GENETIC EVALUATION OF GROWTH AND REPRODUCTIVE PERFORMANCE OF THE AFRIKANER CATTLE BREED

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DECLARATION

I declare that the dissertation hereby submitted to the North West University for the degree of Master of Science in Agriculture in Animal Science (Animal Breeding and Genetics) has not, wholly or in part, been previously submitted by me for any degree at this or any other institution of learning, and that it is my independent work in its entirety, and that all material contained herein has been duly acknowledged.

Signature: ________________________________

Date: 22/11/2018,

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ABSTRACT

The objective of the current study was to estimate genetic parameters for growth and reproductive traits of the South African Afrikaner cattle population, using different genetic models after accounting for known systematic non-genetic effects.

The data originated from records collected between 1966 and 2017, from a population of 260 789 animals. For final analysis, the available data were substantially reduced after removing data with missing information on pedigree or performance records. Performance records available after editing were 27 633 for birth weight (BWT), 70 504 for weaning weight (WWT), 21 624 for yearling weight (YWT) and 23 248 for eighteen months' weight (EWT). A total of 6 502 contemporary groups (herd, year and season of birth) were identified from weight records. Reproduction records available after editing were 45 819 for age at first calving (AFC), 21 695 for calving interval (CI) and 15 157 for accumulated productivity (ACP).

Data were analysed using linear univariate and bivariate models, fitting the animal (AM) and sire-maternal grandsire (S-MGS) models. The S-MGS model was used to analyse data of BWT and WWT which are traits that are expected to be highly influenced by maternal effects. Estimates of (co)variance components were obtained with the commonly used ASREML package.

Using the AM, direct heritability estimates of BWT, WWT, YWT and EWT were 0.28, 0.27, 0.24 and 0.35, respectively. The corresponding maternal heritability estimates were 0.05, 0.12, 0.10 and 0.08, respectively. Similarly, the corresponding total heritability estimates were 0.19, 0.20, 0.24 and 0.32, respectively. From the S-MGS model, direct heritability estimates were the same (0.23) for BWT and WWT, while maternal heritability estimates were 0.18 and 0.19, respectively. The permanent maternal environmental component contributed 4 to 13 % of the total phenotypic variance for the growth traits under consideration.

A negative association was found between direct and maternal effects with a genetic correlation of -0.64, -0.49, -0.22 and -0.26 for BWT, WWT, YWT and EWT, respectively. Using the S-MGS model, estimates of the correlation between direct- and maternal genetic effects improved to -0.28 for BWT and to -0.29 for WWT.

Estimates of direct genetic correlations between BWT and weights at later ages ranged from 0.27 to 0.35. The corresponding estimates of phenotypic correlations ranged from 0.14 to 0.17, indicating a weak observable relationship between BWT and weights at later ages. Estimates of direct genetic correlations for WWT with YWT and EWT were 0.89 and 0.85, respectively while the correlation between YWT and EWT was 0.88.

For reproductive traits, additive genetic variance accounted for the least variation for AFC and CI, resulting in low heritability estimates. Heritability estimates for AFC and CI were 0.093 and 0.096, respectively. The heritability estimate for ACP was of a moderate magnitude (0.39), suggesting that selection on this trait will yield moderate genetic gains.

For growth traits, the estimates of direct and maternal heritability revealed that the genotype of the calf was more important than that of the dam in determining the weight of the calf at all ages.

Keywords: genetic parameters, growth traits, maternal effects, variance components, heritability

TABLE OF CONTENTS

CHAPTER 1

CHAPTER 2

CHAPTER 3

CHAPTER 4

CHAPTER 5

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

1.1 Background

Afrikaner cattle (*Bos taurus africanus*) are a South African landrace breed in accordance with the Animal Improvement Act of South Africa (DAFF, 1998). The Afrikaner cattle breed is considered a Sanga type along other breeds indigenous to Africa, including the Abigar, Ankole, Drakensberger, Nguni (including all other Nguni ecotypes), Tswana and Tuli cattle.

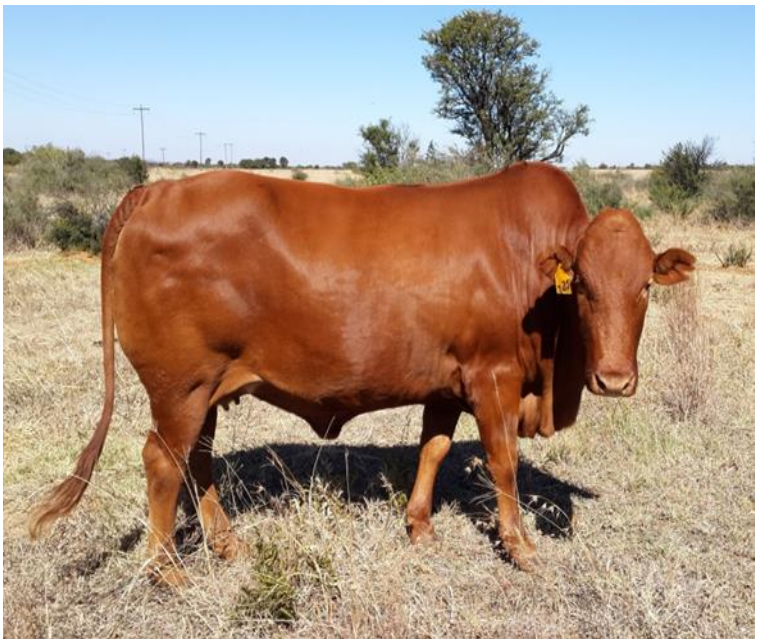


Figure 1.1 Afrikaner cow on dry late autumn native grazing

The first officially registered Afrikaner cattle were recorded in the South African Stud Book register in 1907 and the breed had a pedigree record of more than 260 000 animals in 2017. The breed is hardy, well adapted to the harsh Southern African conditions and reasonably distributed through a wide variety of ecological regions in and around Southern Africa (Pienaar *et al.*, 2014).

The Afrikaner breed has a rich heritage and historical importance in Southern Africa and specifically in South Africa. In 2013, the Afrikaner cattle breed was identified as an indigenous agricultural genetic resource, and was earmarked for conservation by the Department of Agriculture, Forestry and Fisheries. Indigenous cattle form the backbone of sustainable livestock production in many ecological areas of South Africa including the under resourced communal range lands. For instance, the Afrikaner ranked fourth among the ten most dominant breeds in the South African communal and emerging sectors (Scholtz *et al.*, 2008). Compared to exotic breeds, Afrikaner cattle are better adapted to survive and reproduce under harsh semi-arid environmental conditions as well as on areas that were previously not considered suitable for cattle farming. The breed represents therefore, an indigenous gene pool with attributes that are relevant to the environmental conditions of the Southern Hemisphere. The relevance of such attributes is even more important, given the current climatic changes brought by global warming.

