight, EWT= eighteen month weight, ADG1= pre-weaning average daily gain and ADG2= post-weaning average daily gain, means within a row showing the same superscript did not show significant difference.

The results obtained in the current study indicated that BWT, WWT, YWT and EWT of calves increased with dam age. Calves born from dams older than 5 years had the heaviest weight at all ages compared to those born from younger dams (Table 3.3). These results are in agreement with the reported findings (Irgang et al., 1985; Bennett et al., 2008; BIF, 2006; Luna-Nevarez et al., 2010). These authors also observed increases in birth, weaning and yearling weights with dam age. Similar to the results obtained in the current study, Irgang et al. (1985) and Bennett et al. (2008) also reported weaning and yearling weights that increased with dam age up to 5 years. However, contrary to the current findings the authors revealed that the weights remain constant beyond 5 years of dam age. Furthermore, Luna-Nevarez et al. (2010) reported significant ($P<0.05$) dam age effect on birth weight of Brangus cattle and they revealed that birth weight increase with dam age up to 5 years which was similar to the current findings. In addition to that, the authors further stated that the weights remained constant after 5 years until 11 years then declined which was inconsistent with the current results.

The observed weight and growth rate differences with dam age imply that young dams are unable to provide adequate uterine and nutrient environment for growth of the foetus during pregnancy and after birth to weaning. This may be due to the fact that young dams are still growing hence the uterus is not yet fully developed, and besides that the nutrients supplied are partitioned not only for lactation and maintenance but also for the dam's own growth. Despite the ability of Tswana dams older than 9 years to provide adequate prenatal environmental requirements for the growth of foetus they fail to provide sufficient environmental needs for postnatal growth of calves to weaning. This may be attributed to loss of efficiency of the digestive system to mobilise feeds consumed and supply enough nutrients for lactation, maintenance and repair of the worn out tissues.

Generally the current results for ADG1 implied that calves born from young and older dams grow more slowly than their counterparts born from mature dams. The results obtained in the current study are consistent with the findings of Bennett et al. (2008) and Luna-Nevarez et al. (2010). However, the values obtained by Bennett et al. (2008) which ranged between 0.82 and 0.97 kg for pre-weaning average daily gain of different cattle populations were higher than those obtained in the current study. Variation of ADG1 with dam age may be due to the inability of both young and older dams to provide sufficient nutrients for their own growth and repair of worn out tissues, respectively coupled with those required for lactation hence less milk produced for their suckling calves. The dam age effect was not significant for ADG2 and the average growth rate obtained for this period is much lower than that reported. Similar to ADG1, the means obtained for ADG2 by dam age in this study were lower than the values reported by Bennett et al. (2008) for different beef cattle breeds, which were in the range of 0.95 to 0.97 kg.

Although most studies reported dam age effect on birth and weaning weight traits as compared to post weaning growth traits, some literature findings (Bennett et al., 2008; Raphaka and Dzama, 2010) reported significant dam age effect on yearling and eighteen-month weights. In general, similar pattern of dam age effect was observed in the current study, in which the effect persisted beyond weaning age. These results indicate that for accurate genetic evaluation to be performed on both pre-weaning and post-weaning growth performance of Tswana cattle, adjustment for dam age should be taken into consideration.

3.3.3. Phenotypic contrast between selected and control lines

The least square mean values for selected lines and control lines that were obtained from the univariate analysis of BWT, WWT, YWT, EWT and ADGs are presented in Table 3.4. Both the selection lines (S1 and S2) had significantly heavier weights at all ages than the control line (S3). The weight differences also varied significantly between the two selected lines and ranged from 0.28±0.24 kg to 13.04±4.15 kg at birth to eighteen-month olds. The highest mean weight differences were observed between animals in S1 and the control group for all growth traits and ranged from 0.96±0.27 kg to 26.66±4.22 kg at birth to eighteen-month olds. The mean difference between animals in S2 and S3 were 0.68±0.27 kg, 13.83±2.14 kg, 14.90±2.61kg and 13.61±4.20 kg for BWT, WWT, YWT and EWT respectively. The least square means for ADG also showed variation ($P<0.001$) with selection line (Table 3.4). The respective mean differences for ADG1 and ADG2 were 0.08±0.01 kg/day and 0.04±0.003 kg/day between animals in S1 and S3, 0.06±0.01 kg and 0.01±0.003 kg/day between animals in S2 and S3, and 0.02±0.01 kg/day and 0.03±0.003 kg/day between animals in S1 and S2.

Table 3.4: Least square means (± S.E.) of BWT, WWT, YWT and EWT for selected and control lines

Selection line	Trait					
	BWT (kg)	WWT (kg)	YWT (kg)	EWT (kg)	ADG1 (kg/day)	ADG2 (kg/day)
S1	32.0±0.22^a	171.5±2.88^a	174.9±3.22^a	231.3±4.30^a	0.67±0.01^a	0.19±0.01^a
S2	31.7±0.22^b	166.2±2.88^b	169.7±3.21^b	218.2±4.29^b	0.64±0.01^b	0.16±0.01^b
S3	31.1±0.24^c	152.3±2.92^c	154.7±3.27^c	204.6±4.33^c	0.58±0.02^c	0.15±0.01^c

S1=Animals selected at weaning, S2= animals selected at eighteen months of age, S3= unselected animals (control), BWT=Birth weight, WWT= Weaning weight, YWT= Weaning weight, EWT=Eighteen month weight, ADG1=pre-weaning average daily gain and ADG2= post weaning average daily gain. Means within a column showing the same superscript did not show significant difference.

The results for growth traits comparison between selection lines obtained in the current study are in agreement with other findings (Irgang et al., 1985; Koch et al., 2004; Kahi and Hirooka, 2007; Bennett et al., 2008; Enns and Nicoll, 2008) in that the selected lines were heavier than the control line. However, contrary to the current results Irgang et al. (1985) reported that improvement on weaning weight, yearling weight and post weaning gains were achieved by male calves due to selection for post weaning gain than for selection on weaning weight. Likewise, Koch et al. (2004) also found animals selected for yearling weight to be heavier than those selected for weaning weight at both weaning and yearling age. The same authors also reported that both selected lines were heavier than the control line at both weaning and yearling. In general, compared to the unselected control populations, calves selected at weaning had the heaviest weight at all ages than those selected at eighteen months of age, which is in contrast to what has been reported (Irgang et al., 1985; Koch el al., 2004; Kahi and Hirooka, 2007; Bennett et al., 2008; Enns and Nicoll, 2008; Boligon et al., 2010; Boligon et al., 2013).

Weaning weight is associated with the ability of the cow to provide the necessary environmental requirements in the form of milk and care for the calf to grow efficiently while eighteen-months weight is said to be dependent on the animal's own ability to grow hence is influenced by the animal's own genetic makeup (ARC, 2004; Boligon et al., 2010; Boligon et al., 2013). The current results indicated that selecting for weaning weight indirectly improved both yearling and eighteen-month weight which is associated with the animal's ability to grow independently of maternal environmental influence. Therefore the current results implied that the animal's genes responsible for good mothering ability may be the same genes or highly linked with the genes accountable for post weaning growth performance.

Similar to the current results, Irgang et al. (1985) and Koch et al. (2004) reported ADG means for selected populations that were high and significantly different from those of non-selected control populations. Bennet et al. (2008) also reported pre weaning ADG that was significantly increased by selection for postnatal growth, while post weaning ADG remained similar to that of the non-selected control population. The results obtained for both ADG1 and ADG2 in this study generally showed lower estimates than those earlier reported (Bennett et al., 2008; Luna-Nevarez et al., 2010; Casas et al., 2011) which may explain the low growth rate of Tswana cattle breed. The current results imply that selection for weaning weight has the potential to effectively improve growth rate in Tswana breed.

3.4. Conclusion

The study revealed that mass selection for weaning and eighteen-month weights based on phenotypic weight index improved the phenotypic growth performance of Tswana cattle compared to unselected control population. Selection for weaning weight resulted in heavier birth, weaning, yearling and eighteen-month weight traits and higher ADGs than selection for eighteen-month weight. Both calf sex and dam age have significant influence on all growth traits in Tswana cattle, and should always be accounted for whenever genetic evaluation for growth performance of this breed is carried out. Therefore, it can be concluded that mass selection for weaning weight can yield optimal improvement on growth performance of Tswana cattle breed when properly carried out.

Chapter 4

Estimates of covariance component and genetic parameters for growth traits in Tswana cattle mass selected at weaning and eighteen-month weights

4.1. Introduction

Genetic parameter estimates are necessary for the implementation of genetic evaluations, subsequent assessment and quantification of genetic progress that can be achieved through on-going long term selection in economically based multi-trait breeding objectives (Enns and Nicoll, 2008). As a result the importance of genetic parameters such as heritability, correlations and repeatability in traits of economic importance in beef cattle cannot be underrated. On the other hand, these parameters are population specific and hence can by no means be generalised (Irgang et al., 1985). As a consequence, many studies have been conducted in recent years across the world with the aim of estimating both phenotypic and genetic parameters and to evaluate their importance in designing breeding programmes for different beef cattle breeds in different production environments (Chevraux and Bailey, 1977; Davis, 1987; Mercadante et al., 2003; Koch et al., 2004; Yilmaz et al., 2004; Enns and Nicoll, 2008; Boligon et al., 2010; Cervantes et al., 2010; Boligon et al., 2013; Shumbusho et al., 2013). This has led to validation of practically achieved progress with theoretically predicted direct and correlated responses for setting up of more efficient breeding programs.

Van Vleck and Cundiff (1998) and Crews (2006) defined selection of beef animals for breeding to be based on breeding values for growth performance. The genetic potential for early growth traits are known to be influenced by both direct and maternal additive genetic merit (Willham, 1972; Robinson, 1996a). In addition to these genetic effects, Koots et al. (1994) and Robinson (1996b) emphasised that permanent environmental effects also need to be accounted for especially in tropical environments where accidents to the udder and exposure to diseases are likely to occur. Meyer et al. (1993) and Garrick (2010) also asserted that optimization of genetic progress should take the two into consideration. For traits expected to be influenced by maternal effects, genetic evaluation through best linear unbiased prediction (BLUP) involves partitioning of the phenotypic variances and covariances into their direct and maternal genetic, maternal permanent environmental, genetic correlations, and residual components. Due to breed differences in the importance of direct and maternal genetic effects, several studies have been conducted to estimate genetic and phenotypic parameters among weight traits of different breeds (Knights et al., 1984; Smith et al., 1989; Lee et al., 2000; Forni and Albuquerque, 2005).

In an established breeding programme, drawing a genetic trend is a useful tool to evaluate the impact of genetic improvement programme. The trend has to be monitored to check the validity of the predictions made and the direction of genetic change (Intaratham et al., 2008; Bosso et al., 2009). Currently, nothing has been reported on genetic change due to selection in indigenous Tswana cattle in Botswana. The objectives of this study were therefore 1) to estimate variance-covariance components and genetic parameters for growth traits, 2) to evaluate the importance of maternal effects on growth traits of Tswana cattle, and 3) to estimate annual genetic change in growth traits of Tswana cattle selected at weaning and eighteen-months relative to unselected control.

4.2. Materials and methods

4.2.1 Data description and editing

Data of selected Tswana cattle collected from 1995 to 2013, acquired from Department of Agricultural Research (D.A.R.) in Botswana was used in this study. The data consisted of 2940 records for seven months selection line (S1), 3034 for eighteen months selection line (S2) and 1252 records for the unselected control line (S3). In both S1 and S2, mass selection was practiced based on the animal's weight index calculated at weaning (205 days) and at eighteen-months (540 days) of age, respectively. Within S1 and S2 indices were calculated based on pre-adjusted 205 and 540 weights respectively prior to the implementation of mass selection.

The data used in this study comprised of the following: pedigree information i.e. calf identity number (CALFID), sire identity number (SIREID), dam identity number (DAMID) and associated important information such as birth date, sex of the calf, and selection line.

The growth traits that were considered were birth weight (BWT); weaning weight (WWT) recorded at seven months; yearling weight (YWT) recorded at twelve months; eighteen months weight (EWT); pre-weaning average daily gain (ADG1); and post-weaning average daily gain (ADG2). ADG1 and ADG2 were calculated as described in chapter 3. Based on dam age distribution and prior literature, dam age was grouped into three classes or categories namely young (≤5 yr), mature (>5 and ≤9 yr) and old (>9 yr). Weaning, Yearling and eighteen-month weights were pre-adjusted to 205, 365 and 540 days respectively, therefore individual age differences at recording were not fitted as an effect in the analysis models.

Since seasonal mating was practiced, all animals were born from late September to early January. However, there were fewer birth records in September and January than in other months. As a result the birth seasons were regrouped as described in chapter 3 and contemporary group was then formed by concatenating birth year and birth season, and was fitted as sparse fixed effect in a mixed model. The summary of the final data used for genetic analyses in this study is presented in Table 4.1.

Table 4.1: Structure of the data used for genetic parameter estimation

Parameter	Trait					
	BWT	WWT	YWT	EWT	ADG1	ADG2
No of observations	7223	6339	5160	4383	6336	4271
Mean ± S.D. (kg)	31.9±5.2	170.5±30.3	173.7±35.6	225.4±42.4	0.66±0,15	0.18±0.09
No of sires	188	188	188	188	188	188
No of sires of sires	50	50	50	50	50	50
No of sires of dams	136	136	136	136	136	136
No of dams	1662	1662	1662	1662	1662	1662
No of dams of dams	611	611	611	611	611	611
No of dams of sires	88	88	88	88	88	88
No of Cont.	54	54	54	54	54	54
No of generations	1-5	1-5	1-5	1-5	1-5	1-5

Cont. = contemporary group, S.D. = standard deviation, BWT = birth weight, WWT = weaning weight, YWT =yearling weight, EWT =18-month weight, ADG1= pre-weaning average daily gain, and ADG2 = post-weaning average daily gain,

4.2.2. Statistical analysis

Mixed statistical models were used for genetic analysis of calf weight and growth rate traits. Fixed effects fitted were sex, dam age, line, contemporary group, sex by contemporary group and line by contemporary group interactions. An animal model integrating all pedigree information with performance data was used in the analysis of all the traits. In addition to the direct additive genetic effects, maternal genetic and permanent environmental effects on the trait studied were tested by fitting them as additional random effects. Because of the data size and depth of pedigree structure the correlation between direct and maternal effect was not estimable for all the traits. The full model considered for the analysis of BWT, WWT, YWT, EWT, ADG1 and ADG2 was:

$$Y = X\beta + Z_a u_a + Z_m u_m + Z_c u_c + \varepsilon$$

Where; Y = the observed growth trait of the calf (BWT, WWT, YWT, EWT, ADG1 or ADG2), X = the incidence matrix relating fixed effects to the observations of a trait, β = vector of fixed effects which were sex, dam age, selection line, contemporary group and their interaction, Z_a = incidence matrix relating direct additive genetic effects to the observations of a trait, Z_m = incidence matrix relating maternal additive genetic effects to the observations of a trait, Z_c = incidence matrix relating permanent maternal environmental effects to the observations of a trait, u_a = a vector of direct additive genetic effects, u_m = a vector of maternal additive genetic effects, u_c = a vector of permanent maternal environmental effects and ε = a vector of random residual effects.

The random effects in the mixed models were assumed to have the following variance covariance distributions: $[\mu_d', \mu_m', \mu_{pe}', e']' \sim N[(0', 0', 0', 0')', \sum]$ and the variance-covariance structure fitted in the analysis of a single trait genetic models were as follows:

$$\sum\begin{bmatrix} a \\ m \\ pe \\ e \end{bmatrix} = \begin{bmatrix} A\sigma_a^2 & 0 & 0 & 0 \\ 0 & A\sigma_m^2 & 0 & 0 \\ 0 & 0 & I_q\sigma_c^2 & 0 \\ 0 & 0 & 0 & I_n\sigma_e^2 \end{bmatrix}$$

The variance-covariances estimates obtained from the fitted random effects were expected to appear as follows: $\mathrm{Var}(y) = \sigma^2_a + \sigma^2_m + \sigma^2_c + \sigma^2_e$, $\mathrm{Var}(u_a) = A\sigma^2_a$, $\mathrm{Var}(u_m) = A\sigma^2_m$, $\mathrm{Var}(u_c) = I\sigma^2_c$ and $\mathrm{Var}(e) = I\sigma^2_e$. *A* is the numerator relationship matrix and *I* is the identity matrix equal to the number of dams for Var(c) and number of animals for Var(e). These variance-covariances were later used to compute, phenotypic variance (σ^2_p), direct heritability (h^2_a), maternal heritability (h^2_m), the ratios for permanent maternal environmental effects (c^2) and random residual effects (e).