Afrikaner cows are noticeably small to medium sized and have low to moderate maintenance requirements (Bergh *et al.*, 2010). The typical Afrikaner cattle are yellow to red (Fig. 1.1) and to some degree red and white coloured and presents lateral twisting horns (Fig 1.2 & 1.3). Characteristics such as hardiness, outstanding carcass features and the ability to finish off on natural grazing (Bergh *et al.*, 2010) are prominent attributes of Afrikaner cattle (Pienaar *et al.*, 2014). Afrikaner cattle are also known for exceptional walking ability, ease of calving, good mothering ability, longevity and good grazing ability. In recognition of these attributes, the breed is often promoted as a dam line for crossbreeding purposes (Scholtz & Theunissen, 2010) and has already played a vital role in the beef industry both locally and internationally. For instance, the Afrikaner breed has played a fundamental role in the development of at least eight composite breeds worldwide, namely the Africangus, Afrigus, Afrisim, Barzona, Belmont Red, Bonsmara, Hugenoot and Sanganer.

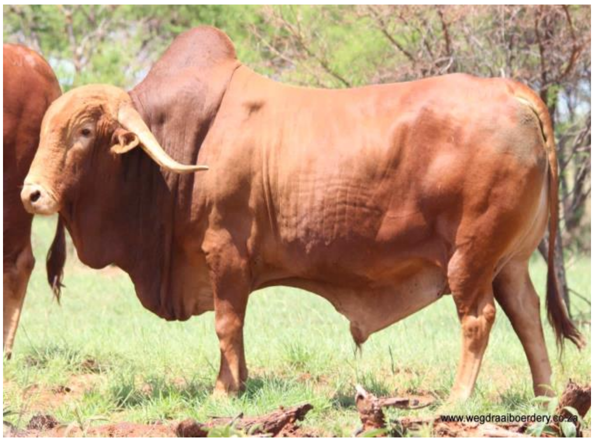


Figure 1.2 Afrikaner bull presenting typical masculine breed characteristics

Figure 1.3 Afrikaner cow presenting typical feminine breed characteristics

In addition, the Afrikaner has been found to compare favourably and even better than some composite and continental beef breeds on meat quality characteristics (Strydom *et al.*, 2000). In support of this point of view, several authors (Page *et al.*, 2002; Banga & Van der Westhuizen, 2004; White *et al.*, 2005) reported the Afrikaner breed to have the highest frequency (up to 97%) of favourable alleles at two meat tenderness gene markers, followed by Bonsmara, Drakensberger, Nguni and Tuli cattle. The Afrikaner is reported to have exceptional good quality meat and is regarded as the ideal minimum care and maximum profit breed (Strydom *et al.*, 2000). Such attributes can only further enhance the popularity of the breed for beef production and crossbreeding purposes.

On the other hand, the effects of climate change, particularly global warming, have a potential to force producers into crossbreeding, in an attempt to improve profitability and production efficiency. The most probable approach is likely going to involve the use of indigenous breeds like the Afrikaner as dam lines, and breeding them with large exotic sire breeds (Scholtz & Theunissen, 2010). The success of such crossbreeding operations, particularly terminal crossbreeding will depend on continued supply of pure-bred replacement heifers to make up for the losses of mature pure-bred cows in the herd. This is therefore, likely to create a continual demand for pure bred animals which may as a result, indirectly aid to further advance the national objectives of conservation programmes of Afrikaner cattle. In agreement, Scholtz & Theunissen (2010) postulated that the most important advantage of any system of terminal crossbreeding utilizing indigenous breeds is that, the conservation of the indigenous breeds can be ensured through the required constant stream of purebred indigenous females. Proper crossbreeding designs should however be developed, because utilization of crossbreeding in beef production with reference to Southern African countries is not properly planned and largely ineffective (Theunissen *et al.*, 2013).

It is important to note that indiscriminate crossbreeding often poses a risk of dilution and degradation of the genetic makeup of indigenous parent stock (Edea *et al.*, 2013; Rahman *et al.*, 2013). Adapted genetic material cannot be replaced and its loss can negatively affect the capacity of breeders to adapt to changes in the respective production environments (Hanotte *et al.*, 2010; Edea *et al.*, 2015). There is a worldwide drive for effective management of indigenous genetic resources as they could be most valuable in selection and breeding programs in times of biological stress such as famine, drought and disease epidemics (Food and Agriculture Organization of the United Nations, FAO, 2010). In South Africa, adaptability of the Afrikaner breed is likely to be central to such conservation drives.

Genetic diversity of indigenous cattle breeds is a key to sustaining the wellbeing of farming and pastoral communities that predominantly rely on low-input production systems (Edea *et al.*, 2013). There is an appreciable gradual increase in studies that investigate genetic diversity of indigenous South African cattle. Information about genetic diversity and population structure among cattle breeds is indispensable for understanding of environmental adaptation (Vali *et al.*, 2008; Groeneveld *et al.*, 2010), genetic improvement, as well as utilization and conservation of cattle breeds (Edea *et al.*, 2015). Among the South African landrace cattle breeds, the Afrikaner seems to present the least level of genetic diversity (Hunlun & Bonthuys, 2013; Makina *et al.*, 2014). The Afrikaner further demonstrated lower genetic diversity measures (as measured by Hz) in comparison with indigenous breeds in other parts of Africa (Pienaar *et al.*, 2014). The low level of genetic diversity within the Afrikaner population may represent a definite challenge for the breed. Programmes for improving the genetic diversity should be considered, particularly by the elite breeders who serve as suppliers of genetic material in a form of stud bulls. In support of this suggestion, it is believed that common genetic exchange between locales under managed breeding schemes is predominantly male-mediated (MacHugh *et al.*, 1997; Zeder *et al.*, 2006). In agreement, Makina *et al.* (2014) suggested the exchange of bulls from different genetic pools as an appropriate approach for increasing diversity in the Afrikaner population. Failure to improve genetic diversity may decrease prospects for tackling the likely productivity improvement challenges and inbreeding control, as well as the effective utilization of breed specific characteristics.

On the other hand, the Afrikaner cattle population seems to have the least level of genetic admixture among the South African indigenous and locally-developed breeds (Makina *et al.,* 2014). This is indeed good for the Afrikaner breed, and should be maintained because genetic admixture is known to dilute embedded local adaptation due to introduction of unadapted foreign genotypes in a given population.

1.2 Problem statement

Genetic parameters for growth traits in Afrikaner cattle were previously reported by Groeneveld *et al.* (1998). However, that study was limited to the performance measured on growth traits up until 1996 (two decades ago). Similarly, studies that reported on genetic parameters for reproductive traits in Afrikaner cattle in the recent times are rather scanty (see, Rust & Groeneveld, 2001; Rust & Groeneveld, 2002; Rust *et al.*, 2009). There is therefore, a paucity of recent information on the genetic parameters for a full range of growth and reproductive traits as well as their correlations, especially from large field data sets for the Afrikaner breed in South Africa.

The first step in the implementation of genetic evaluation for a specific breed is the knowledge of relevant genetic parameters for economically important traits (Maiwashe *et al.*, 2009). Genetic parameter estimates are necessary for designing of breeding objectives; implementation of breeding programmes as well as for the evaluation of progress made regarding genetic improvement. Furthermore, genetic parameter estimates for economically important traits are needed for accurate and unbiased prediction of breeding values, to predict direct- and correlated selection responses (Wasike *et al.*, 2006; Van Niekerk & Neser, 2006) and to develop appropriate selection criteria. Afrikaner cattle are farmed primarily under extensive conditions and the use of large field data in the estimation of genetic parameters is practically inevitable. Given the importance of estimates of genetic parameters as outlined above, the paucity of recent information on the genetic parameter estimates for a full range of growth and reproductive traits in the Afrikaner cattle population need to be addressed.

1.3 Research aim and objectives

The overall aim of the current study was to evaluate and analyse the historical dataset to estimate variances and covariances for a range of economically important growth and female fertility traits of the South African Afrikaner cattle population.

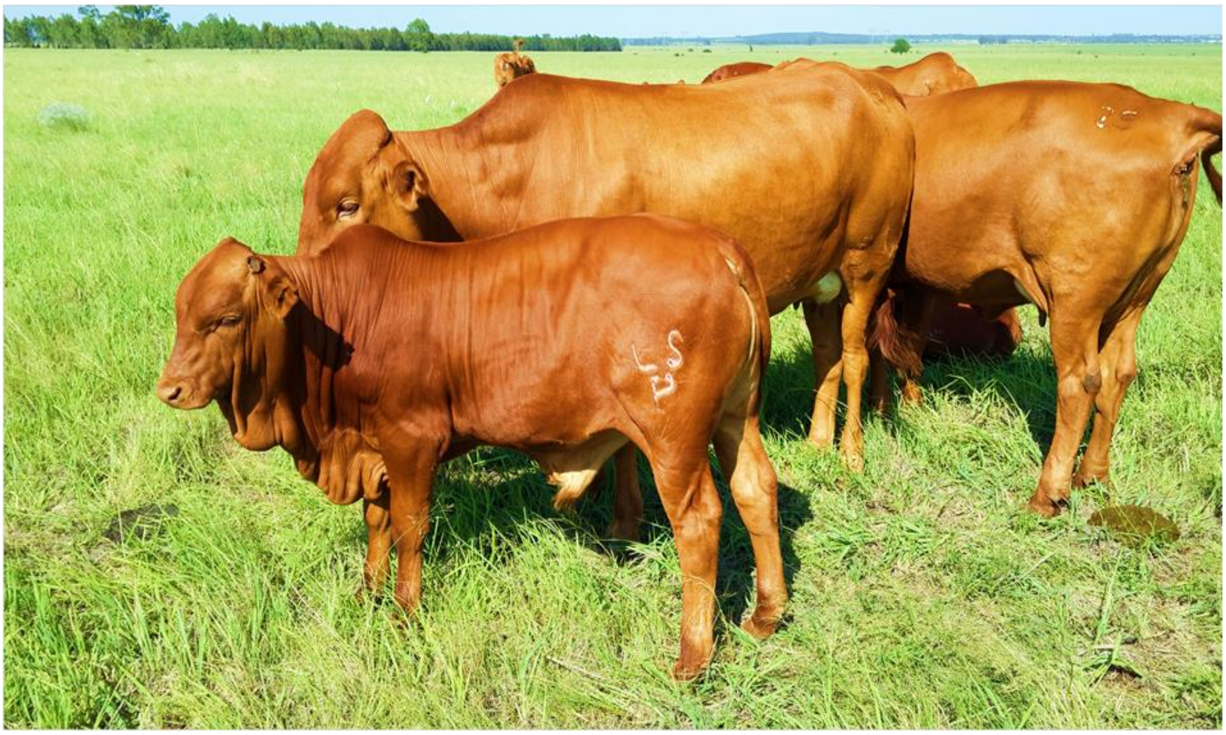
1.3.1 To achieve the overall aim, the study focused on the following specific objectives:

a) Estimation of genetic parameters for growth and reproductive traits using different genetic models after accounting for known systematic non-genetic effects;

b) Estimation of genetic and phenotypic associations among growth traits; and

c) Estimation of genetic and phenotypic associations among reproductive traits in Afrikaner cattle**.**

The results from this study will be valuable for providing practical reference points for use in the national genetic evaluation of this breed and for updating available literature on genetic parameters. The latter can be used in designing breeding objectives for improvement of the pure-bred Afrikaner population. In addition, the results should be helpful to determine the long-term growth and reproductive performance impact due to previous selection based on indicator traits. The results should also prove to be useful in the design of the anticipated Afrikaner based crossbreeding programmes in response to the deteriorating extensive farming environmental conditions. This is important, particularly in light of climate change and the consequential quest to improve beef production efficiency.



A typical dehorned four months old Afrikaner calf with dam, on lush green pastures

CHAPTER 2

LITERATURE REVIEW

2.1 Relevance of indigenous cattle

In nearly all cases, domestic animals came from purebred stocks of indigenous breeds (Zeder *et al.*, 2006). Indigenous breeds, also termed autochthonous or native breeds form a subset of locally adapted breeds (FAO, 2015) which can survive and produce under harsh environments (Scholtz & Mamabolo, 2016). Indigenous livestock breeds have always played an important role in the lives of the people of Sub-Saharan Africa (Bosso *et al.*, 2009) and their relevance in the current climatic times is of high importance. This is so because the South African beef production industry is uniquely characterised by adverse production environments and the subsequent diverse management practices between farms. Central to this characteristic of the beef industry is the different types of cattle that are often utilised including indigenous breeds.