4.2.3 Model comparison procedure

Analysis of genetic parameters and covariances was carried out by fitting univariate and bivariate animal models that ignored one or two of the maternal effects to the data using ASREML programme (Gilmour et al., 2015). These models were numbered as follows: model 1: h^2_a; model 2: h^2_a and h^2_m; model 3: h^2_a, h^2_m, c^2. The models were then compared using the log likelihood ratio test (LR), which was calculated as minus twice the difference between the Log L of models under comparison. To declare the difference as significant, the likelihood ratio was compared with the tabulated χ^2 statistics with the number of degrees of freedom taken as the difference in the number of parameters fitted between the two models. Using the best model for each trait, phenotypic and genetic covariances, and correlations among traits were estimated through bivariate analyses. Based on the LR test, model 3 was identified to be the best for BWT, WWT and ADG1. Model 2 was suitable for YWT and EWT while Model 1 was suitable for ADG2.

4.3. Results and discussion

4.3.1. Variance components and genetic parameter estimates for growth traits

Estimates of variance components and genetic parameters for each trait obtained from the three statistical models are presented in Tables 4.2 and 4.3, respectively. When one of maternal effects was included in a model (Models 2 and 3) for BWT, WWT and ADG1, both direct genetic variance and the corresponding direct heritabilities were substantially reduced. The estimates obtained for both maternal genetic and environmental variances were significantly different from zero and showed substantial contribution to the overall phenotypic variances. The LR was significantly improved compared to the model fitting only direct genetic effect (Model 1). The maternal genetic variance estimate for YWT obtained from Model 2 was significantly different from zero. However, the estimates obtained for maternal effects when Models 2 and 3 were fitted for EWT and ADG2 were not significantly different from zero and did not show any important contribution to the phenotypic variance, despite the improved LR as compared to the model containing only direct genetic effect.

Table 4.2: Estimates of variance components (± S.E.) for BWT, WWT, YWT, EWT, ADG1 and ADG2 from univariate models

Estimate	Model		
	1	2	3
BWT (kg^2)			
σ^2_a	6.10±0.73	3.03±0.66	3.01±0.52
σ^2_m		1.63±0.31	0.99±0.47
σ^2_c			0.71±0.41
σ^2_e	19.46±0.61	20.51±0.55	20.41±0.48
σ_P^2	25.57±0.48	25.16±0.45	25.12±0.44
WWT (kg^2)			
σ^2_a	220.70±16.36	127.82±17.02	128.29±13.40
σ^2_m		93.47±9.47	53.26±14.41
σ^2_c			37.78±13.47
σ^2_e	273.37±11.45	292.43±11.47	289.07±9.98
σ_P^2	494.06±10.44	513.72±11.33	508.41±9.67
YWT (kg^2)			
σ^2_a	245.10±24.66	202.84±27.30	204.22±24.09
σ^2_m		36.00±11.01	19.05±16.21
σ^2_c			18.18±15.61
σ^2_e	440.79±18.76	445.07±18.83	441.43±17.66
σ_P^2	685.89±15.62	683.92±15.64	682.89±13.51
EWT (kg^2)			
σ^2_a	457.38±42.43	427.51±46.98	428.88±43.77
σ^2_m		39.47±17.62	15.78±24.34
σ^2_c			26.89±21.87

σ^2_e	558.02±30.02	551.99±30.65	546.06±21.77
σ_P^2	1015.40±25.94	1019.00±26.42	1017.60±22.08
ADG1 (g^2)			
σ^2_a	5117.6±398.6	2816.4±398.9	2844.05±289.55
σ^2_m		1919.8±211.9	941.20±311.58
σ^2_c			936.49±310.18
σ^2_e	6878.2±283.5	7186.6±274.4	7087.73±229.77
σ_P^2	11996.0±252.7	11923.0±257.9	11809.0±216.48
ADG2 (g^2)			
σ^2_a	1712.3±231.4		
σ^2_e	3810.7±182.9		
σ_P^2	5522.9±137.7		

S.E. = standard error, σ^2_a = direct variance; σ^2_m = maternal variance; σ^2_c = permanent maternal environmental variance; σ^2_e = residual error variance; σ_p^2 = phenotypic variance; ADG1 = pre-weaning average daily gain and ADG2 = post-weaning average daily gain.

Although the inclusion of one of the maternal effects in Models 2 and 3 substantially reduced the direct genetic variances and the corresponding heritability estimates for BWT, WWT, YWT and ADG1 compared to Model 1. The two models did not show any considerable differences between each other in terms of both direct genetic variances and the corresponding heritability estimates. Besides, the magnitude of the estimates for both maternal genetic and maternal permanent environmental effects from Models 2 and 3 were more or less the same (Tables 4.2 and 4.3). There was a significant improvement on the LR, and a minor change in the magnitude of direct genetic variances and the corresponding heritabilities for EWT when one of the maternal effects was included in the analysis model (Models 2 and 3). The LR did not improve when model 3 was fitted for ADG2, while the magnitude of both maternal genetic and maternal permanent environmental variances and the respective heritability estimate from both models 2 and 3 were negligible and not different from zero.

Table 4.3: Heritability and permanent environmental proportion estimates (S.E.) for BWT, WWT, YWT, EWT, ADG1 and ADG2 estimated from univariate analysis.

Estimate	Model		
	1	2	3
BWT (-2 log LR)		30.62***	32.06***
h^2_a	0.24±0.03	0.12±0.03	0.12±0.03
h^2_m		0.06±0.01	0.04±0.02
c^2			0.03±0.02
WWT (-2 log LR)		829.08***	837.36***
h^2_a	0.45±0.03	0.25±0.03	0.25±0.03
h^2_m		0.18±0.02	0.11±0.03
c^2			0.07±0.03
YWT (-2 log LR)		13.06***	14.40***
h^2_a	0.36±0.03	0.30±0.04	0.30±0.04
h^2_m		0.05±0.02	0.03±0.02
c^2			0.03±0.02
EWT (-2 log LR)		5.98*	7.12*
h^2_a	0.45±0.03	0.42±0.04	0.42±0.04
h^2_m		0.04±0.02	0.02±0.03
c^2			0.03±0.02
ADG1 (-2 log LR)		131.56***	140.06***
h^2_a	0.43±0.03	0.24±0.03	0.24±0.03
h^2_m		0.16±0.02	0.08±0.03
c^2			0.08±0.03
ADG2 (-2 log LR)			
h^2_a	0.31±0.04		

S.E. = standard error, h2a = heritability for direct genetic effects; h2m = heritability for maternal genetic effects; c2 = permanent maternal environmental proportion; ADG1 = pre-weaning average daily gain and ADG2 = post-weaning average daily gain. * = P<0.05, **= P<0.01 and *** = P<0.001

Direct heritability estimates for BWT, WWT, YWT, EWT, ADG1 and ADG2 were 24%, 45%, 36%, 45%, 43% and 31% respectively, from Model 1 while the corresponding heritability estimates from Models 2 and 3 were similar (Table 4.3). The range of direct heritability values obtained in the current study were consistent with those reported by Meyer (1997) for BWT and WWT in Australian beef cattle and Demeke et al. (2003) for BWT in Ethiopian indigenous breeds and their crosses. Direct heritability value obtained for ADG2 in the current study was similar to the value reported by Raphaka and Dzama (2011) for the same breed. On the other hand, they reported high direct heritability value for BWT and lower values for WWT, EWT and ADG1 than those obtained in the current study. In general, the current heritability estimates for various growth traits are within the range of values reported for other breeds (Groeneveld et al., 1998; Costa et al., 2011; Boligon et al., 2010). The magnitude of direct genetic variances and associated heritabilities currently obtained were generally high for WWT, YWT, EWT and ADGs which implied that generally there is sufficient genetic variation to implement genetic improvement through well planned selection.

Maternal genetic heritabilities from Model 2 were 4%, 11%, 3%, 2% and 8% for BWT, WWT, YWT, EWT and ADG1 respectively (Table 4.3). The range of values obtained for maternal genetic heritabilities for various traits are within the range of estimates reported in literature (Groeneveld et al., 1998; Demeke et al., 2003; Iwaisaki et al., 2005) for BWT, (Meyer, 1997; Costa et al., 2011; Boligon et al., 2012) for WWT, (Groeneveld et al., 1998; Boligon et al., 2010; Costa et al., 2011) for YWT and EWT, and (Demeke et al., 2003; Raphaka and Dzama, 2011; Boligon et al., 2012) for ADGs. Permanent maternal environmental proportions from Model 3 were 3%, 7%, 3%, 3%, and 8% for BWT, WWT, YWT, EWT and ADG1 respectively and not significantly different from zero for BWT, YWT and EWT. The results showed that both maternal genetic and maternal environmental variances decreased by a large amount from WWT to EWT. However, a notable change observed on the magnitude of parameters and an improvement on LR between Model 1 and Model 3 indicated that the exclusion of maternal genetic effect may result in, to some extent, biased estimates of genetic predictions and genetic parameters for BWT, WWT, YWT and ADG1 in Tswana cattle. The current results are consistent with the findings by Thompson (1976) and Costa et al. (2011) who reported that maternal genetic effect remained present after weaning to yearling weight and mature weight. However, the inclusion of maternal effects did not substantially affect the estimates of direct genetic variances and the corresponding heritabilities for EWT and ADG2 in the current study. According to some reported findings, the opinions as to whether to consider the effects when computing estimated breeding values for EWT and ADG2 (EBV) seem to be contradictory (Meyer, 1999; Rumph et al., 2002; Costa et al., 2011). Despite that, Thompson (1976) emphasised that if a trait is affected by maternal effects even to a smaller degree, the effects had to be considered in the model to avoid biased and inflated direct heritability estimates.

Although Meyer (1992) argued that modern genetic evaluation of post weaning weight traits tend to exclude maternal effects in the estimation of genetic parameters hence estimation of direct genetic effects and direct heritabilities might be inflated. The current study suggests that the inclusion of maternal effects in EWT and ADG2 analyses may have little or no effect on the estimated direct genetic variances and the corresponding direct heritabilities in Tswana cattle.

The maternal permanent environmental effect explained roughly 3% to 8% of the variability in growth traits. The estimates for maternal permanent environmental effects followed the same pattern to maternal genetic effects. Estimates were large at younger age (WWT) and declined towards EWT. When compared with genetic parameters the maternal permanent environmental effects were generally smaller. However, the observed influence of this effect beyond weaning was not significant, suggesting that maternal permanent effects could even be excluded in the genetic analysis of YWT. As a result, the current findings conformed to the argument by Costa et al. (2011) that failure to account for maternal effects may result in to a certain extent but not greatly biased estimates of genetic predictions and genetic parameters in post weaning growth traits. The same authors further stated that the resultant bias of EBV may be very small or even unnoticeable but the effects should be included in the analysis. Similar to the value obtained in Model 2 for maternal genetic heritability estimate, the zero value obtained for maternal permanent environmental effect in Model 3 for ADG2 may be attributed either to these effects being none influential on this trait or statistical artefact due to insufficient records hence incomplete censoring.

Direct and maternal genetic covariances and correlations were not estimable for all growth traits and ADGs. According to Robinson (1996a) and Meyer (1997) the estimation of this effect is not simple and shows strong dependence on the data structure hence it should be set to zero. In addition to that, Boligon et al. (2011) also suggested that since direct and maternal genetic covariance is dependent on data structure, it should be set to zero when estimating genetic parameters for early growth traits from the data set with insufficient structure i.e. small proportion of cows with phenotypic information, small number of progenies and poorly linked pedigree relationships.

4.3.2. Phenotypic and genetic correlations

Estimates of direct and maternal heritabilities for BWT, WWT, YWT, EWT, ADG1 and ADG2 obtained through bivariate analyses did not show any notable deviation from those obtained through univariate analyses.

Estimates of phenotypic and genetic correlations among BWT, WWT, YWT, EWT, ADG1 and ADG2 are presented in Table 4.4. Genetic correlation estimates were all positive and ranged from 0.19 to 0.98 (Table 4.4) indicating low to high genetic association between the traits. The positive correlations between the traits suggest that selection for one trait may result in a correlated response in another trait. The correlations between BWT and any of WWT, YWT, EWT and ADG1 were low to medium and ranged from 0.19 to 0.36. This therefore signalled low chances of increased BWT hence minimal risk associated with calving difficulty when selecting for increased WWT, YWT, EWT or ADG1. The current values obtained for correlations are consistent with those reported by Raphaka and Dzama (2010) for the same breed and Maiwashe et al. (2002) for Bonsmara breed. High correlation values obtained between WWT and each of ADG1, YWT, and EWT indicate that an increase in any of these weight traits can be attained through selection for WWT, hence the current results are in agreement with the findings of Burrow et al. (2001) and Raphaka and Dzama (2010). Genetic correlation between YWT and EWT was also very high signifying that selection for one of these traits can actually yield correlated response in the other. The inestimable genetic correlation between pre-weaning traits with ADG2 suggest that the estimates may be low due to compensatory growth effects (Raphaka and Dzama, 2010; Corbet et al., 2006).

Table 4.4: Estimates of direct genetic (above diagonal) and phenotypic (below diagonal) correlations and their respective S.E. between BWT, WWT, YWT, EWT, ADG1 and ADG2 in Tswana cattle obtained using bivariate analysis

Trait	BWT	WWT	YWT	EWT	ADG1	ADG2
BWT	-	0.31 ±0.07	0.33 ±0.08	0.36±0.08	0.19±0.07	-
WWT	0.19±0.01	-	0.98±0.02	0.82±0.04	0.99±0.02	-
YWT	0.18±0.02	0.64±0.01	-	0.91±0.03	-	0.55±0.08
EWT	0.20±0.02	0.57±0.01	0.66±0.01	-	0.82±0.04	0.70±0.06
ADG1	-	0.94±0.01	-	0.40±0.03	-	-
ADG2	-	-	0.35±0.02	0.71±0.01	-	-

S.E. = standard error, BWT = birth weight, WWT = weaning weight, YWT =yearling weight, EWT =18-month weight, ADG1= pre-weaning average daily gain, and ADG2 = post-weaning average daily gain.

Phenotypic correlations obtained in this study were generally lower than the corresponding genetic correlation estimates. This has also been observed in some reviews (Mohiuddin, 1993; Koots et al., 1994) and it was suggested that estimates of lower phenotypic correlations compared to the corresponding genetic correlations will arise where the genes governing the two traits are similar but the environments affecting the expression of these traits have low correlation (Searle, 1961). As was the situation with the genetic correlations, phenotypic correlations were lowest between BWT and all the other traits. This may indicate that BWT will not be enhanced by selecting for increased WWT and post weaning weight traits hence no threat of increasing chances of difficult calving can be encountered.

4.3.3 Genetic trends for growth traits and average daily gains

Genetic trends estimated by averaging predicted breeding values for growth traits and average daily gains of animals in selected and control lines are shown in Figures 4.1 to 4.6 and Table 4.5. Although the trends fluctuated over the entire period of selection, the distinct feature in genetic trends is exhibited in the two selected lines. The two lines showed positive trends in progression of average breeding values from 1995 to 2013 in various traits. However, genetic trends for EWT of selection line 1 did not show any significant progression and were not distinctive from those of the control line. Genetic trends for various traits in the control line were low and fluctuated below and above zero without any clear direction of change for the better part of the selection period as anticipated, although a significant positive progression was observed in WWT. However, trends for BWT of selection line 2 and the control line surprisingly exhibited genetic progression toward a negative direction (Figure 4.1). The trends estimates for both lines were not significantly different from zero (Table 4.5).