The history and biogeography of cattle populations in Africa is characterised by a complex interaction of ecological, genetic and anthropological factors (MacHugh *et al.*, 1997) that resulted in cattle that are highly adapted to harsh tropical environments. Unlike other continents, Africa is abundantly endowed with an assortment of indigenous breeds that are adapted to the continent’s prevailing harsh (Scholtz, 1988, 2005) and spatially dissimilar environmental conditions. These harsh conditions often include periodic droughts characterised by seasonal nutritional shortages, endemic diseases and an array of internal and external parasites (FAO, 2015). To the benefit of Africa, the indigenous breeds evolved under such conditions and have adapted well to these conditions. For instance, in a local study, a 24-hour period of water deprivation did not reduce feed intake in case of the Afrikaner, whereas that of an exotic breed (Hereford) was reduced by 24% (Bonsma, 1980).

Unfortunately, the role that indigenous cattle breeds can play in providing animal-source food and associated economic and social benefits is not always recognized. In agreement, and describing African indigenous cattle, Hanotte *et al.* (2010) recognised a world of Darwinian adaptations that awaits to be discovered, understood, and utilised. This is so, notwithstanding that beef cattle make up a high percentage of the meat-producing ruminants (Rust & Rust, 2013) in Africa, and many African indigenous cattle are beef producing breeds. Adaptability traits of the indigenous breeds are of cardinal importance and make these breeds a viable alternative for sustainable livestock production.

Most ruminant livestock (e.g. cattle, sheep, goats) are kept under extensive production systems (Scholtz *et al.*, 2013a), in the more arid regions of the country which often receive less than 500 mm of rain per year (Meissner *et al.*, 2013). These extensive farming systems are often characterised by compromised climatic and nutritional conditions. As a result, pure breeding with indigenous breeds becomes the only viable production strategy applied by stock farmers under such conditions (Scholtz & Theunissen, 2010).

On the other hand, there is a general consensus that Southern Africa will become drier and warmer as a result of climate change (Engelbrecht *et al.*, 2009; Meissner *et al.*, 2013; Scholtz *et al.*, 2013a). This anticipated change will have a negative effect on livestock production environments (Scholtz *et al.*, 2013b) and related production outputs (Rust & Rust, 2013). These environmental changes may make it more difficult to raise some breeds in the geographical areas where they have traditionally been kept (FAO, 2015), increasing therefore the need for more hardy and adapted breeds. Balancing growth and reproductive performance in beef cattle managed under these harsh environments is often very challenging. Additionally, an array of parasites and diseases are showing increasing resistance to known remedies which makes the natural parasite tolerance of indigenous breeds all the more valuable (FAO, 2015). Indigenous breeds like the Afrikaner and Nguni cattle are therefore, likely to have a vital role to play in the beef industry, due to their adaptability to the tropical production environment (Scholtz, 1988, 2005; Bergh *et al.*, 2010), which facilitates their greater ability to grow and reproduce in semi-arid conditions.

2.2 Traits of economic importance

The primary goal of animal breeding is to genetically improve production and reproduction traits in animal populations (Snyman & Olivier, 2002). This is because in a beef cattle production system, the traits with the most impact in cow-calf production systems can be separated mainly into two groups: growth and reproduction. The traits of economic importance (reproduction and production traits) in beef cattle are typically those that influence income and the related costs of production. Fertility traits are the most important traits to consider in breeding objectives for beef cattle (Cavani *et al.*, 2015), and should be included in breeding goals at a greater rate than the present extent. Growth rate and the associated efficiency of gain are inseparable to traits of economic importance in the beef industry. Growth rate has a direct effect on net return and is positively correlated to efficiency of gain, weight, and the value of the retail product in beef production (BIF, 2010). Development of effective genetic evaluation and improvement programmes requires knowledge of the genetic parameters (genetic variance of each trait and covariances among traits) for these economically important production traits (Safari *et al.*, 2005; Maiwashe *et al.*, 2009). There is also a constant need for estimates of phenotypic and genetic parameters to be updated and refined using new methods of analysis (Van Wyk *et al.*, 2008) in order to facilitate accurate multiple-trait breeding value predictions for traits of economic importance.

2.2.1 Growth traits

The weight behaviour of animals is of great interest in genetic breeding programs for beef cattle that utilize weight standardized at different ages as selection criteria (Araújo *et al.*, 2014). Growth traits are often described by performance of an animal at various stages of the growth curve (Newman & Coffey, 1999). Growth traits influence various aspects of production, ranging from maintenance requirements to cull cow value. In addition, these traits influence carcass (Pariacote *et al.,* 1998) as well as reproductive traits (Burrow, 2001) and thus directly affect revenue in beef production. Growth traits are however often affected by the adaptability of the animal to the production environment (Gaughan *et al.*, 1999; Burrow, 2001). The latter is mainly because expression of these traits is dependent on both the animal’s inherent growth ability and on the production environment (Mackinnon *et al.*, 1991; Davis, 1993).

Growth traits therefore, form the basis of selection criteria in many genetic improvement programmes. This is also due to their early expression and ease of measurement. Growth is influenced by the genes of the individual animal, the environment provided by the dam, and other natural environmental effects (Albuquerque and Meyer 2001). According to Boligon *et al*. (2011), these traits are positively correlated to others of economic importance, and presents heritability estimates of a medium magnitude in response to selection. However, selecting for these traits can have unfavourable effects on other traits of economic importance such as dam mature size, early fat deposition and reproductive traits (Grossi *et al.*, 2008; Boligon *et al.*, 2011; Boligon *et al.*, 2013). As a result, several indices consisting of a number of traits (see, Grossi *et al.*, 2008; Chud *et al.*, 2014; Eler *et al.*, 2014) are often employed in beef cattle genetic evaluations in an attempt to account for both the productive and reproductive traits during selection albeit with modest potential for genetic gain.

2.2.1.1 Variance components and genetic parameters for growth traits in beef cattle

An animal's genetic potential is measured by estimating the probable parent to progeny transferable (additive) genetic merit for a specific trait. (Co)variance components are always attributed to specific effects (animal or environmental) and contribute therefore to a better understanding of the genetic mechanism of such effects on the observed phenotypic variation. For instance, the birth weight of an animal and its early growth rate till weaning, is determined not only by its own genetic potential but also by the maternal environment (Meyer, 1992).

Genetic parameters and variance components are frequently estimated using records obtained from data collected by farmers participating in performance recording often through national animal performance improvement recording schemes. Knowledge of variance components and genetic parameters is required for predicting breeding values (Neser *et al.*, 2012) as well as for designing breeding programmes for genetic improvement (Eler *et al.*, 1995). This is more so considering that, biological variation is an important aspect of genetic progress since the aim of selective breeding is dependent on reliable identification of animals with superior genes to form parents of the next generation (Falconer & Mackay, 1996). Variance components are therefore useful for depicting the genetic variability existent in populations (Raphaka, 2008).