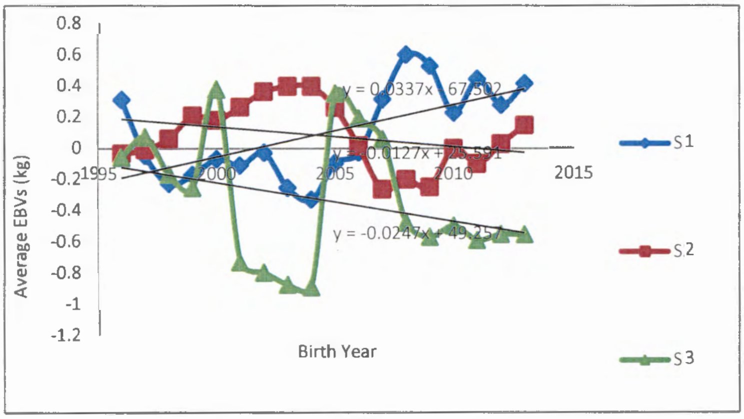

Figure 4.1: Genetic trends for estimating mean direct breeding values for BWT of Tswana cattle selected for weaning (S1), 18-months (S2) and the control population (S3).

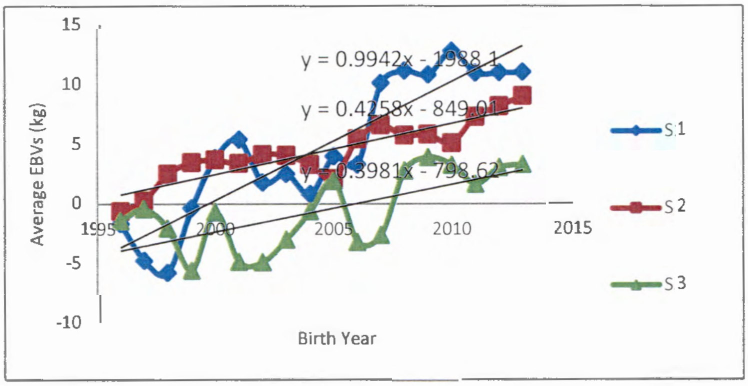

Figure 4.2: Genetic trends for estimated mean direct breeding values for WWT of Tswana cattle selected for weaning (S1), 18-months (S2) and the control population (S3).

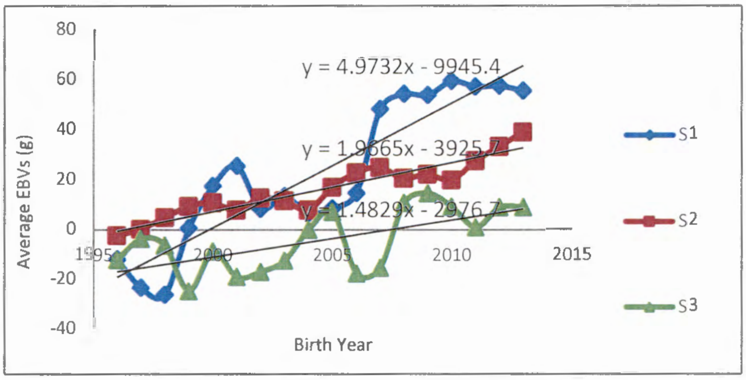

Figure 4.3: Genetic trends for estimated mean direct breeding values for pre-weaning average daily gain of Tswana cattle selected for weaning (S1), 18-months (S2) and the control population (S3).

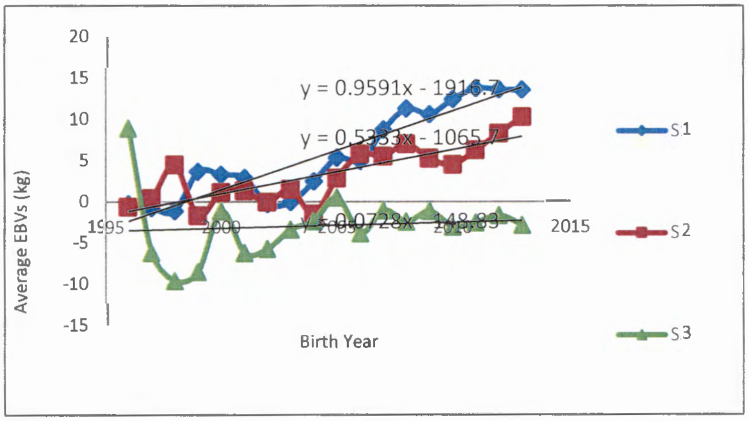

Figure 4.4: Genetic trends for estimated mean direct breeding values for YWT of Tswana cattle selected for weaning (S1), 18-months (S2) and the control population (S3).

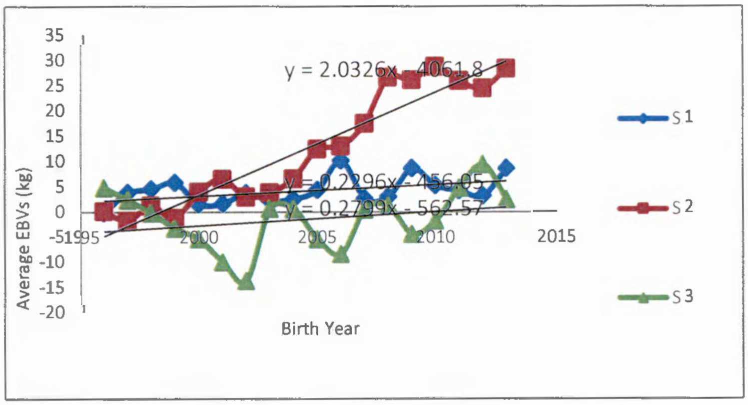

Figure 4.5: Genetic trends for estimated mean direct breeding values for EWT of Tswana cattle selected for weaning (S1), 18-months (S2) and the control population (S3).

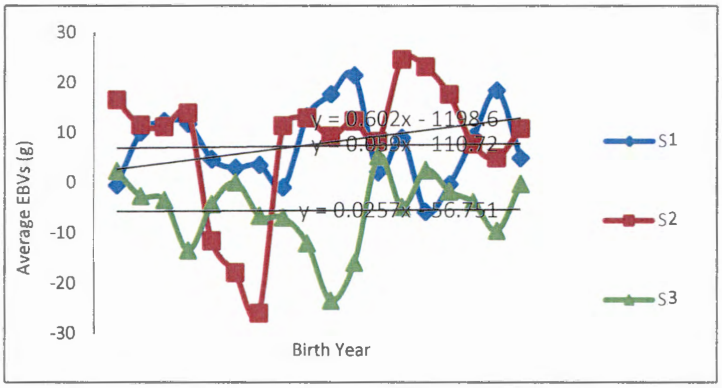

Figure 4.6: Genetic trends for estimated mean direct breeding value for post weaning average daily gain of Tswana cattle selected for weaning (S1), 18-months (S2) and the control population (S3).

The regression values obtained for BWT were 0.034±0.011 kg/year, -0.013±0.009 kg/year and -0.025±0.018 kg/year in S1, S2 and S3 respectively (Table 4.5). The values obtained currently for S2 and S3 were lower while the one for S1 was within the range of values; 0.061 kg/year, 0.015 kg/year, 0.024 kg/year and 0.090 kg/year as reported for BWT by Plasse et al. (2002) in selected Brahman cattle, Ferraz et al. (2000) in Santa Gertrudis, Assan (2013) in Tuli cattle and Tawah et al. (1993) in Gudali cattle respectively. The respective annual genetic trends obtained for WWT in S1, S2 and S3 were 0.99±0.12 kg/year, 0.43±0.05 kg/year and 0.40±0.11 kg/year. The values obtained for WWT in the current study were within the range of values reported for selected Hereford and Angus cattle (0.63 to 1.03 kg/year) by Baker et al. (1991); for Brahman cattle (0.155 kg/year) by Plasse et al. (2002); for Thai indigenous cattle (0.04 kg/year) by Intaratham et al. (2008); and for Tuli cattle (0.02 kg/year) by Assan (2010). The annual fluctuations of estimated genetic trend values for BWT and WWT may be due to the circumstance that selection of reproducing animals was based on phenotypic indices which may not always be a true reflection of the allied breeding values.

Annual changes in breeding values obtained in the current study for YWT were 0.96±0.10 kg/year, 0.53±0.10 kg/year and 0.07±0.19 kg/year in S1, S2 and S3 respectively (Figure 4.4). The value reported for EWT in the current study for S2 was consistent with the previously reported values ranging from 0.19 to 0.72 kg/year by Enns and Nicoll (2008) in selected New Zealand Angus nucleus herd while the respective values obtained for S1 and S3 were higher and lower than the reported ranges. The respective annual genetic changes obtained for EWT were 0.23±0.11 kg/year, 2.03±0.17 kg/year and 0.28±0.26 kg/year in S1, S2 and S3 (Figure 4.5). The values obtained in the current study for EWT in S1 and S3 were within the previously reported range of 0.13 kg/year to 0.49 kg/year (Plasse et al., 2002; Wasike et al., 2006; Enns and Nicoll, 2008) while the one obtained for EWT in S2 was higher.

Genetic trends currently obtained for ADG1 and ADG2 were generally high and low respectively (Figures 4.3 and 4.6). The values currently obtained for ADG1 were 4.97±0.57 g/year, 1.97±0.17 g/year and 1.48±0.44 g/year in S1, S2 and S3, respectively. The corresponding values of 0.06±0.35 g/year, 0.60±0.60 g/year and 0.03±0.34 g/year were obtained for ADG2 in S1, S2 and S3 which were all not significantly different from zero. Even though the values obtained in the current study for ADG1 in S2 and S3 were fairly closer to the reported values of 1.92 g/year by Beffa (2005) in Afrikaner cattle and 1.57 g/year by Tawah et al. (1993) in selected Wakwa cattle, respectively. The value currently obtained for S1 was way too high. The values currently obtained for ADG2 in S1 and S3 were far lower than the range of 0.13 g/year to 0.29 g/year previously reported in selected New Zealand Angus nucleus herd (Enns and Nicoll, 2008) while the one currently obtained for S2 was almost similar to the value of 0.66 g/year reported by Tawah et al. (1993) in selected Gudali cattle. The deviations of annual mean breeding values for BWT, WWT, YWT and ADG1 between the two selection lines demonstrated effective improvement in S1 than in S2. The high annual breeding values obtained for both EWT and ADG2 in S2 were contrary to the findings of Rakwadi (2010) who reported no clear genetic improvement in Brahman, Tuli and Bonsmara breeds selected for EWT. The unselected control line exhibited generally lower annual breeding values for all traits than the two selected lines which may be due to sudden change in genotype of the selected lines over the years of selection (Yaehgoobi et al., 2011).

Table 4.5: Genetic gains per year estimated as regression coefficients of the predicted annual breeding values of animals born in the selected lines and control line

Selection line	Trait					
	BWT (kg/year)	WWT (kg/year)	YWT (kg/year)	EWT (kg/year)	ADG1 (g/year)	ADG2 (g/year)
S1	0.034 ± 0.011^{NS}	$0.99 \pm 0.12^{***}$	$0.96 \pm 0.11^{***}$	0.23 ± 0.11^{NS}	$4.97 \pm 0.57^{***}$	0.06 ± 0.35^{NS}
S2	-0.013 ± 0.009^{NS}	$0.43 \pm 0.05^{***}$	$0.53 \pm 0.10^{***}$	$2.03 \pm 0.17^{***}$	$1.97 \pm 0.17^{***}$	0.60 ± 0.60^{NS}
S3	-0.025 ± 0.018^{NS}	$0.40 \pm 0.11^{**}$	0.07 ± 0.19^{NS}	0.28 ± 0.26^{NS}	$1.48 \pm 0.44^{**}$	0.03 ± 0.34^{NS}

^{NS}Regression coefficient not significantly different from zero,* and *** regression coefficient significantly differ from zero at ($P<0.05$), ($P<0.01$) and ($P<0.001$) respectively, BWT = birth weight, WWT = weaning weight, YWT =yearling weight, EWT =18-month weight, ADG1= pre-weaning average daily gain, and ADG2 = post-weaning average daily gain.

The current estimates for annual genetic gain indicated that in all traits, annual genetic gains were significantly enhanced among selected lines compared to the unselected control line. The directions of genetic change were desirable for all the traits except for BWT in eighteen months selection line and the control population. Both significant genetic progression in WWT of the control line and genetic change towards negative direction in BWT of the eighteen months selection and control lines were not anticipated and the cause could not be well identified in the current study. However, it may be attributed to asymmetry of selection response due to maternal effects, random drift or inbreeding depression (Falconer, 1989). High genetic gain for EWT in S2 demonstrates that selection for eighteen-month weight enhanced breeding value for EWT than selection for weaning weight. This clearly indicates the potential for improvement in the rate of change in annual genetic gain if an effective selection program was to be implemented.

4.4. Conclusion

Direct genetic variances and corresponding heritability estimates obtained in the current study for WWT, YWT, EWT, ADG1 and ADG2 were high demonstrating the breed's potential for genetic improvement if planned selection has to be carried out. Maternal genetic effects had significant influence on BWT, WWT, YWT and ADG1while maternal permanent environmental effects had significant influence on BWT, WWT and ADG1 hence the effects should be accounted for when estimating breeding values and genetic parameters for these growth traits and pre-weaning ADG in Tswana cattle. High genetic correlations among growth traits suggested that selection for any of the growth traits from weaning weight to eighteen months weight and average daily gains can result in correlated responses in other traits. Low genetic correlation between birth weight and other growth traits and average daily gains indicated the low chances of increased birth weight due to selection for increased growth traits and average daily gains hence minimal risks of dystocia. The two selected lines significantly enhanced annual genetic gain for all growth traits and ADG1 but not ADG2. However, genetic gain for EWT was optimally improved in selection line 2 than in selection line1. The control line exhibited significant annual genetic gain in WWT which was not anticipated and perhaps attributed to asymmetry of selection response. In general the study revealed that selection has yielded positive response over the years hence presents an opportunity for planned selection program to improve growth traits of the Tswana cattle breed.

Chapter 5

Environmental and genetic factors influencing reproductive traits and calf survival to weaning in Tswana cattle selected for early growth traits

5.1. Introduction

Reproductive efficiency has been described as a fundamental goal in beef cattle production (Dickerson, 1970; Milagres et al., 1979; Meacham and Notter, 1987). Janson (1980) and Magalhaes Silva et al (2017) also reported variation in reproduction efficiency to be associated with variation in management and nutrition. They further noted that genetic variation of reproductive efficiency is very low and estimated heritability to vary between 0 and 10%. Although beef cattle improvement has traditionally focused on production traits, breeding programs should consider all traits of economic importance to optimise genetic gain (Phocas et al., 1998; Albera et al., 2004). Gutierrez et al. (2007) reported that calving-interval is one of the major reproductive traits to be taken into consideration. Calving interval affects the efficiency of beef cattle production, if it is not well managed (Opsomer et al., 2000; Lamming and Royal, 2001; Lopez-Gatius et al., 2001). Prolonged calving interval is suggested to be either caused by failure of cyclic cows to show oestrous or by failure of the cows to recommence cycling after calving especially if the production management is not conducive and both pre- and postpartum nutritional requirements of the cows are not well met (Mwaanga and Janowski, 2000; Stevenson, 2001; De Rensis et al., 2008).

The American Simmental Association (ASA, 1986) stated that the inclusion of reproductive competency measures in performance evaluation programs would allow producers to identify superior bulls with early conception and easy breeding characters. The practice of culling non-pregnant females has commonly been a recommended management approach to advance production efficiency in beef cattle (Azzam and Azzam, 1991; Dziuk and Bellows, 1993). Age at first calving is also described as a good indicator of cow fertility influencing the overall herd productivity (Gutierrez et al., 2002). Dams calving at a young age tend to be more resourceful in beef production system since a decrease in age of heifers at first calving increases the average number of calves weaned per cow during its entire production life hence improving the cow's lifetime productivity (Yilmaz et al., 2004; Marshall et al., 1990).