Due to changes in management, selection programs, analysis methods (Koots *et al.*, 1994a, Gutierrez *et al.*, 2007) and data structure (Meyer, 1992, Clément *et al.*, 2001; Wasike *et al.*, 2006, Boligon *et al.*, 2012), genetic parameters can differ among cattle breeds and from year to year (Robinson, 1996; Lôbo *et al*., 2000). Furthermore, genetic variances and associated parameters are characteristics of a population from which they were derived, and their expression is often affected by environmental conditions (Demeke *et al.*, 2003). Thus, for comprehensive livestock improvement programs, regular computation of these parameters is necessary to evaluate progress made and its direction.

Typically, variance components are partitioned into genetic and environmental components. However, their inefficiency to explain the true variance structure have encouraged the use of more complex models which attribute variance to both direct and indirect sources of variation (Falconer & Mackay, 1996). Generally, the variance and covariance components estimated with such models are direct and maternal genetic variances, the maternal permanent environmental variance, the residual variance, and direct- and maternal genetic covariance (Dodenhoff *et al*., 1999; David *et al*., 2015).

In animal breeding, the animal model is extensively used for estimating genetic parameters (Meyer, 1992) because it allows for the combined use of all relationships and performances to improve accuracy of estimations (Clément *et al.*, 2001). However, despite the theoretical advantages of the animal model, some data and model conditions often affect the validity and precision of the estimation of variance components (Clément *et al.*, 2001; Wasike *et al*., 2006, Boligon *et al*., 2012). For instance, in growth traits, estimation of maternal effects and their covariance components is inherently problematic since direct- and maternal effects are generally confounded (Baker, 1980; Willham, 1980).

Furthermore, the expression of the maternal effects is sex-limited, lags behind by one generation and occurs late in life for the females (Baker, 1980; Willham, 1980; Roehe & Kennedy, 1993). The most appropriate model for growth trait analyses should at least include both direct and maternal additive genetic effects (Meyer, 1992), the covariance between the two genetic effects as well as permanent environmental effects due to the dam (Robinson 1996; Meyer, 1997; Van Wyk *et al.*, 2008). Maternal effects seem to constitute a considerable source of variation in suckled offspring. This is because for mammalian species, apart from their genetic contribution, dams have an advantageous opportunity to wield an added effect on the offspring phenotype by also influencing the offspring through the environment that they provide.

Commonly, genetic parameters of importance are direct additive, maternal additive and permanent maternal environmental heritabilities as well as genetic, phenotypic and environmental correlations.

For background purposes, selected literature estimates of genetic parameters for birth weight (BWT), weaning weight (WWT), yearling weight (YWT) and weight at 18 months of age (EWT) in beef cattle are presented in Table 2.1. Literature values for direct and maternal heritability estimates for BWT vary from 0.07 (direct) and 0.04 (maternal) (Diop

& Van Vleck, 1998) to 0.68 (direct) (Abera *et al.*, 2011) and 0.24 (maternal) (Smith, 2010). For WWT, the same values vary from 0.07 (direct) (Plasse *et al.*, 2002) and 0.04 (maternal) (Boligon *et al*., 2012) to 0.60 (direct) and 0.30 (maternal) (Gutierrez *et al*., 1997). For YWT, literature values for direct and maternal heritability estimates vary from 0.11 (direct) (Beffa *et al.*, 2009) and 0.04 (maternal) (Meyer, 1992) to 0.70 (direct) and 0.38 (maternal) (Smith, 2010). For EWT, literature values for direct and maternal heritability estimates vary from 0.08 (direct) (Wasike, 2006) and 0.03 (maternal) (Groeneveld *et al.*, 1998; Pico *et al.*, 2004) to 0.42 (direct) (Corbet *et al.*, 2006) and 0.16 (maternal) (Diop & Van Vleck, 1998).

Table 2.1. Selected literature estimates for genetic parameters (h^2_a, h^2_m, r_{am}, c^2) for growth traits in beef cattle

Breed	**Country**	**Model**	h^2_a	h^2_m	r_{am}	c^2	**Reference**
			Birth weight (BWT)				
Hereford	Australia	UAM	0.41	0.08	0.29	0.05	Meyer, 1992
Afrikaner	SA	MAM	0.52	0.07	-0.57	-	Groeneveld *et al.*, 1998
Hereford	America	UAM	0.45	0.10	0.15	0.01	Dodenhoff *et al.*, 1998
Gobra	Senegal	UAM	0.07	0.04	-0.17	0.04	Diop & Van Vleck, 1998
Hanwoo	Korea	UAM	0.09	0.04	0.61	-	Choi *et al.*, 2000
Brahman	Venezuela	UAM	0.33	0.08	-0.37	0.03	Plasse *et al.*, 2002
Brahman	Venezuela	UAM	0.42	0.07	0.06	0.01	Plasse *et al.*, 2004
Brahman	SA	UAM	0.28	0.11	-0.36	-	Pico *et al.*, 2004
Bon & Bel Red	SA	UAM	0.23	0.10	-0.09	0.00	Corbet *et al.*, 2006
Limousin	SA	UAM	0.09	0.05	-0.64	0.04	Van Niekerk & Neser, 2006
Afrikaner	Zimbabwe	UAM	0.38	0.15	-	-	Beffa *et al.*, 2009
Tswana	Botswana	UAM	0.31	0.11	0.33	-	Raphaka, 2008
Nellore	Mexico	UAM	0.59	0.17	-0.90	-	Martínez *et al.*, 2010
Simbra	SA	UAM	0.56	0.24	-0.75	-	Smith, 2010
Horro	Ethiopia	UAM	0.68	0.12	-0.76	0.18	Abera *et al.*, 2011
Nellore	Brazil	UAM	0.37	0.11	-0.68	-	Araujo *et al.*, 2014