However, harmonizing growth and reproductive performance in beef cattle managed in tropical regions is challenging (Luna-Nevarez et al., 2010), since the variations in body size and milk production in cattle results in varied nutrient requirements for growth, maintenance and reproduction (Arango and Van Vleck, 2002; MacNeil, 2005). Luna-Nevarez et al. (2010) observed opposing relationship between cow size and fertility in Brangus cattle and further suggested maturing rate index to be negatively correlated with both age at first calving and calving interval.

Besides age at first calving and calving interval, calf survival also has a major impact on herd economic efficiency as it reduces beef farm income and affects the number of animals available for selection, thus influencing both selection intensity and genetic progress (Gianola, 1982; Gianola and Foulley, 1983; Magalhaes Silva et al., 2017). Guerra et al. (2006) and Cecchinato et al. (2010) stated that survival trait has a binomial phenotypic expression, but with underlying continuous genetic and environmental influences. Casellas et al. (2006) reported that calf survival and longevity are traits of interests to animal breeders due to their effects on economic performance and animal welfare. However, there is no previous study reported on the reproductive as well as calf survival traits for Tswana cattle in Botswana. The objective of this study was therefore to determine the environmental and genetic factors influencing age at first calving, calving interval and calf survival to weaning in Tswana cattle selected for weaning and eighteen-month weights.

5.2. Materials and methods

5.2.1. Data description

Data obtained from DAR, consisting of records as described in the third chapter was used in this study. Data was edited and extracted for records as shown in Table 5.1 below which were then used for analysis of age at first calving, calving interval, and calf survival to weaning. Calving interval (CI) was derived as the difference between the two subsequent calving dates.

Fixed effects fitted for the analysis of the reproductive traits were selection line, calving season and calving year. Since seasonal mating was practiced which started in January and ended in March, calving seasons started in September and ended in January. Few animals calved in the months of September and January therefore calving or birth seasons were categorized into 3 groups as follows: season 1 comprised cows that calved in September and October, season 2 comprised those that calved in November while season 3 comprised cows that calved in December and January.

Table 5.1: Summary statistics for data used for analysis of age at first calving, calving interval and calf survival to weaning

Parameter	Number of observations		
	CS	AFC	CI
Total number of animals with records	7223	818	1804
No of animals survived to weaning	6515		
No of animals died before weaning	708		
No of generations	5	4	4
No of sires with progeny	188	136	121
No of dams with progeny	1659	611	496
Calf sex (levels)	2	2	2
Birth/calving season	3	3	3
BWT (kg)		-	Covariate

CS = calf survival, AFC = age at first calving, CI = calving interval, BWT = birth weight of calf.

5.2.2. Statistical analysis

5.2.2.1. Analysis of reproductive traits

Variance components for age at first calving and calving interval were estimated by fitting univariate individual animal models in ASREML program (Gilmour et al., 2015). Calving interval was estimated using repeatability model. These variance components were later used to compute, phenotypic variance (σ^2_p), direct heritability (h^2_d), the ratios for permanent maternal environmental effects (h^2_c) and random residual effects (h^2_e). Fixed effects fitted for both calving interval and age at first calving were selection line, calving year and season. The mixed statistical model used for analyzing data of calving interval and age at first calving was as follows:

$$Y = X\beta + Z_d u_d + Z_c u_c + \varepsilon$$

Where,

Y = the observed reproductive trait of the cow (age at first calving and calving interval)

X = the incidence matrix relating fixed effects to the observations of a trait

β = vector of fixed effects,

Z_d = incidence matrix relating direct additive genetic effects the observations of a trait,

Z_c = incidence matrix relating permanent environmental effects to the observations of a trait.

u_d = a vector of direct additive genetic effects,

u_c = a vector of permanent cow environmental effects

and ε = a vector of random residual effects.

The random effects in the mixed models are assumed to have the following distributions: $[\mu_d', \mu_{pe}', e']' \sim N\ [(0', 0', 0')', \sum]$. The age at first calving was analyzed using a univariate mixed model with animal direct genetic as the only random effect other than the residual term. Expected variance-covariance structure fitted in the genetic analysis model was as follows:

$$\Sigma = \begin{bmatrix} A\sigma_d^2 & 0 & 0 \\ 0 & I_q\sigma_c^2 & 0 \\ 0 & 0 & I_n\sigma_e^2 \end{bmatrix}$$

Where I_q is an identity matrix equal to number of cows (qxn); I_n is an identity matrix with the size equal to n x n; A is numerator relationship among the animals; σ_d^2, σ_c^2, σ_e^2 are additive genetic, permanent environmental and residual variances respectively.

5.2.2.2. Analysis of pre-weaning survival trait

Calf survival was coded as 1 if the calf was born alive and survived to weaning age and 0 if the calf was born as still birth or born alive but died before reaching weaning age. Since calf survival was analysed as a binomial trait, log-linear logistic model was fitted to analyse the data. The fixed effects fitted for calf survival trait were selection line, dam age, sex, linear and quadratic birth weight effects and contemporary group formed from concatenating year and month of birth as described in chapters 3 and 4 of this study. All fixed factors were fitted as class variables except birth weight which was fitted as a covariate.

The model was used to analyse pre-weaning mortality as a binary outcome such that it postulated a random variable called liability: λ_i where i=1...,n and the observed binary response: y_i was the result of the following relationship;

$$y_i = \begin{Bmatrix} 0 \text{ if } \lambda_i < \tau \\ 1 \text{ if } \lambda_i \geq \tau \end{Bmatrix}$$

Where; τ = fixed threshold,

λ= liability assumed to be normally distributed with a mean, μ and a covariance matrix, R = $I\sigma^2_e$, where σ^2_e is the residual variance,

y = observation of binary response corresponding to the calf survived to weaning or not.

Due to the unidentifiable threshold and σ^2_e, the parameters were set to arbitrary values ($\tau = 0$ and $\sigma^2_e = 1$) to represent the origin and scale of measurement respectively. It was assumed the vector of liabilities, given μ, followed the distribution; $\lambda|\mu \sim N(\mu,I)$. The probability that observation *i* is scored as 1, given a model parameter vector, Θ was defined as;

$$\Pi = \text{Prob}(y_i = 1|\mu_i) = \text{Prob}(\lambda_i > 0|\Theta) = \Phi(\mu_i)$$

Where $\Phi(\mu_i)$ is the standard normal cumulative distribution function.

Fixed statistical model was fitted to the data using GENMOD procedures with logit as a link function in Statistical Analysis System (SAS, 2012) to identify environmental factors significantly influencing survival. The general form of the fixed model fitted for calf survival was as outlined below;

$$Y_{ijklmn} = s_i + d_j + y_k + m_l + b_m + e_{ijklmn}$$

Where;

$Y_{ijklmno}$ is the observation of the calf survival to weaning in the nth selection line, b_m is the mth linear or quadratic birth weight effect, s_i is the ith sex of the calf effect, d_j is jth dam age at calf's birth, y_k is kth contemporary group effect, m_l is lth effect of the sire and e_{ijklmn} is random residual error distributed independently with mean zero and common variance, $\sigma^2_{e.}$

5.2.2.3. Estimation of genetic parameters for calf pre-weaning survival

To estimate the genetic parameters for calf survival, generalised mixed linear logistic model with logit as link function was fitted to the data using ASREML program (Gilmour et al., 2015).

The genetic parameters for the preweaning survival were estimated using a sire model as shown below;

$$\lambda_{ijklmn} = \mu + b_i + (b_i)^2 + s_j + y_k + p_l + s_m + e_{ijklmn}$$

Where; λ_{ijklmn} is the value of liability for a calf n, μ = general mean, b_i = linear birth weight, $(b_i)^2$ = quadratic birth weight, s_j = sex of the calf, y_k = year and month of birth, p_l = age of the dam, and s_m = random sire effect distributed as N(0, $A\sigma_s^2$) and e_{ijklm} is residual term distributed as N(0, $I\sigma_e^2$).

5.3. Results and discussion

5.3.1. Factors influencing reproductive traits

The results for the analysis of environmental factors affecting both age at first calving and calving interval are shown in Table 5.2. The two traits were significantly influenced (P<0.001) by selection line, calving year and season.

Table 5.2: Least square means (± S.E.) for selection lines and calving seasons

Effect	Trait	
Selection line	Age at first calving (months)	Calving interval (days)
S1	40.34 ± 0.46^a	569.21 ± 9.85^a
S2	41.44 ± 0.46^b	554.49 ± 10.17^b
S3	39.66 ± 0.60^a	536.97 ± 13.87^c
Birth/Calving season		
October	41.75 ± 0.51^a	625.95 ± 7.93^a
November	40.37 ± 0.48^b	473.78 ± 6.40^b
December	39.30 ± 0.53^b	414.65 ± 6.77^c

S.E. = standard error; ***regression coefficients differ significantly from zero (P<0.0001), S1 = selected for weaning weight, 2 = selected for 18 month weight and S3 = unselected control population.

5.3.1.1. Selection line

The results indicated that age at first calving was not significant between the control population (S3) and animals selected for weaning weight (S1). However animals selected for eighteen months weight (S2) calved at older age than the other two lines (Table 5.2). The result revealed that selection for eighteen months weight increased age at first calving by 1.78 and 1.10 months when compared to the control population and animals selected for weaning weight, respectively. The results are consistent with the findings by Luna-Nevarez et al. (2010) who reported a negative relationship between improved growth traits (birth weight, yearling weight and post weaning ADG) and age at first calving in Brangus cattle managed under desert production system. Cooke et al. (2013) also established that both increased birth weight and growth rate led to increased age at first calving in Holstein heifers. Meyer et al. (1991), likewise reported low and negative association between age at calving and growth traits in Australian beef cattle. However, contrary to the current results Mercadante et al. (2003) reported that selection for post-weaning growth traits did not compromise reproductive performance of the cows.

The current results showed that calving interval significantly varied with selection line. The shortest (536.97±13.87) calving interval was observed in the unselected control population while longest (569.21±9.85) was witnessed in the population selected for weaning weight. The current results are consistent with some literature reports (Albera et al., 2004; Luna-Nevarez et al., 2010; Berry and Evans, 2014) that described negatively correlated responses on reproduction of cows selected for growth rate. However, since the animals were grazing on a natural pasture, the variation may be attributed to lack of improved pasture quality to match the nutritional requirements for relatively larger cows from the selected lines and failure of management to cull cows that failed to conceive in mating season.

5.3.1.2. Birth/Calving season

The mean difference in age at first calving remained non-significant between animals that calved in November and December. However, the trait differed significantly between October and the other two calving seasons. Age at first calving for those that calved in October was 1.38 and 2.45 months greater than for those calved in November and December, respectively. The estimates obtained currently for age at first calving were consistent with the range reported by Berry and Evans (2014) of 936±51.4 days in Irish beef cattle, McHugh et al. (2014) of 660 to 1278 days in Irish beef cattle and Luna-Nevarez et al. (2010) of 722.4±19 days in Brangus cattle. However, since seasonal mating was practiced in the current study the increased age at first calving in October may be due to the circumstance that animals born in this season were exposed to breeding at the same time as those born in the later seasons hence their chances of being younger at first mating season and ultimately at calving were eliminated.

Calving interval varied significantly between the three calving seasons. The longest calving interval was exhibited in cows that calved in October followed by those that calved in November and December. Cows that calved in December exhibited the shortest calving interval. Calving interval for cows that calved in October were 152.17 and 211.30 days longer than those that calved in November and December, respectively. However, the difference between calving intervals of cows that calved in seasons November and December was 59.13 days. The values for calving interval obtained in the present study are within the range of 300 to 799 days reported by McHugh et al. (2014) for Irish beef cattle and by Luna-Nevarez et al. (2010) of 414.9±5.4 in for Brangus cattle. The current results also agreed with the findings by Short et al. (1990) who reported that calving season is one of the factors mostly associated with *postpartum anoestrus* hence influencing calving interval. Hansen (1985) also acknowledged the seasonal effect on postpartum interval and stated that it was due to nutrition and other factors such as genotype and suckling. However, Sharpe et al. (1986) concluded that not much can be done through management to correct seasonal effects rather than adjusting for them. Since mating season which started in January and ended in March was practiced in the current study, prolonged calving interval may be attributed to the situation that cows calving in October had to wait until January to be served with a bull compared to those calving in November and December which waited for a short period to be served with a bull or calved with the bull around. The other reason may be that grazing on natural pasture was practiced and the rain season starts in September and end in April hence cows calving in October possibly had poor body condition score at calving and also may not have had adequate postpartum nutrition compared to those that calved in November and December when adequate nutritious pasture is well established. Therefore good body condition score at calving and adequate postpartum nutrition improved the chances for both postpartum cycling and re-conception rate of cows that calved in November and December hence shortening their calving intervals (Short et al., 1990 and Berry and Evans, 2014).

5.3.1.3. Birth/Calving year

The least square mean estimates of calving interval and age at first calving ranged from 447± 22 days in 1999 to 577±22 days in 2010 and 35.6 ± 3.63 months in 1999 to 48.4 ± 0.83 months in 2011 for calving and birth year, respectively (the detailed data is not shown). The results showed a clear regression on the performance of the cows for the two traits. The declining trend observed on both traits over the years in the current study seems to be in agreement with the previous literature reports by Do et al. (2013) and Oltenacu and Broom (2010) that selection for high growth and milk performance in cattle generally is accompanied by a decline in reproductive performance unless the increased nutritional requirements of the cows is maintained through supplementary feeding. Since the animals in the current study were dependent on natural pasture for the better part of their nutritional needs the results may indicate a continuous deterioration in pasture quality over the years. Hence, this call for improving the quantity and quality of grazing pasture as well as implementation of supplementary feeding strategy in order to keep up with the continuous improvement on livestock performance through selection.

5.3.2. Factors influencing calf survival to weaning

5.3.2.1. Selection line, Calf sex and dam age effects

There was no significant difference in pre-weaning survival of calves among the selection lines, while calf survival was significantly affected by calf sex and dam age (Table 5.3). The female calves survival was 1% higher ($P<0.05$) than male calves. This may be attributed to male calves being born heavier than their female counterparts hence more calving difficulties and dystocia cases that lead to high mortality in male calves than in females especially those calves born from primiparous cows.

Calf survival rate increased from 90% for young dams aged less than 5 years to 93% for mature dams aged 5 to 9 years. However, calf survival rate was not significantly different between mature dams, aged between 5 to 9 years and older dams aged above 9 years (Table 5.3). Variation in calf survival with dam age may be attributed to young dams being either prone to calving difficulty or failing to meet the calf's environmental and nutritional requirements during prenatal and postnatal period hence leading to weak calves with low birth weight being born and failing to survive to weaning age.

Table 5.3: Least square means (± S.E.) for calf survival to weaning by selection line, dam age, calf sex and regression coefficient (± S.E.) for calf birth weight

Effect	Means ± S.E.
Selection line	
S1	0.91 ± 0.007^{a}
S2	0.91 ± 0.006^{a}
S3	0.92 ± 0.009^{a}
Sex of the calf	
Male	0.904 ± 0.005^{a}
Female	0.910 ± 0.007^{b}
Dam age (years)	
≤5	0.904 ± 0.008^{a}
>5 to ≤9	0.932 ± 0.006^{b}
>9	0.937 ± 0.007^{b}
Birth Weight	
Linear	$0.0550\pm0.0061^{***}$
Quadratic	$-0.0008\pm0.0001^{***}$

S.E. = standard error; *** = P<0.001, S1 = selected for weaning weight, 2 = selected for 18 month weight and S3 = unselected control population.

The results of the current study are consistent with the findings by Goyache et al. (2003) who reported an average survival rate difference of 0.15% to 2.44% in favour of female calves at different pre-weaning ages in beef cattle. Likewise, Tarres et al. (2010) observed that calving difficulty varies with calf sex and is more extreme in male calves than in their female counterparts.

The lower calf survival observed in the current study for younger dams might be attributed to calving difficulties and inability of providing sufficient nutrients for weaker calves during the nursing stage. Cole et al. (2007) reported that calving difficulty negatively affect calf survival via prolonged hypoxia and associated potential traumas. Tarres et al. (2010) reported that calving difficulty is one of the factors leading to reduced pre-weaning calf survival, and it extremely affects young primiparous dams aged less than 5 years than mature dams aged 5 years and older. On the other hand, Correa et al. (2000) reported that dystocia and calving difficulty are not the main cause of death in tropical beef breeds.

In general, the range of values (90% to 94%) obtained for calf survival rate in Tswana cattle in the current study is within the range of values reported for other beef breeds by Cervantes et al. (2010) for Asturiana de los Valles beef cattle (80 to 94%), by Magalhaes Silva et al. (2017) for Nellore cattle (93%) and by Guerra et al. (2006) for multibreed beef cattle (91%).

5.3.2.2. Birth weight effect

Both linear and quadratic birth weight effects had significant ($P<0.001$) influence on calf survival (Table 5.3). The implication of the result is that the calf survival rate increased with increasing weight of calves towards average weight and then declined with increasing calf birth weight. This may happen as a result of some calves being born with extremely lighter and heavier weight than average birth weight leading to death from various stressful environmental factors including inability of the dams to care and provide sufficient nourishment required for early growth.

The results are consistent with a report by Bunter et al. (2014) who observed higher mortality rate in Brahman and tropical composite calves with low birth weight. The same authors further found that generally pre-weaning mortality in beef cattle is associated with calving difficulty and extreme birth weights. Riley et al. (2004) and Vostry et al. (2014) reported that new born calves with low vigour were frequently observed in *Bos indicus*. The authors further established that most pre-weaning deaths occurred within thirty days after birth and cited calf weakness as the major cause of death, followed by diarrhoea and navel inflammation. Magalhaes Silva et al. (2017) also found that factors most significantly associated with mortality for large number of calves were production environment presented by site-year and low birth weight more so than high birth weight.

5.3.3. Variance component and genetic parameter estimates for reproductive traits

Direct genetic and environmental variances contributed 10% and 90% to the phenotypic variance of age at first calving, while the direct genetic and environmental variance contributions to the phenotypic variance of calving interval were 7% and 93% respectively. The permanent environmental variance estimate for the calving interval was zero (Table 5.4). This might indicate lack of predicting ability of current calving interval for the future calving interval within a cow.

Table 5.4: Variance components and heritability estimates (± S.E.) for age at first calving and calving interval

Parameter	Trait	
	Age at first calving	Calving interval
σ^2_a	2.47±1.85	2150.3±792.50
σ^2_e	22.83±2.1	29979±1184.5
σ^2_{pe}	-	0.0
σ^2_p	25.306±1.27	32129±1088

h^2_a	0.10±0.07	0.07±0.02
h^2_e	0.90±0.07	0.93±0.02

S.E. = standard error, σ^2_a = direct genetic variance; σ^2_e = residual variance; σ^2_{pe} = permanent environmental variance; σ^2_p = phenotypic variance; h^2_a = direct heritability and h^2_e = environmental proportion.

Direct heritability estimate currently obtained for age at first calving was 0.10±0.07 and it did not differ significantly from zero. The estimate was low and within the lower range of reported values. For example, the reported heritability values range from 0.11 to 0.31 (Makgahlela et al., 2008; McHugh et al., 2014; Berry and Evans, 2014; Park and Lee, 2013; Solemani-Baghshah et al., 2014; Gutierrez et al., 2002) in beef and dairy cattle. Direct heritability estimate obtained in the current study for the calving interval was 0.07±0.02. This estimate was also low but significantly different from zero. Direct heritability value obtained in the current study was comparable with the range of 0.01 to 0.06 as reported (Gutierrez et al., 2002; Berry and Evans, 2014; McHugh et al., 2014) for beef cattle. The results show that in general heritability for reproductive traits is very low and also they are lowly repeatable. As it has been established in several previous studies, the high estimates of environmental variance obtained for the two traits indicate that significant performance improvement on the two traits can be attained through modifying environmental factors associated with cow management.

5.3.4. Variance components and genetic parameter estimates for calf survival to weaning

The results presented in Table 5.5 show that the sire variance for the survival accounts only for 10% of the phenotypic variance. This result indicates that much of the phenotypic variance for calf survival may be defined by other components other than direct genetic effects possibly by environmental components.

Table 5.5: Variance components and heritability estimates (± S.E.) for calf survival to weaning

Parameter	Estimate
σ^2_s	0.062±0.040
σ^2_a	0.249±0.159

σ^2_e	3.290±0.040
σ^2_p	3.352±0.040
h^2	0.074±0.045

S.E. = standard error, σ^2_s = sire variance, σ^2_a = genetic variance, σ^2_p = phenotypic variance = $\sigma^2_e + \sigma^2_s$ and h^2 = heritability = $4(\sigma^2_s) / (\sigma^2_e + \sigma^2_s)$

The lower estimate for direct genetic effect obtained in the current study is in line with the findings by Gregory and Maurer (1991) and Von-Keyserlingk and Weary (2007). These authors reported that pre-weaning mortality has an important maternal component which decreased from birth to weaning period. The authors further described maternal effects to be in the form of intrauterine effects, milk production and protection provided through behaviour and passive immunity (colostrum). The lower estimate currently obtained for direct genetic variance was not significantly different from zero. However it is well documented that that survival is one of the traits with low heritability and most of the variation comes from other environmental aspects (Cox, 1972; Prentice and Gloekler, 1978; Casellas et al., 2006; Cecchinato et al., 2010; Cervantes et al., 2010; Bunter et al., 2014 and Magalhaes Silva et al., 2017). Therefore a significant improvement on calf survival rate may be attained through improvement on the environmental part such a management system.

The current direct heritability estimate of 0.074±0.045 is consistent with other reported heritability estimates (Guerra et al., 2006; Schmidek et al., 2013 and Magalhaes Silva et al., 2017) for pre-weaning calf survival ranging from 0.02±0.02 to 0.190±0.078 for the Nellore and multibreed beef cattle. Schmidek et al. (2013) observed higher genetic variability for calf survival during the perinatal period up to 2 to 3 days after birth compared to the rest of the pre-weaning period. In general, the low and non-significant genetic component found in the current results as shown in Table 5.5 reveals that there is insufficient genetic variability to improve calf survival to weaning through genetic selection.

5.4. Conclusion

The current study revealed that both age at first calving and calving interval have low direct heritability and are more influenced by environmental factors than genetic effects. The low repeatability estimate for calving interval proved the trait to be poorly repeatable. Improvement of these traits can therefore rapidly be achieved through modification of the management aspects than selection for these traits.

Sex of the calf, dam age and birth weight significantly influenced calf survival to weaning. The significant influence of birth weight on calf survival to weaning trait suggests that management intervention in the form of proper assistance by veterinarians during birth should be in place to avoid pre-weaning death of calves born with very low and high birth weights. Calf survival to weaning had low and non-significant genetic variability indicating that this trait is largely affected by environmental effects hence may not improve rapidly through genetic selection.

Chapter 6

Environmental and genetic components influencing mature cow weight in Tswana cattle selected for early growth traits

6.1. Introduction

Mature body weight and milk production potential are well known essential mechanisms in determining the production competence of beef cows (McMorris et al., 1986; Montano-Bermudez et al., 1990; Miller and Wilton, 1999) and cows with high mature weight require more energy for maintenance. As a consequent, increasing mature cow weight should generally be considered undesirable for the breeding herd as Fiss and Wilton (1992) asserted. In addition, the inclusion of mature cow size in selection programme to improve feed efficiency of the cow herd has been emphasised (Garrick, 2010; Crook et al., 2010). Fiss and Wilton (1989) further added that elevated maintenance cost associated with large mature cows is detrimental in any breeding program. Mature cow weight can therefore be considered in genetic evaluation together with some genetically correlated traits measured earlier in life to account for culling in field data

(Kaps et al., 1999). The aim of this study was to investigate the impact of mass selection for weaning weight (S1) and eighteen months weight (S2) on mature cow weight (MWT) compared to the unselected control line (S3) in Tswana cattle.

6.2. Materials and methods

6.2.1. Animal management

The animals were generally grazed on veld as a main source of food from birth to maturity and occasionally supplemented with mineral/nutritional licks during severe draught and winter seasons.

6.2.2. Data description

Data obtained from Department Of Agricultural Research in Botswana consisting of records as described in the chapter 3 which focussed on environmental factors affecting early growth traits, were extracted for traits as listed in Table 6.1 below and used for cow weight analysis.

Table 6.1: Summary statistics of the data used for analysis of mature cow weight

Observation	No of observations	Average	SD	Min	Max
Total number of records	19301				
Dams	610				
Sires	137				
No of generations	4				
Contemporary group	54				
Cow weight (kg)		428.7	69.9	157	670
Cow age (years)		7.2	2.8	2.0	17.6

6.2.3. Statistical analysis

6.2.3.1. Environmental effects and genetic parameters for mature cow weight

Using the records from data collected on selected Tswana cattle obtained from DAR as described in the data description section above, analysis of mature cow weight was undertaken using a mixed model. The analyses were performed such that they utilized the entire observations recorded for each cow. The fixed effects fitted for mature cow weight were selection line, contemporary group, cow age in years fitted as covariate (linear and quadratic) and the interaction between cow age and selection line. Contemporary group was derived by concatenating season and year of weighing. Variance and covariance components were estimated by fitting repeatability animal models to the data using the ASREML program (Gilmour et al., 2015). Genetic parameters were then derived from the variance components. Correlations between mature cow weight and early growth traits were estimated by fitting bivariate animal models. Mature cow weight for each cow was taken as the average of all the individual cow weight observations recorded at different parturition and weaning dates. Only animals with all the records for early growth traits (birth, weaning, yearling, and eighteen months weights) and mature cow weight traits were extracted and used for the estimation of correlations. The general form of the model for the estimation of variance components with their expected variance-covariance structure were as outlined below:

$$Y = X\beta + Z_d u_d + Z_c u_c + \varepsilon$$

Where,

Y = the observed mature cow weight trait

X = the incidence matrix relating fixed effects to the observations,

β = vector of fixed effects,

Z_d = incidence matrix relating direct additive genetic effects to the observations,

Z_c = incidence matrix relating permanent environmental effects to the observations,

u_d = a vector of random direct additive genetic effects,

u_c = a vector of random permanent environmental effects

and ε = a vector of random residual effects.

The random effects in the mixed models were assumed to have the following distributions:

$[\mu_d', \mu_c', e']' \sim N[(0', 0', 0')', \Sigma]$

$$\Sigma = \begin{bmatrix} A\sigma_d^2 & 0 & 0 \\ 0 & I_q\sigma_c^2 & 0 \\ 0 & 0 & I_n\sigma_e^2 \end{bmatrix}$$

Where; A is a numerator relationship matrix among all animals, σ^2_d is the direct genetic variance; I_q and I_n are identity matrices equal to the number of dams and number of animals with observation respectively; σ^2_c and σ^2_ε are permanent environment variance and error (temporary environmental) variance respectively.

6.3. Results and discussion

6.3.1. Factors influencing mature cow weight trait

6.3.1.1. Selection line

Mature cow weight varied significantly with selection line. Mature cow weight among the selection lines ranged from 393.93±4.71 kg to 445.98±4.6 kg (Table 6.2). The lightest cow weight was observed in unselected control line (S3) while the heaviest cow weight was detected in the eighteen months weight selection line (S2).

Table 6.2: Least square means (± S.E.) for selection lines

Selection line	Cow weight (kg)
S1	441.16±4.62^{a}
S2	445.98±4.62^{b}
S3	393.93±4.71^{c}

^{a,b,c} means with different superscript differ significantly ($P<0.05$), S.E. = standard error, S1= selection for weaning weight, S2 = selection for 18 months weight and S3 = unselected control population.

The results revealed that selection for weaning weight and eighteen months weight significantly increased mature cow weight. However, selection for eighteen months weight increased mature cow weight more than as selection for weaning weight did. The current results are consistent with the report by Nephawe (2004) that an increase in overall growth at saleable age of calves (weaning and slaughter weight) may increase mature cow size, which the author further stated is of concern in the beef production system due to the cost of energy required to maintain mature cow weight. Boligon et al. (2013) also reported positive and medium correlation between mature cow weight and both weaning and yearling growth traits in selected Nellore cattle. Furthermore, Boligon et al. (2010) and Forni et al. (2007) revealed that selection of young animals for greater weight may result in heavier animals at adult age owing to indirect correlated response.

6.3.1.2. Cow age

Both linear and quadratic dam age significantly influenced mature cow weight and their effects varied with selection line. Cow weight increased linearly with the age of the cows at rates of 28.16±1.64 kg, 38.65±0.48 kg and 40.46±0.5 kg per annum in S3, S1 and S2 lines, respectively. In the three lines, the cow weight reached a maximum value between 8 and 10 years of age and declined thereafter at rate of 1.16±0.10 kg, 1.98±0.07 kg and 2.05±0.07 kg per annum in S3, S1 and S2 lines, respectively (Figure 6.1). In general, both the rates of increase and decrease in cow weight with age were significantly slower in control population than in the two selected lines.

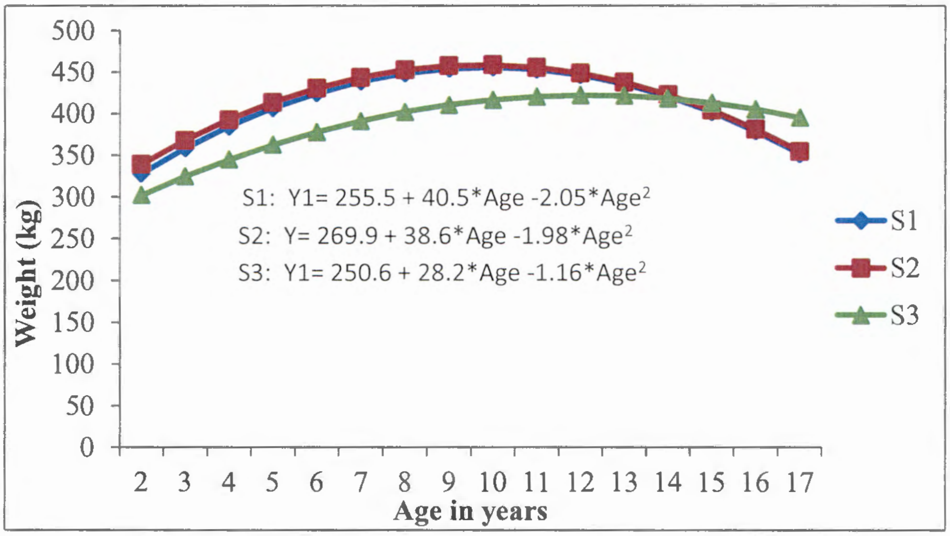

Figure 6.1 Predicted cow weight with age for the three selection lines. (S1= selection for weaning weight, S2 = selection for 18 months weight and S3 = unselected control population)

The results agreed with the findings by Nephawe (2004) who reported that cow weights demonstrated an increasing trend at early ages, a flush pattern at intermediate ages, and a declining trend at latter ages. Crook et al. (2010) also revealed a quadratic relationship between age of cow (in years) and cow weight at calving and at weaning. The same authors further stated that cow weights at calving and at weaning amplified rapidly with age up to around six years, after which the rate of change with age diminished. Variation of cow age effect with selection line may be due to the fact that the magnitude of the influence of the two selection criteria differs, with eighteen months weight selection displaying more change. Therefore, the cow's loss of efficiency to mobilize nutrients towards production and maintenance as it ages coupled with deterioration on the grazing pasture mostly affected the animals from the selection lines with greater mature cow weight than those unselected control cows with less mature weight.

6.3.2. Estimates of genetic parameters for cow weight trait

The results indicate that direct genetic, permanent and temporary environmental variances constituted significant proportions of the phenotypic variance of mature cow weight (Table 6.3). Direct genetic effect constituted 26% of the phenotypic variance while temporary environmental effect constituted 54%. Permanent environmental effect was accountable for 20% of the phenotypic variance, indicating that mature cow weight is moderately repeatable.