Table 2.1 Continued…

Breed	**Country**	**Model**	h_a^2	h_m^2	r_{am}	c^2	**Reference**
			Weaning weight (WWT)				
Angus	Australia	UAM	0.20	0.14	0.22	0.04	Meyer, 1992
Hereford	Australia	UAM	0.14	0.13	-0.59	0.23	Meyer, 1992
Asturiana de los Valles	Spain	UAM	0.60	0.30	-0.73	-	Gutierrez *et al*., 1997
Afrikaner	SA	MAM	0.23	0.13	-0.44	-	Groeneveld *et al.*, 1998
Brahman	Venezuela	MAM	0.13	0.14	0.28	0.09	Plasse *et al*., 2004
Brahman	SA	UAM	0.14	0.06	-	0.07	Pico *et al.*, 2004
Boran	Kenya	UAM	0.12	0.14	-0.25	0.16	Wasike, 2006
Bon & Bel Red	SA	UAM	0.14	0.19	-0.21	0.16	Corbet *et al*., 2006
Limousin	SA	UAM	0.19	0.12	-0.70	0.17	Van Niekerk & Neser, 2006
Afrikaner	Zimbabwe	UAM	0.12	0.20	-0.42	0.31	Beffa *et al.*, 2009
Tswana	Botswana	UAM	0.20	0.15	0.69	-	Raphaka, 2008
Nellore	Mexico	UAM	0.29	0.17	-0.90	-	Martínez *et al.*, 2010
Simbra	SA	UAM	0.67	0.33	-093	-	Smith, 2010
Horro	Ethiopia	UAM	0.53	0.21	-0.71	0.16	Abera *et al.*, 2011
Nellore	Brazil	UAM	0.18	0.04	0.13	0.12	Boligon *et al*., 2012
Nellore	Brazil	UAM	0.35	0.05	-0.35	-	Araujo *et al.*, 2014
			Yearling weight (YWT)				
Hereford	Australia	UAM	0.15	0.11	-0.48	0.05	Meyer, 1992
Angus	Australia	UAM	0.33	0.04	0.49	0.03	Meyer, 1992
Afrikaner	SA	MAM	0.17	0.06	-0.41	-	Groeneveld *et al.*, 1998
Brahman	Venezuela	AMMP	0.07	0.14	-0.13	0.16	Plasse *et al*., 2002
Brahman	SA	UAM	0.14	0.05	-	0.03	Pico *et al.*, 2004
Boran	Kenya	UAM	0.19	0.34	-0.58	0.04	Wasike, 2006
Bon & Bel Red	SA	UAM	0.26	0.08	0.35	0.03	Corbet *et al.*, 2006
Afrikaner	Zimbabwe	UAM	0.11	0.22	-0.46	0.25	Beffa *et al.*, 2009
Nellore	Mexico	UAM	0.24	0.15	-0.86	-	Martínez *et al.*, 2010
Simbra	SA	UAM	0.70	0.38	-0.85	-	Smith, 2010

Table 2.1. Continued…

Breed	Country	Model	h_a^2	h_m^2	r_{am}	c^2	Reference
			Eighteen months' weight (EWT)				
Hereford	Australia	UAM	0.22	0.04	-0.20	0.09	Meyer, 1992
Afrikaner	SA	MAM	0.17	0.03	-0.18	-	Groeneveld *et al.*, 1998
Gobra	Senegal	UAM	0.14	0.16	-0.28	0.04	Diop & Van Vleck, 1998
Brahman	Venezuela	MAM	0.13	0.08	0.49	0.01	Plasse *et al.*, 2002
Brahman	SA	UAM	0.18	0.03	-	0.04	Pico *et al.*, 2004
Brahman	Venezuela	MAM	0.22	0.05	0.34	0.01	Plasse *et al.*, 2004
Boran	Kenya	UAM	0.08	0.04	-0.14	0.10	Wasike, 2006
Bon & Bel Red	SA	UAM	0.42	0.15	-0.38	0.00	Corbet *et al.*, 2006
Limousin	SA	UAM	0.24	-	-	0.08	Van Niekerk & Neser, 2006
Tswana	Botswana	UAM	0.31	-	-	-	Raphaka, 2008
Afrikaner	Zimbabwe	UAM	0.20	0.11	-0.42	0.14	Beffa *et al.*, 2009

h_a^2 and h_m^2 are the direct additive and maternal additive heritability's respectively; r_{am} is the genetic correlation between direct additive and maternal additive effects and $c^2 = \sigma_c^2/\sigma_p^2$ is the fraction of phenotypic variance due to permanent environment. Bon & Bel Red = Bonsmara & Belmont Red; MAM = Multivariate Animal Model; SA = South Africa; UAM = Univariate Animal Model

2.2.2 Reproductive traits

Reproduction is arguably the most economically important factor in the efficiency and profitability of most cow-calf operations (Urioste *et al.*, 2007; Minick Bormann & Wilson, 2010; Moreira *et al*., 2015) and its improvement should form a key part of the breeding objectives of any breed. This is mainly because reproductive traits describe the animal's ability to conceive, give birth to a live calf and to successfully suckle the calf to weaning (Davis, 1993). This weaned calf is principally the only output in beef cow-calf enterprises, making reproductive efficiency a key determinant of profitability in most cow-calf operations (Diskin & Kenny, 2014).

Furthermore, improvements in reproductive performance can be up to 4-fold more important than improvements in end-product traits in a conventional cow-calf operation selling market calves at weaning (Melton, 1995; Cammack *et al.*, 2009). Therefore, improving reproductive performance has a direct and positive influence on production efficiency. Improved production efficiency of a herd, even if only minor changes on genetic structure of the population were made, should therefore lead to greater profitability (Cavani *et al.*, 2015). Substantial financial losses may occur if the cow does not calve regularly (annually) during her reproductive life or if the first calving occurs at an advanced age (Silva *et al.*, 2003; Santana *et al.*, 2012).

For use in routine evaluations, it is difficult to identify economically important traits relating to reproduction (Rust & Groeneveld, 2002). Reproductive performance is commonly evaluated by analysing an array of female reproductive traits. However, use of reproductive information as a selection tool often presents difficulties. Because reproductive traits are generally considered lowly heritable (Rust & Groeneveld, 2002; Minick Bormann and Wilson, 2010), little emphasis has traditionally been placed on them in genetic improvement programs (BIF, 2010). In general, reproductive performance receives comparatively little attention in most genetic evaluation programmes, particularly for beef cattle. For example, calf tempo and scrotal circumference are the only fertility traits in a list of 17 traits that forms part of the national beef cattle evaluation programme in South Africa (Maiwashe *et al.*, 2009).

A number of reproductive traits have been identified and measured in a multitude of ways including but not limited to age at first calving, calving success, calving rate, days to first breeding, days from first insemination to conception, pregnancy rate, calving interval, longevity, calf tempo; retention tempo and stayability (Rust & Groeneveld, 2002; Urioste *et al.*, 2007; Cammack *et al.*, 2009; Buzanskas *et al.*, 2010). According to Berry and Evans (2014), reproductive traits that are routinely measured on commercial animals in most international dairy and beef cattle populations may be simply separated into: (1) interval traits, (2) binary traits and (3) count traits. However, reproductive performance is a complex trait that has many components (Van der Westhuizen *et al.*, 2001; Rust & Groeneveld, 2001), and no completely satisfactory measure of reproductive performance has been found yet (Urioste *et al.*, 2007; Rust *et al.*, 2009). For instance, calving rate is a lifetime measure of the reproductive performance of a cow, but requires records of herd entry and exit dates as well as the pregnancy status of cows exiting the herd to enable this trait to be computed correctly (Rust & Groeneveld, 2001). This information is however rarely available in the South African recording system (Rust *et al.*, 2009).