Table 6.3: Variance components and heritability estimates (± S.E.) for cow mature weight

Parameter	Mature cow weight
σ^2_a	799.55±105.95
σ^2_c	599.79±86.77
σ^2_e	1641.5±17.51
σ_P^2	3062.6±62.90
h^2_a	0.26±0.03
h^2_c	0.20±0.03
h^2_e	0.54±0.01
r	0.46±0.01

S.E. = standard error; σ^2_a = direct variance; σ^2_c = permanent environmental variance; σ^2_p = phenotypic variance; σ^2_e = error variance; h^2_a = direct heritability; h^2_c = permanent environmental proportion; r = repeatability (calculated as $\frac{\sigma_a^2+\sigma_c^2}{\sigma_P^2}$, Falconer and Mackay, 1996) h^2_e = temporary environmental proportion.

Direct heritability estimate of 0.26±0.03 currently obtained for mature cow weight of Tswana cattle is comparable with the range of values: 20.9±10.3, 19.3±9.3, 38.5±15.8 and 39.9±13.7 reported for Aberdeen Angus, South Devon, Limousin and Simmental, respectively by Roughsedge et al. (2005) and 0.29±0.04 and 0.37±0.04 reported for the South African Simmental by Crook et al. (2010). The significant heritability estimate indicates that the trait can be included in the selection indices for growth traits to control its unfavourable increase due to indirect response to selection for early growth traits in Tswana cattle. The ratio of the total phenotypic variance of cow weight due to permanent environmental effects associated with the cow accounted for approximately 20%. Mature cow weight in Tswana cattle appear to be a moderately repeatable trait as signified by the magnitude of total animal variance as a fraction of the phenotypic variance (46%). The results are slightly lower but comparable with those obtained by Nephawe (2004) for the Bonsmara cattle in South Africa, and Nephawe et al. (2004) using data of multi-bred beef cattle from the Germplasm Evaluation Project at the United States Meat

Animal Research Centre. The results showed that temporary environmental variance which is attributable to random unaccountable effects accounted for a significant proportion of total phenotypic variance.

6.3.3 Estimates of correlations between mature cow weight and early growth traits

Phenotypic and genetic correlations between early growth traits (weaning, yearling and eighteen months weights) and mature cow weight were significantly different from zero. The genetic correlation amongst BWT and MWT was not substantially different from zero. Both genetic and phenotypic correlations between early growth traits and mature cow weight increased substantially from birth weight to eighteen months weight. All the estimates for genetic correlations were positive and higher than the corresponding phenotypic correlations except only for birth weight where the estimated values were practically similar (Table 6.4).

Table 6.4: Estimates (± S.E.) of genetic and phenotypic correlations between mature cow weight and early growth traits obtained from bivariate analysis

Trait	Genetic correlation	Phenotypic correlation
BWT	0.15±0.17	0.15±0.04
WWT	0.56±0.13	0.27±0.03
YWT	0.84±0.19	0.19±0.03
EWT	0.58±0.13	0.31±0.03

S.E. = standard error, BWT = birth weight, WWT= weaning weight, YWT= yearling weight and EWT= eighteen months weight

The current results are comparable to the findings by Roughsedge et al. (2005) who reported genetic correlations between mature cow weight and weaning weight and post weaning weight ranging between 0.66 and 0.98 for mixed beef cattle. Costa et al. (2011) reported genetic correlations ranging from 0.66±0.06 to 0.85±0.07 between mature cow weight and early growth weight traits (weaning and yearling weights) of Angus cattle. The stronger genetic correlations witnessed in the current results may indicate that more or less identical set of genes influence both mature cow weight and early growth traits. Similar to the values obtained in the current study, Rigatieri et al. (2012) reported low and positive phenotypic correlations ranging from 0.26±0.02 to 0.49±0.02 between mature cow weight and early growth traits (weaning and yearling weights) and weight gains (pre-weaning gain and yearling gain). The low phenotypic correlations between mature cow weight and early growth traits currently obtained reveals weaker environmental correlations among these traits which may be attributed to the variation in the influence of effects such as random environmental effects, dominance and epistasis genetic effects on these traits. The high genetic correlation between mature cow weight and early growth traits suggest that selection for increased early growth weights may lead to increased mature cow weight hence the trait should also be included in the selection program to avoid adverse indirect response.

6.4. Conclusion

Both selection line and cow age significantly influenced the mature cow weight trait in Tswana cattle. The two selection approaches resulted in heavier cows at maturity. The pattern of cow weight changes with age was higher and similar for the two selection lines than for the unselected control line. Mature cow weight exhibited significant genetic variability with moderate repeatability. Cow weight exhibited high genetic correlations with early growth traits (weaning, yearling and eighteen months weights). The current results suggest that in practicing mass selection for early growth traits, caution must be taken to avoid undesirable change in mature cow weight by considering mature weight as part of the selection index.

Chapter 7

General conclusions and recommendations

7.1. Exploiting genetic variation

The genetic merit of beef cattle is fundamental to the profitability and sustainability of the beef production industry. Evaluation of genetic merit in beef cattle starts with the identification and adjustment for environmental factors influencing the traits under consideration. The profitability and sustainability of beef production industry are dependent on the continuous improvement of the genetic merit of beef cattle for economically important traits. The current results indicated the existence of substantial genetic variation in growth and mature cow weight traits of Tswana cattle, suggesting the possibility of genetic improvement through application of effective selection programs. However, the observed genetic change in growth traits has shown less consistency over the past twenty years for phenotypic mass selection in Tswana cattle. On the other hand, variation in phenotypic performance has been detected in some reproductive traits perhaps due to change in management practices. The pre-weaning calf survival trait analysed in the current study showed weak evidence of genetic variation, thus improvement through genetic selection might be possible but slow. For improved performance to be attained in growth traits, farmers should be advised to select their animals based on genetic merit by using the estimated breeding values generated from multiple trait analysis. To maximize genetic change, breeders and farmers should consider maternal genetic effects in selection programs for pre-weaning growth traits.

7.2. Developing the breeding objective

Breeding objectives should sufficiently be related with the profitability and sustainability of an enterprise in order to benefit both the producer and the consumer. Growth, reproductive and survival traits are the main targets in genetic improvement of beef cattle and should be considered in defining the breeding objectives. The inclusion of traits in the breeding objectives should be based on their identified influence on the profit hence only economically important traits should be incorporated in the breeding objective. Traits that are identified for inclusion in the breeding objective should be considered simultaneously for genetic improvement. Since the presence of several traits considered in a selection program involves placing appropriate weights on the traits, the weights should be proportional to the extent to which the traits affect the profit. Establishment of economic values for traits should take into account all economic parameters affecting the operation of the enterprise. Traits of economic importance identified as growth and mature cow weight traits in the current study should be considered in defining the breeding objective for Tswana cattle in Botswana. Economic values for these traits have to be established taking into consideration various beef markets located in different regions within the country and abroad.

7.3. Implementing multi-trait selection

Successful implementation of multi-trait selection is dependent on the use of genetic parameters and economic values which are combined through the use of selection index. The genetic parameters estimated for traits analysed in the current study contribute towards such goal. The best selection method should be based on genetic parameters rather than phenotypic indices as has been the case for growth traits in the current project. Estimation of breeding values for all traits included in the breeding objective should be done through Best Linear Unbiased Program since this will help utilizing the relationship amongst traits and animals thereby improving the accuracy of the predictions. During the selection, estimated breeding values should be weighted by economic values. In case of highly correlated traits such as WWT and YWT and ADG1, the use of WWT as an indicator trait in the selection program may be possible with correlated responses anticipated in both YWT and ADG1. Since the use of economic selection indices enables breeders and producers to evaluate different breeding programs in monetary terms while genetic progress and economic returns are sensitive to changes in economic values, the economic values should be periodically updated. The updating process should entail recalculating index weights for selection purposes thus helping breeders and producers to place appropriate weights on index traits hence benefitting the breeding program. The selection index to be considered for Tswana cattle productivity and economic efficiency may consist of growth, mature cow weight, reproductive and meat quality traits. However, both genetic parameters and economic values for these traits in Tswana cattle breed are yet to be adequately established. Therefore the Botswana beef production industry should be advised to mobilize the formation of effective Tswana cattle breed association that will establish the breeding objectives and economic values for these traits in the breed to be used for redesigning the breeding programs.

7.4. Recommendation for further studies

Although numerous studies have been conducted on genetic parameter estimates for growth, reproductive and calf survival traits in different well established beef breeds, there is lack of information available on these traits for indigenous beef cattle breeds in Botswana. The current study focused on identifying environmental effects and estimating genetic parameters for growth, reproductive and calf survival traits in Tswana cattle. This study has established basic genetic information for these traits. However, more studies focusing on estimating genetic parameters for these traits need to be conducted to check for the consistency of the estimates and assist in genetic improvement of Tswana breed in the country. Since the implementation of an efficient breeding program for one breed in a multi breed industry may result in a more significant genetic improvement in that breed than other breeds, developing economic breeding programs for other indigenous cattle breeds in Botswana may also be the way forward for the country's beef production industry.

Data used in this study were collected from a project conducted in one site of the department of agricultural research and the results may be considered unrepresentative to all production environments in the country hence there is a need for more similar studies to be conducted in the same breed involving different farms located in different regions in the country. In addition, studies should be conducted to establish economic values for all traits of economic importance identified to be included in the selection index and ultimately to calculate the index weights to be placed against these traits.

7.5. Recommendations on improved record taking and quality of measurements on economically important traits in the future breeding efforts

Good record keeping means noting down all important details and events, in a simple and clear manner that can help provide information for future activities. Excellent records are a cornerstone of building a financially successful livestock enterprise and greatly help in the development of livestock industry of any country. Therefore record keeping is a must in any country's livestock production sector. The records can be used for improved breeding decision making at farm level and collectively to bring about the desired genetic improvement and conservation in the sector and at large in the country. Recording keeping on performance as well as pedigree at farm level is the area that has always appeared to be the most neglected management technique in Botswana beef cattle producers. It will therefore be of great importance for Botswana's beef production industry to be advised to organize effective breeders associations that will assist in educating and changing the perception of farmers towards record taking and quality measurements on economically important traits. The whole process will thus help farmers think of their farms as businesses, and to realize that good record keeping and management actually also influence the production and profitability of the farm. For effective improvement of the country's future breeding efforts, both commercial and emerging Tswana cattle producers need to be assisted to realize that performance records are important in the overall national herd genetic evaluation and improvement. At farm level as well as nationally, performance records can be used to keep track of all animals and for the identification of individual animals with the right characteristics for future breeding. The importance of accurate breeding records will therefore help to measure the productive efficiency of the national Tswana cattle herd and enable genetic improvement for economically important traits through culling and selection. Therefore, an up to date and accurate performance and pedigree record of each individual animal will be necessary.

The important records to be emphasized at farm level should include pedigree or parentage, growth and reproductive traits. In addition there is a need to establish central performance testing system to record feedlot performance, feed efficiency and meat quality traits to have a complete beef performance improvement programme for Tswana cattle breed and other beef breeds in the country.

References

Aaron, D. K., R. R. Frahm, and D. S. Buchanan. 1986. Direct and Correlated Responses to Selection for Increased Weaning or Yearling Weight in Angus Cattle. I. Measurement of Selection Applied. J. Anim. Sci. 62, 54-65.

Albera, A., A. F. Groen, and P. Carnier. 2004. Genetic relationships between calving performance and beef production traits in Piemontese cattle. J. Anim. Sci. 82, 3440-3446.

Animal Production and Range Research Unit (APRRU), Annual Report. 1992. Livestock and Range Research in Botswana, Ministry of Agriculture, Private Bag 0033 Gaborone Botswana.

Animal Production and Range Research Unit (APRRU), Annual Report. 1993. Livestock and Range Research in Botswana, Ministry of Agriculture, Private Bag 0033 Gaborone Botswana.

Animal Production and Range Research Unit (APRRU), Annual Report. 1999. Livestock and Range Research in Botswana, Ministry of Agriculture, Private Bag 0033 Gaborone Botswana.

Arango, J. A. and L. D. Van Vleck. 2002. Size of beef cows: early ideas, new developments. Genet. Mol. Res. 1: 51-63.

Archer, J. A., R. M. Herd, P. F. Arthur, and P. F. Parnell. 1998. Correlated responses in rate of maturation and mature size of cows and steers to divergent selection for yearling growth rate in Angus cattle. Livest. Prod. Sci. 54: 183-192.

ASA. 1996. Simmental sire selection. Amer. Simmental Assoc., Bozeman, MT.

Assan, N. 2010. Direct and maternal genetic effects and trends for weaning weight in local Tuli cattle of Zimbabwe. Intern. J. Trop. Agric. Food Sys. 3: 206-216.

Assan, N. 2013. Estimates of genetic, environment and phenotypic trends in indigenous Nguni cattle of Zimbabwe: Implication for management and breeding program. Sci. J. Anim. Sci 12: 360-368.

Azzam, S. M. and A. M. Azzam. 1991. A Markovian decision model for bee cattle replacement that considers spring and fall calving. J. Anim. Sci. 69: 2329-2341.

Baker, R. L., C. A. Morris, D. L. Johnson, J. C. Hunter, and S. M. Hickey. 1991. Results of selection for yearling or 18-month weight in Angus and Hereford cattle. Livest. Prod. Sci. 29: 277-296.

Beffa, L. M. 2005. Genotype X enviroment interaction in Afrikaner cattle. PhD Thesis, Department of Animal, Wildlife and Grasslands, University of the Free State, Bloemfontein, South Africa.

Beffa, L. M., J. B. Van Wyk, and G. J. Erusmus. 2009. Long-term selection experiment with Afrikaner cattle. 2. Genetic parameters and genotype X environment interaction for calf growth traits. S. Afr. J. Anim. Sci. 39: 98-105.

Bennett, G. L. and K. E Gregory. 2001. Genetic (co)variances for calving difficulty score in composite and parental populations of beef cattle: II. Reproductive, skeletal, and carcass traits. J. Anim. Sci. 79: 52-59.

Bennett, G. L., R. M. Thallman, W. M. Snelling, and L. A. Kuehn. 2008. Experimental selection for calving ease and postnatal growth in seven cattle populations. II. Phenotypic differences. J. Anim. Sci. 86: 2103-2114.

Berry, D. P. and R. D. Evans. 2014. Genetics of reproductive performance in seasonal calving beef cows and its association with performance traits. J. Anim. Sci. 92: 1412-1422.

Berry, D. P., F. Buckley, P. Dillon, R. D. Evans, M. Rath, and R. F. Veerkamp. 2003. Genetic parameters for body condition score, body weight, milk yield, and fertility estimated using random regression models. J. Dairy Sci. 86: 3704-3717.

Berry, D. P., J. F. Kearney, K. Twomey, and R. D. Evans. 2013. Genetics of reproductive performance in seasonal calving dairy cattle production systems. Ir. J. Agric. Food Res. 52: 1-16.

Boligon, A. A., J. A. Silva, R. C. Sesana, J. C. Sesana, J. B. Junqueira, and L. G. Albuquerque. 2010. Estimation of genetic parameters for body weights, scrotal circumference, and testicular volume measured at different ages in Nellore cattle. J. Anim. Sci. 88: 1215-1219.

Boligon, A. A., L. G. Albuquerque, M. E. Z. Mercadante, and R. B. Lobo. 2008. Models for genetic evaluation of Nelore cattle mature body weight. J. Anim. Sci. 86:2840-2844.

Boligon, A. A., M. E. Z. Mercadante, and L. G. Albuquerque. 2011. Genetic associations of conformation, finishing precocity and muscling visual scores with mature weight in Nelore cattle. Livest. Sci. 135: 238-243.

Boligon, A. A., M. E. Z. Mercadante, S. Forni, R. B. Lobo, and L. G. Albuquerque. 2010. Covariance functions for weights from birth to maturity in Nellore cows. J. Anim. Sci. 88: 849-859.