Furthermore, improvement of cow fertility in beef cattle is considered to be potentially limited (Davenport *et al.*, 1965; Dearborn *et al.*, 1973; Rust & Groeneveld, 2001). This is because heritability estimates of female fertility traits from published reports are generally low and often close to zero (Koots *et al.*, 1994a; Rust & Groeneveld, 2002; Cammack *et al.*, 2009), indicating that environmental effects account for a large proportion of the variation in these traits (Corbet *et al.*, 2006). Moreover, most reproductive traits are phenotypically expressed in limited categories, notwithstanding that diverse combinations of genetic as well as environmental influences determine the phenotype (Rust & Groeneveld, 2002). For example, some reproductive traits are threshold type, which do not present continuous phenotypic expression and makes genetic evaluations more difficult (Cavani *et al.*, 2015). Additionally, selection based on reproductive traits is limited in beef cattle, because beef cattle are predominantly raised extensively and this makes data collection and herd measurements more complicated (Eler *et al.*, 2014).

2.2.2.1 Variance components and genetic parameters for reproductive traits in beef cattle

Estimating breeding values for fertility traits, especially in females presents difficulties in data collection and analysis. This is mainly because the expression of reproductive ability is often constrained by the management system employed as well as the particular recording scheme used for the breed (Rust & Groeneveld, 2001). As a result, there are limited ways to evaluate fertility on a between-herd basis other than heifer pregnancy (Minick Bormann & Wilson, 2010). Low heritability is commonly reported for most measures of reproductive performance in beef cattle.

In spite of their low heritability, reproduction traits should be further studied and their inclusion in the selection criteria must be evaluated in order to improve reproductive efficiency in beef cattle (Grossi *et al*., 2016). The estimation of genetic parameters is a key component in evaluating the potential to genetically improve reproductive performance in beef herds (Berry and Evans, 2014), and for obtaining indices to maximize response to selection (Cavani *et al.*, 2015). The use of indices is mainly because, owing to difficulty in establishing an indicator trait that simultaneously represents productive and reproductive traits, indices consisting of several traits are often employed in genetic evaluation (Grossi *et al.*, 2008).

For background purposes, selected literature estimates of genetic parameters for some reproductive traits in beef cattle are presented in Table 2.2. Direct heritability estimates for age at first calving (AFC) vary from 0.03 (Buzanskas *et al*., 2013) to 0.40 (Van der Westhuizen *et al*., 2001). For calving interval (CI), heritability estimates vary from 0.01 (Van der Westhuizen *et al*., 2001) to 0.125 (Gutierrez *et al*., 2002). Accumulated Productivity (ACP) has not been extensively reported on, nevertheless, available ACP heritability estimates vary from 0.11 (Chud *et al*., 2014) to 0.24 (Duitama *et al*., 2013).

Table 2.2. Selected literature estimates for genetic parameters (h_a^2, r_g, r_p) and their respective standard errors (SE) for commonly reported reproductive traits in female beef cattle

Breed	Country	Model	h_a^2 ± se	r_g (AFC-ACP)	r_p (AFC-ACP)	Reference
			Age at First Calving (AFC)			
Crossbreds	South Africa	MAM	0.40			Van der Westhuizen *et al*., 2001
A- de los Valles	Spain	MAM	0.24 ± 0.018			Gutierrez *et al*., 2002
Bons & Belm Red	South Africa	UAM	0.13 ± 0.06			Corbet *et al*., 2006
Nellore	Brazil	MAM	0.07 ± 0.040	-0.33 ± 0.04	-0.36	Grossi *et al*., 2008
Angus	America	MAM	0.28 ± 0.060			Minick Bormann & Wilson, 2010
Nellore	Brazil	MAM	0.11			Lôbo *et al*., 2011
Canchim	Brazil	MAM	0.03 ± 0.01			Buzanskas *et al*., 2013
Crossbreds	Ireland	MAM	0.31 ± 0.016			Berry & Evans, 2014
Nellore	Brazil	MAM	0.20 ± 0.020			Moreira *et al*., 2015
Tabapuã	Brazil	MAM	0.09 ± 0.020	–0.60 ± 0.18	–0.34 ± 0.04	Bernardes *et al*., 2015
Brahman	Brazil	MAM	0.10			Cavani *et al*., 2015
Nellore	Brazil		0.12			Rizzo *et al*., 2015
Nellore	Brazil	TRM	0.15			Santana Jr. *et al*., 2015
Mpwapwa	Tanzania	RAM	0.13 ± 0.110			Chawala *et al*., 2017
Crossbreds	South Africa	MAM	0.01	-0.03		Van der Westhuizen *et al*., 2001
A- de los Valles	Spain	MAM	0.13 ± 0.020	0.23 ± 0.078		Gutierrez *et al*., 2002
Bons & Belm Red	South Africa	UAM	0.04 ± 0.010	0.44 (0.08)	-0.28 ± 0.01	Corbet *et al*., 2006

Table 2.2. Continued…

Breed	Country	Model	$h_a^2 \pm se$	r_g (CI – AFC)	r_p (CI – AFC)	Reference
Calving Interval (CI)						
Canchim	Brazil	MAM	0.06 ± 0.020	0.23 ± 0.020	-0.08 ± 0.01	Buzanskas *et al*., 2013
Crossbreds	Ireland	MAM	0.02 ± 0.004	-	-	Berry & Evans, 2014
Brahman	Brazil	MAM	0.02	-0.13	-0.05	Cavani *et al.*, 2015
Nellore	Brazil	MAM	0.06 ± 0.030	-	-	Grossi *et al*., 2016
Tabapuã	Brazil	MAM	0.08 ± 0.040	0.74 ± 0.28	-0.11 ± 0.03	Bernardes *et al*., 2015
Nellore	Brazil		0.11			Rizzo *et al*., 2015
Mpwapwa	Tanzania	RAM	0.10 ± 0.05		-0.10 ± 0.0	Chawala *et al*., 2017

Breed	Country	Model	$h_a^2 \pm se$	r_g (CI – ACP)	r_p (CI – ACP)	Reference
Accumulated Productivity (ACP)						
Nellore	Brazil	MAM	0.14 ± 0.060			Grossi *et al*., 2008
Brahman	Colombia	MAM	0.24± 0.040	-0.40 ± 0.12	-0.31 ± 0.04	Duitama *et al*., 2013
Nellore	Brazil	UAM	0.11 ± 0.020			Chud *et al*., 2014
Tabapuã	Brazil	MAM	0.18 ± 0.060	-0.83 ± 0.02	-0.57 ± 0.040	Bernardes *et al*., 2015
Nellore	Brazil	MAM	0.17 ± 0.030	-0.40 ± 0.27	-0.32	Grossi *et al*., 2016

A- de los Valles = Asturiana de los Valles; MAM = Multitrait Animal Model, UAM = Univariate Animal Model, TRM = Two-trait Regression Model, RAM = Repeatability Animal Model, r_g = genetic correlation, r_p = phenotypic correlation.