Boligon, A. A., R. Carvalheiro, and L. G. Albuquerque. 2013. Evaluation of mature cow weight: Genetic correlations with traits used in selection indices, correlated responses, and genetic trends in Nellore cattle. J. Anim. Sci. 91: 20-28.

Boligon, A. A., R. J. Pereira, D. R. Ayres, and L. G. Abuquerque. 2012. Influence of data structure on the estimation of additive genetic direct and maternal covariance for early growthtraits in Nellore cattle. Livest. Sci. 145: 212-218.

Bosso, N. A., E. H. Van der Waaij, K. Agyemang, and J. A. M. Van Arendok. 2009. Genetic parameters for growth traits in N'Dama cattle under tsetse challenge in Gambia. Liv. Res. Rural Dev. 21: 223-231.

Buddenberg, B. J., C. J. Brown, Z. B. Johnson, J. E. Dunn, and H. P. Peterson. 1989. Heritability estimates of pregnancy rate in beef cows under natural mating. J. Anim. Sci. 67: 2589-2594.

Bullock, K. D., J. K. Bertrand, and L. L. Benyshek. 1993. Genetic and environmental parameters for mature weight and other growth measures in Polled Hereford cattle. J. Anim. Sci. 71: 1737-1741.

Bunter, K. L., D. J. Johnston, M. L. Wolcot, and G. Fordyce. 2014. Factors associated with calf mortality in tropicallyadapted beef breeds managed in extensive Australian production systems. Anim. Prod. Sci. 54: 25-36.

Burrow, H. M. 2001. Variances and covariances between productive and adaptive traits and temperament in a composite breed of tropical beef cattle. Livest. Prod. Sci. 70: 213-233.

Casellas J., J. Tarres, J. Piedrafita, and L. Varona. 2006. Parametric boostrap for testing model fitting in the proportional hazards framework: An application to the survival analysis of Bruna dels Pirineus beef calves. J. Anim. Sci. 84: 2609-2616.

Cecchinato, A., O. González-Recio, E. López de Maturana, L. Gallo, and P. Carnier. 2010. A comparison between different survival and threshold models with an application to piglet preweaning survival in a dry-cured ham-producing crossbred line. J. Anim. Sci. 88: 1990-1998.

Cerventes, I., J. P. Gutierrez, I. Fernandez, and F. Goyache. 2010. Genetic relationship among calving ease, gestation length, and calf survival to weaning in Austriana de los Valles beef cattle breed. J. Anim. Sci 88: 96-102

Chevraux, D. J. and C. M. Bailey. 1977. Selection for Postweaning Growth Rate in a Closed Line of Hereford Cattle. J. Anim. Sci. 44: 352-359.

Cole, J. B., G. R. Wiggans, P. M. Van Raden, and R. H. Miller. 2007. Stillbirth (co)variance components for a sire-maternal grandsire threshold model and development of calving ability index for sire selection. J. Dairy Sci. 90: 2489-2496.

Cooke, J. S., Z. Cheng, N. E. Bourne and D. C. Wathes. 2013. Association between growth rates, age at first calving and subsequent fertility, milk production and survival in Holstein-Friesian heifers. Open J. Anim. Sci. 3: 1-12.

Corbet, N. J., R. K. Shepherd, H. M. Burrow, J. Van der Westhuizen, P. E. Strydom, D. J. Bosman. 2006. Genetic parameters for growth and fertility. Evaluation of Bonsmara and Belmont Red cattle breeds in South Africa. 2Aust. J. Exp. Agric. 46: 213-223.

Correa, E. S., P. De Andrade, K. Euclides Filho, and R. G. de Alves. 2000. Avaliacao de um sistema de producao de gado de corte. 1 Desempenho reproductivo. Rev. Bras. Zootecn. 29 (2): 2209-2215.

Costa, R. B., I. Misztal, M. A. Elzo, J. K. Bertrand, L. O. C. Silva, and M. Lukaszewicz. 2011. Estimation of genetic parameters for mature weightin Angus cattle. J. Anim. Sci. 89: 2680-2686.

Cox, D. R. 1972. Regression models and life tables (with discussion). J. Royal Stat. Soc. Series B34: 187-220.

Crews, D. H. 2006. Age of dam and sex of calf adjustments and genetic parameters for gestation length in Charolais cattle. J. Anim. Sci. 84: 25-31.

Crook, B. J., F. W. C. Neser, and M. J. Bradfield. 2010. Genetic parameters for cow weight at calving and at calf weaning in South African Simmental cattle. S. Afr. J. Anim. Sci. 40(2): 140-145.

Davis, M. E. 1987. Divergent Selection for Postweaning Feed Conversion in Beef Cattle: Predicted Response Based on an Index of Feed Intake and Gain vs Feed:Gain Ratio. J. Anim. Sci. 65: 886-895.

De Rensis, F., F. Lopez-Gatius, T. Capelli, E. Molima, M. Techakumphu, and R. J. Scaramuzzi. 2008. Effects of season on luteal activity during the post-partum period of dairy cows in temperate areas. Anim. Consort. 2(4): 554-559.

Deese, R. E. and M. Koger. 1967. Heritability of fertility in Brahman and crossbred cattle. J. Anim. Sci. 26: 984-987.

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

Dickerson, G. E. 1969. Techniques for research in quantitative animal genetics, In: techniques and procedures in animal science research. Amer. Soc. of Anim. Sci. Champaign, Il.

Dickerson, G. E. 1970. Efficiency of animal production-molding the biological components. J. Anim. Sci. 30: 849-859.

Dickerson, G. E., N. Künzi, L. V. Cundiff, R. M. Koch, V. H. Artaud, and K. E. Gregory. 1974. Selection Criteria for Efficient Beef Production. J. Anim. Sci. 39: 659-673.

Do, C., N. Wasana, K. Cho, Y. Choi, T. Choi, B. Park, and D. Lee. 2013. The Effect of Age at First Calving and Calving Interval on Productive Life and Lifetime Profit in Korean Holsteins. Asian Australas. J. Anim. Sci. 26: 1511-1517.

Donoghue, K. A., R. Rekaya, J. K. Bertrand, and I. Misztal. 2004. Genetic evaluation of calving to first insemination using natural and artificial insemination mating data. J. Anim. Sci. 82: 362-367.

Dziuk, P. J. and R. A. Bellows. 1983. Management of reproduction of beef cattle, sheep and pigs. J. Anim. Sci. 57: 355-379.

Enns, R. M. and G. B. Nicoll. 2008. Genetic change results from selection on an economic breeding objective in beef cattle. J. Anim. Sci. 86: 3348-3357.

Eriksson, S., A. Nasholm, K. Johansson, and J. Philipsson. 2004. Genetic parameters for calving difficulty, stillbirth, and birth weight for Hereford and Charolais at first and later parities. J. Anim. Sci. 82: 375-383.

Evans, J. L., B. L. Golden, R. M. Bourdon, and K. L. Long. 1999. Additive genetic relationships between heifer pregnancy and scrotal circumference in Hereford cattle. J. Anim. Sci. 77: 2621-2628.

Falconer, D. S. 1989. Introduction to quantitative genetics (3rd edition). John Wiley & Sons,Inc., 605 Tird Avenue, New Yok, USA.

Falconer, D. S. and T. F. C. Mackay. 1996. Introduction to quantitative genetics (4th edition). Longmans Green, Harlow, Essex, UK.

Ferraz, J. B. S., J. P. Eler, and P. M. T. Ribeiro. 2000. Genetic study of Santa Getrudis cattle in Brazil. Liv. Res. Rural Dev. 20: 130-137.

Ferreira, J. L., L. B. Lopes, T. Bresolin, J. A. S. Garcia, S. Minharro and R. B. Lobo. 2015. Effect of age of dam on weight of calfin the genetic assessment of Zebu cattle in random regressionmodels. Acta Sci. Anim. Sci. 37: 203-208.

Fiss, C. F. and J. W. Wilton. 1989. Effects of Breeding System, Cow Weight and Milk Yield on Reproductive Performance in Beef Cattle. J. Anim. Sci. 67: 1714-1721.

Fiss, C.F. and J.W. Wilton. 1992. Contribution of breed, cow weight, and milk yield to the traits of heifers and cows in four beef breeding systems. J. Anim. Sci. 70: 3686-3696.

Flores, A. G. 1971. A study of calving interval. Retrospective Theses and Dissertations. Iowa State University. Paper 4452.

Forni, S. and L. G. Albuquerque. 2005. Estimates of genetic correlations between days to calving and reproductive and weight traits in Nelore cattle. J. Anim. Sci. 83: 1511-1515.

Forni, S., M. Piles, A. Blasco, L. Varona, H. N. Oliveira, R. B. Lobo, and L. G. Albuquerque. 2007. Analysis of beef cattle longitudinal data applying a non-linear model. J. Anim. Sci. 85: 3189-3197.

Garrick, D. J. 2006. Genetic improvement in beef cattle - Assessing the ramifications of genetic change. Proc. 8th World Congr. Gen. Appl. Livest. Prod., Belo Horizonte, Brazil. 03-17.

Garrick, D. J. 2010. An animal breeding approach to the estimation of genetic and environmental trends from field populations. J. Anim. Sci. 88: E3-E10.

Gianola, D. 1982. Theory and analysis of threshold characters. J. Anim. Sci. 54: 1079-1096.

Gianola, D., and J. L. Foulley. 1983. Sire evaluation for ordered categorical data with a threshold model. Genet. Sel. Evol. 15: 201-223.

Gilmour, A. R., B. J. Gogel, B. R. Cullis, and R. Thompson. 2015. ASReml user guide. Release V4.1. VSN International Ltd., Hemel Hempstead, UK.

Goyache, F., J. P. Gutierrez, I. Alvarez, I. Fernandez, L. J. Royo, and E. Gomez. 2003. Genetic analysis of calf survival at different preweaning ages in beef cattle. Livest. Prod. Sci. 83: 13-20.

Gregory, K. E., and R. R. Maurer. 1991. Prenatal and Postnatal maternal contributions to reproductive, maternal, and size related traits of beef cattle. J. Anim. Sci. 69: 961-976.

Gregory, K. E., L. V. Cundiff, and R. M. Koch. 1995. Genetic and phenotypic (co)variances for production traits of female populations of purebred and composite beef cattle. J. Anim. Sci. 73: 2235-2242.

Groeneveld, E., B. E. Mostert, and T. Rust. 1998. The covariance structure of growth traits in Afrikaner beef cattle. Livest. Prod. Sci. 55: 99-107.

Guerra, J. L. L., D. E. Franke, and D. C. Blouin. 2006. Genetic parameters for calving rate and calf survival from linear, threshold, and logistic models in a multibreed beef cattle population. J. Anim. Sci. 84: 3197-3203.

Gutiérrez, J. P., F. Goyache, I. Fernández, I. Alvarez, and L. J. Royo. 2007. Genetic relationships among calving ease, calving interval, birth weight, and weaning weight in the Asturiana de los Valles beef cattle breed. J. Anim. Sci. 85: 69-75.

Gutiérrez, J. P., I. Álvarez, I. Fernández, L. J. Royo, J. Díez and F. Goyache. 2002. Genetic relationships between calving date, calving interval, age at first calving and type traits in beef cattle. Livest. Prod. Sci. 78: 215-222.

Hansen, M., M. S. Lund, J. Pedersen, and L. G. Christensen. 2004.Gestation length in Danish Holsteins has weak genetic associations with stillbirth, calving difficulty, and calf size. Livest. Prod. Sci. 91: 23-33.

Hansen, P. J. 1985. Seasonal modulation of puberty and the postpartum anestrus in cattle: A review. Livest. Prod. Sci. 12: 309-327.

Intaratham, W., S. Koonawootrittriron, P. Sopannarath, H. U. Graser, and S. Tumwasom. 2008. Genetic parameters and annual trends for birth and weaning weights of a Northeastern Thai indigenous cattle line Asian-Austr. J. Anim. Sci. 21: 478-483.

Irgang, R., E. U. Dillard, M. W. Tess, and O. W. Robison. 1985. Selection for Weaning Weight and Postweaning Gain in Hereford Cattle. I. Population Structure and Selection Applied. J. Anim. Sci. 60: 1133-1141.

Iwaisaki, H., S. Tsuruta, I. Misztal, and J. K. Bertrand. 2005. Genetic parameters estimated with multitrait and linear spline-random regression models using Gelbvieh early growth data. J. Anim. Sci. 83: 757-763.

Janson, L. 1980. Studies on fertility traits in Swedish dairy cattle. II. Genetic parameters. Acta Agr. Scand. 30: 427-436.

Jenkins, T. G. and C. L. Ferrell. 1994. Productivity through weaning of nine breeds of cattle under varying feed availabilities. I. Initial evaluation. J. Anim. Sci. 72: 2787-2797.

Kaps, M., W. O. Herring, and W. R. Lamberson. 1999. Genetic and environmental parameters for mature weight in Angus cattle. J. Anim. Sci. 77: 569-574.

Kattnig, R. M., J. A. Winder, J. D. Wallace, and C. C. Bailey. 1993. Evaluation of biological efficiency of free-grazing beef cows undersemidesert conditions. J. Anim. Sci. 71: 2601-2607.

Kirkpatrick, M., W. G. Hill, and R. Thompson. 1994. Estimating the covariance structure of traits during growth and aging, illustrated with lactation in dairy cattle. Genet. Res., Camb. 64: 57-69.

Kirkpatrick, M., D. Lofsvold, and M. Bulmer. 1990. Analysis of the inheritance and evolution of growth trajectories. Genetics 124: 979-993.

Knights, S. A., R. L. Baker, D. Gianola, and J. B. Gibb. 1984. Estimates of Heritabilities and of Genetic and Phenotypic Correlations among Growth and Reproductive Traits in Yearling Angus Bulls. J. Anim. Sci. 58: 887-893.

Koch, R. M. and J. W. Algeo. 1983. The beef cattle industry: *changes* and challenges. J. *Anim.* Sci. 57(2): 28-43.

Koch, R. M., L. V. Cundiff, K. E. Gregory, and L. D. Van Vleck. 2004. Genetic response to selection for weaning weight or yearling weight or yearling weight and muscle score in Hereford cattle: Efficiency of gain, growth, and carcass characteristics. J. Anim. Sci. 82: 668-682.

Koots, K. R., J. P. Gibson, C. Smith, and J. W. Wilton. 1994. Analysis of published genetic parameter estimates for beef production traits: 1. Heritability. Anim. Breed. Abstr. 62: 309-338.

Lai, X. and K. K. W. Yau. 2008. Long-term survivor model with bivariate random effects: Applications to bone marrow transplant and carcinoma study data. Stat. Med. 27: 5692-5708.

Lamming, G. E. and M. D. Royal. 2001. Overian hormone patterns and subfertility in dairy cows. In: fertility in high- producing dairy cows, British society of animal science, Edinburg, UK. Occasional Publication 26: 105-118.

Lee, J. W., S. B. Choi, Y. H. Jung, J. F. Keown, and L. D. Van Vleck. 2000. Parameter estimates for direct and maternal genetic effects on yearling, eighteen-month, and slaughter weights of Korean native cattle. J. Anim. Sci. 78: 1414-1421.

Lombard, J. E., F. B. Garry, S. M. Tomlinson, and P. B. Garber. 2006. Impacts of dystocia on health and survival of dairy calves. J. Dairy Sci. 90: 1751-1760.

López de Torre, G., J.J. Candotti, A. Reverter, M.M. Bellido, P. Vasco, L.J. García, and J.S. Brinks. 1992. Effects of growth curve parameters on cow efficiency. J. Anim. Sci. 70: 2668-2672.

Lopez-Gatius, F., P Santolaria, J. Yaniz, J. Rutllant, and M. Lopez-Bejar. 2001. Persistent overian follicles in dairy cows: a therapeutic approach. Theriogenology. 56: 649-659.

Luna-Nevarez, P., D. W. Bailey, C. C. Bailey, D. M. VanLeeuwen, R. M. Enns, G. A. Silver, K. L. DeAtley, and M. G. Thomas. 2010. Growth characteristics, reproductive performance, and evaluation of their associative relationships in Brangus cattle managed in a Chihuahuan Desert production system1. J. Anim. Sci. 88: 1891-1904.

MacNeil, M. D. 2005. Genetic evaluation of the ratio of calf weaning weight to cow weight. J. Anim. Sci. 83: 794-802.

Magalhaes Silva, L. C., F. Baldi, C. Aboujaoude, G. C. Venturini, L. G. Albuquerque, and M. J. R. Paranhos da Costa. 2017. Genetic parameter estimates for prenatal and postnatal mortality in Nellore cattle. J. Anim. Breed. Genet. 134: 27-33.

Maiwashe, A. N., M. J. Bradfield, H. E. Theron, and J. B. Van Wyk. 2002. Genenetic parameter estimates for body measurements and growth in South African Bonsmara cattle. Livest. Prod. Sci. 75: 293-300.

Makgahlela, M. L., C. B. Banga, D. Norris, K. Dzama, and J. W. Ngambi. 2008. Genetic analysis of age at first calving and calving interval in South African Holstein cattle. Asian J. Anim. Vet. Adv. 3(3): 197-205.

Marshall, D.M., W. Minqiang and B. A. Freking. 1990. Relative calving date of first-calf heifers as related to production efficiency and subsequent reproductive performance. J. Anim. Sci. 68: 1812-1817.

Martinez, G. E., R. M. Koch, L. V. Cundiff, K. E. Gregory, and L. D. Van Vleck. 2004. Genetic parameters for six measures of length of productive life and three measures of lifetime production by 6 yr after first calving for Hereford cows. J. Anim. Sci. 82: 1912-1918.

Martínez-Velázquez, G., K. E. Gregory, G. L. Bennett, and L. D. Van Vleck. 2003. Genetic relationships between scrotal circumference and female reproductive traits. J. Anim. Sci. 81: 395-401.

McCurley, J. R. and J. B. McLaren. 1981. Relationship of Body Measurements, Weight, Age and Fatness to Size and Performance in Beef Cattle. J. Anim. Sci. 52: 493-499.

McHugh, N., A. R. Cromie, R. D. Evans, and D. P. Berry. 2014. Validation of national genetic evaluations for maternal beef cattle traits using Irish field data J. Anim. Sci..92: 1423-1432.

McMorris, M. R., J. W. Wilton, and W. C. Pfeiffer. 1986. Breeding System, Cow Weight and Milk Yield Effects on Various Economic Variables in Beef Production. J. Anim. Sci. 63: 1373-1383.

Meacham, N. S. and D. R. Notter. 1987. Heritability estimates for calving date in Simmental cattle. J. Anim. Sci. 64: 701-705.

Melton, B. E. 1995. Conception to consumption: The economics of genetic improvement. In: Proc. Beef Improvement Federation 27th Research Symposium and Annual Meeting, Sheridan, WY.

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

Meyer, K. 1992. Bias and sampling covariances of estimates of variance components for due to maternal effects. Genet. Select. Evol. 24: 487-509.

Meyer, K. 1997. Estimation of genetic parameters for weaning weight of beef cattle accounting for direct-maternal environmental covariances. Livest. Prod. Sci. 52: 187-199.

Meyer, K. 1998. 'DXMRR'- A program to estimate covariance functions for longitudinal data by Restricted Maximum Likelihood. Proc. 6 World Congr. Genet. Appl. Livest. Prod., Armidale, Australia 27: 465-466.

Meyer, K. 1999. Estimation of genetic and phenotypic covariance functions for post weaning growth and mature weight of beef cows. J. Anim. Breed. Genet. 116: 181-205.

Meyer, K. 2000. Random Regression to model phenotypic variation in monthly weights of Australian beef cows. Livest. Prod. Sci. 65: 19-38.

Meyer, K., K. Hammond, M. J. Mackinnon, and P. F. Parnell. 1991. Estimates of covariance between reproduction and growth in Australian beef cattle. J. Anim. Sci. 69: 3533-3543.

Meyer, K., M. J. Carrick, and B. J. Donnelly. 1993. Genetic parameters for growth traits of Australian beef cattle from a multibreed selection experiment. Journal of Animal Science 71: 2614-2622.

Milagres, J. E., E. U. Dillard and O. W. Robinson. 1979. Heritability estimates for some measures of reproduction in Hereford heifers. J. Anim. Sci. 49: 668-674.

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

Mohiuddin, G. 1993. Estimates of genetic and phenotypic parameters of some performance traits in beef cattle. Anim. Breed. Abstr. 61: 495-522.

Montaño-Bermudez, M. and M. K. Nielsen. 1990. Reproductive performance and variation in body weight during annual cycles for crossbred beef cows with different genetic potential for milk. J. Anim. Sci. 68: 2289-2296.

Mwaanga, E. S. and T. Janowski. 2000. Anoestrus in dairy cows, prevalence and clinical forms. Reproduction in Domestic Animals. 35: 193-200.

Nephawe, K. A. 2004. Application of random regression models to the genetic evaluation of cow weight in Bonsmara cattle of South Africa. S. Afr. J. Anim. Sci. 3: 166-173.

Nephawe, K. A., L.V. Cundiff, M.E. Dikeman, J. D. Crouse, and L. D. Van Vleck. 2004. Genetic relationships between sex-specific traits in beef cattle: Mature weight, weight adjusted for body condition score, height and body condition score measurement of cows and carcass traits of their steer relatives. J. Anim. Sci. 82: 647-653.

Niebel, E. and L. D. Van Vleck. 1982. Selection with Restriction in Cattle. J. Anim. Sci. 55: 439-457.

Oltenacu, P. A. and D. M. Broom. 2010. The impact of genetic selection for increased milk yield on the welfare of dairy cows. Anim. Welf. 19: 39-49.

Opsomer, G., Y. T. Grohn, J. Hertl, M. Coryn, H. Deluyker and A. de Kruif. 2000. Risk factor for post-partum overian dysfunctionin high-producing dairy cows in Belgium: a field study. Theriogenology. 53: 841-857.

Owens, F. N., P. Dubeski, and C. F. Hanson. 1993. Factors that alter the growth and development of ruminants. J. Anim. Sci. 71: 3138-3150.

Pedrosa, V. B., J. P. Eler, J. B. S. Ferraz, J. A. II V. Silva, S. Ribeiro, M. R. Silva, and L. F. B. Pinto. 2010. Parâmetros genéticos do peso adulto e características de desenvolvimento ponderal na raça Nelore. (In Portuguese.) Rev. Bras. Saude Prod. Anim. 11: 104-113.

Phocas, F., C. Bloch, P. Chapelle, F. Becherel, G. Renand, and F. Menissier. 1998. Developing a breeding objective for a French purebred beef cattle selection program. Livest. Prod. Sci. 57: 49-65.

Phocas, F. and J. Sapa. 2004. Genetic parameters for growth, reproductive performance, calving ease and suckling performance in beef cattle heifers. Anim. Sci. 79: 41-48.

Plasse, D., O. Verde, J. Arango, L. Camaripano, H. Fossi, R. Romero, C. M. Rodriguez, and J. L. Rumbos. 2002. (Co) variance components, genetic parameters and annual trends for calfweight in Brahman herd kept on floodable savanna. Genet. Mol. Res. 119: 282-297.

Prentice, R. L. and L. A. Gloeckler. 1978. Regression analysis of grouped survival data with application to breast cancer data. Biometrics. 34: 57-67.

Pryce, J. E. and R. F. Veerkamp. 2001. The incorporation of fertility indices in genetic improvement programmes. In: M. G. Diskin, editor, Fertility in the high-producing dairy cow. Occasional Publication No 26. British Society of Animal Science, Edinburgh, Scotland. p. 223-236.

Rakwadi, E. 2010. Estimation of genetic and phenotypic parameters for growth traits of three beef cattle breeds raised under ranch conditions in Botswana. MSc. dissertation, University of Malawi, Bunda College. Malawi.

Randel, R. D. and T. H. Welsh Jr. 2013. Joint Alpharma-Beef Species Symposium: Interactions of feed efficiency with bee heifer reproductive development. J. Anim. Sci. 2013. 91:1323-1328.

Raphaka, K. and K. Dzama. 2010. Genetic analyses for growth traitsof two indigenous beef cattle breeds in Botswana. Livest. Sci. 129: 194-199.

Regatieri, I. C., A. A. Boligon, F. Baldi, and L. G. Albuquerque. 2012. Genetic correlations between mature cow weight and productive and reproductive traits in Nellore cattle. Genet. Mol. Res. 11 (3): 2979-2986.

Riley, D. G., C. C. Chase Jr., T. A. Olson, S. W. Coleman, and A. C. Hammond. 2004. Genetic and non-genetic influences on vigor at birth and preweaning mortality of purebred and high percentage Brahman calves. J. Anim. Sci. 82: 1581-1588.

Robinson, D. L. 1996a. Estimation and interpretation of direct and maternal genetic parameters for the weights of Australian Angus cattle. Livest. Prod. Sci. 45: 1-11.

Robinson, D. L. 1996b. Models which might explain negative correlations between direct and maternal genetic effects. Livest. Prod. Sci. 45: 111-122.

Roughsedge, T., P. R. Amer, R. Thompson, and G. Simm. 2005. Genetic parameters for a maternal breeding goal in beef production. Anim. Sci. 83: 2319-2329.

Rumph, J. M., R. M. Koch, K. E. Gregory, L. V. Cundiff, and L. D. Van Vleck. 2002. J. Anim. Sci. 80: 583-590.

Santana, M. L., Eler, J. P., Bignardi, A. B. and J. B. S. Ferraz. 2013. Genetic associations among average annual productivity, growth traits, and stayability: A parallel between Nelore and composite beef cattle. J. Anim. Sci. 91: 2566-2574.

SAS. 2012. SAS systems version 9.4, Institute Inc., Cary, NC, US.

Schaeffer, L. R. and J. C. M. Dekkers. 1994. Random regression animal models for test-day production in dairy cattle. Proc. 5th World Congr. Genet. Appl. Livest. Prod., Guelph, Canada. 18: 443-446.

Jamrozik, J., J. Bphmanova and L. R. Schaeffer. 2010. Selection of lactatins of knots for linear splines in random regression test-day models. J. Anim. Breed. Genet. 127: 87-92.

Schmidek, A., M. J. R. Paranhos, M. E. Z. da Costa Mercadante, L. M. Toledo, S. Cyrillo, and R. H. Branco. 2013. Genetic and non-genetic effects on calf vigor at birth and preweaning mortality in Nellore calves. R. Bras. Zootecn. 42: 421-427.

Searle, S. R. 1961. Phenotypic , genetic and environmental correlations. Biometrics 17: 474-480.

Sharpe, P. H., D. R. Gifford, P. F. Flavel, M. G. Nottle, and D. T. Armstrong. 1986. Effect of melatonin on postpartum anestrus in beef cows. Theriogenology. 26(5): 621-629.

Short, R. E., R. A. Bellows, R. B. Staigmiller, J. G. Berardinelli, and E. E. Custer. 1990. Physiological mechanisms controlling anestrus and infertility in postpartum beef cattle. J. Anim. Sci. 68: 799-816.

Shorten, P. R., C. A. Morris, and N. G. Cullen. 2015. The effect of age, weight, and Sire on pregnancy rate in cattle. J. Anim. Sci. 93: 1535-1545.

Shumbusho, F., J. Raoul, J. M. Astruc, I. Palhiere, and J. M. Elsen. 2013. Potential benefits of genomic selection on genetic gain of small ruminant breeding programs. J. Anim. Sci. 91: 3644-3657.

Silveira, J. C., C. McManus, A. S. Mascioli, L. O. C. Silva, A. C. Silveira, J. A. S. Garcia, and H. Louvandini. 2004. Fatores ambientais e parâmetros genéticos para características produtivas e reprodutivas em um rebanho Nelore no estado do Mato Grosso do Sul. (In Portuguese.) Rev. Bras. Zootec. 33: 1432-1444.

Smith, B. A., J. S. Brinks, and G. V. Richardson. 1989. Estimation of Genetic Parameters among Reproductive and Growth Traits in Yearling Heifers. J. Anim. Sci. 67: 2881-2885.

Solemani-Baghshah, S., S. Ansari-Mahyari, M. A. Edriss and H. Asadollahpour-Nanaei. 2014. Estimation of Genetic and Phonotypic Trends for Age at First Calving, Calving Interval, Days Open and Number of Insemination to conception for Isfahan Holstein Cows. Int J Adv Biol Biom Res. 2(5): 1307-1314.

Stevenson, J. S. 2001. A review of oestrus behaviour and detection in dairy cows. In: fertility in high-producing dairy cows, British society of animal science, Edinburg, Uk. Occasional Publication. 26: 43-62.

Tarres, J., J. Casellas, and J. Piedrafita. 2005. Genetic and environmental factors influencing mortality up to weaning of Bruna dels Pirineus beef calves in mountain areas. A survival analysis. J. Anim. Sci. 83: 543-551.

Tarres, J., M. Fina, and J. Piedrafita. 2010. Parametric bootstrap for testing model fitting of threshold and grouped data models: An application to the analysis of calving ease of Bruna dels Pirineus beef cattle. J. Anim. Sci. 88: 2920-2931.

Tawah, C. L., D. A. Mbah, J. F. O. Rege, and H. Oumate. 1993. Genetic evaluation of birth and weaning weight of Gudali and two synthetic Wakwa beef cattle populations underselection in Cameroon: Genetic and phenotypic parameters. Anim. Prod. 57: 73-79.

Thompson, R. 1976. The estimation of maternal genetic variances. Biometrics. 32: 903-917.

Urioste, J. I., I. Misztal, and J. K. Bertrand. 2007. Fertility traits in spring-calving Aberdeen Angus cattle. 1. Model development and genetic parameters. J. Anim. Sci. 85: 2854-2860.

Van Vleck, L. D. and L. V. Cundiff. 1998. Sex effects on breed of sire differences for birth, weaning, and yearling weights. J. Anim. Sci. 76: 1528-1534.

Varona, L., C. Moremo, L. A. Garcia-Cortes, and J. Altariba. 1997. Multiple trait genetic analysis of underlying biological variables of production functions. Livest. Prod. Sci. 47: 201-210.

Varona, L., C. Moreno, and J. Altarriba. 2009. A model with heterogeneous thresholds for subjective traits: Fat cover and conformation score in the Pirenaica beef cattle. J. Anim. Sci. 87: 1210-1217

Von-keyserlingk, M. A. G. and D. M. Weary. 2007. Maternal behavior in cattle. Horm. Behav. 52: 106-113.

Vostry, L., Z. Vesela, A. Svitakova, and H. V. Vostra. 2014. Comparison of models for estimating genetic parameters and predicting breeding values for birth weight and calving ease in Czech Charolais cattle. Czech J. Anim. Sci. 59: 302-309.

Wasike, C. B., E. D. Llatsia, J. M. K. Ojango, and A. K. Kahi. 2006. Genetic parameters for weaning weight of Kenyan Boran cattle accounting for direct-maternal genetic covariance. S. Afr. J. Anim. Sci. 36: 275-281.

Willham, R. L. 1972. The Role of Maternal Effects in Animal Breeding: III. Biometrical Aspects of Maternal Effects in Animals. J. Anim. Sci. 35: 1288-1293.

Winder, J. A., C. C. Bailey, M. G. Thomas, and J.Holechek. 2000. Breed and stocking rate effects on Chihuahuan Desert cattle production. J. Range Manage. 53: 32-38.

Yaeghoobi, R., A. Doosti, A. M. Noorian, and A. M. Bahrami. 2011. Genetic parameters and trends of milk and fat yield in Holstein dairy cattle of West Provinces of Iran. Int. J. Dairy Sci. 6: 142-149.

Yilmaz, A., M. E. Davis, and R. C. M. Simmen. 2004. Estimation of (co)variance components forreproductive traits in Angus beef cattle divergently selected for blood serum IGF-I concentration. J. Anim. Sci. 82: 2285-2292.