2.3 Correlations

Correlation among traits is generally an indicator of the consistency and reliability of the association between two characteristics or traits in a population. Correlations are important as they aid in prediction of response to selection in one trait due to selection on another. According to Falconer and Mackay (1996), the magnitude of change in a trait when indirect selection is applied on another trait, can be obtained by knowing the heritability of the two traits and the correlation between them. Generally, correlations are partitioned into phenotypic, genetic and environmental correlations (Wasike *et al.*, 2009). Correlations can be negative or positive, varying between the values of -1.0 and 1.0 implying a negative and a positive relationship, respectively. Thus, positively correlated pairs of characteristics will change in the same direction whereas negatively correlated pairs, change in opposite directions. Correlations are considered favourable when selection for a particular trait results in a desirable change in a second trait/s of economic importance.

Other correlations of particular importance are those between different values for the same trait in a population, i.e. a correlation between direct- and maternal effects on growth traits. Although a negative correlation in this instance is unfavourable, negative correlations are commonly reported in the literature for most livestock species. For example, most studies reported a negative genetic correlation between direct- and maternal effects on growth traits (Eler *et al.*, 1995; Haile-Mariam & Kassa-Mersha, 1995; Diop & Van Vleck, 1998; Demeke *et al.*, 2003; Pico, 2004; Van Niekerk & Neser, 2006; Meyer & Tier, 2012; David *et al*., 2015). In contrast, the studies of Koch (1972), Trus & Wilton (1988) as well as Meyer (1992) suggested that there is little association between these effects. As a result, some authors have suggested setting the direct-maternal genetic correlation to zero for genetic evaluation purposes (Boligon *et al.*, 2012; David *et al*., 2015).

The cause of the relatively large negative correlation between direct- and maternal genetic effects is still not quite clear (Robison, 1996; Meyer, 1997; Groeneveld *et al.*, 1998; Boligon *et al.*, 2012; David *et al*., 2015). In general, accurate estimation of genetic correlations between direct- and maternal genetic effects for growth traits appears to be largely dependent on data structure, particularly with regard to the proportion of dams with their own phenotypic information, the number of progeny per dam, and available pedigree relationships (Clément *et al.*, 2001; Boligon *et al.*, 2012). There are however many other propositions for the negative correlation between direct- and maternal genetic effects and the list is still growing.

Regarding reproduction, there are clear benefits for including correlated predictor traits in national multitrait genetic evaluations (Berry & Evans, 2014). This is more so considering that the choice of a selection criterion does not only depend on how much the trait is subject to transmission from parent to offspring, but also on its correlation with other traits (Boligon *et al.*, 2013; Cavani *et al.*, 2015). However, there are no studies that evaluated the correlated impact on reproduction, resulting from genetic selection on other economically important traits in Afrikaner cattle. Given its importance for the genetic improvement, studies that estimate genetic correlations between reproductive and productive traits are quite necessary (Cavani *et al.*, 2015). This study will explore the most probable correlations between traits, aiming at identifying economically important traits that presents higher heritability whilst also presenting a positively correlated influence on reproductive traits.

2.4 Genetic and phenotypic trends

Genetic trends reflect the amount of genetic improvement (or lack thereof) for a particular trait in a population over time. The study of genetic trends over time in traits that are under direct and/or correlated selection permits evaluation of the results of the selection program adopted and can where necessary, contribute to the evaluation of traits that should be included in selection indices (Boligon *et al.*, 2013). Comparison of genetic and phenotypic trends can be helpful in assessing whether genetic improvement is translated into superior performance, on which the remuneration for producers is often based (Dube *et al.*, 2012). Therefore, phenotypic and genetic trend lines can help farmers to assess selection responses and also compare alternative methods for genetic improvement (Javed *et al.*, 2007; Ramatsoma *et al.*, 2014).

Other than the study of Jordaan *et al.* (2014) on genetic and phenotypic trends for calf weaning weight and dam weight at weaning, genetic and phenotypic trends on most traits for the Afrikaner cattle have not been reported yet. To effectively implement selection criteria, knowledge of these trends is essential, and it is against this background that future studies of Afrikaner cattle should determine the genetic and phenotypic trends of growth and reproductive traits. The results of such studies will allow for evaluation of whether any significant and sustained genetic progress in the desired direction has been achieved for growth and reproductive traits in this population.

2.5 Genetic models for estimating genetic parameters

Our theoretical and empirical understanding of the quantitative genetic models particularly for variance components due to direct and maternal effects comes from earlier work on variance component models (e.g. Henderson, 1953; Willham, 1972, 1980; Baker, 1980; Falconer & Mackay 1996).

Genetic evaluations provide information that can aid in breeding decisions for increased long-term performance of animals and herds (McHugh *et al.*, 2014). In quantitative genetics, the objective is to separate additive genetic variances and covariances from other sources of variance (Eaglen *et al.*, 2012). A form of mixed-effects model known as the ‘Animal model’ is often used to decompose phenotypic variance into different genetic and environmental sources as well as to estimate key parameters such as the heritability of a trait or the genetic correlations between traits (Wilson *et al.*, 2010; Varona *et al.*, 2015; Holand & Steinsland, 2016). The most commonly used parameterization accounts for the direct polygenic additive genetic effects inherent to each individual and for several systematic effects (e.g. rearing status, sex, herd, season of birth, etc.), as well as the residual source of variation (Varona *et al.*, 2015).

However, some traits may also be affected by maternally associated effects that are either genetic or environmental in origin. The contribution of maternal genetic effect on an offspring is always equal in proportion, to the paternal genetic effect. However, maternal environmental effect exerts an added external influence on the progeny phenotype extending therefore the maternal influence proportion. Maternal genetic effects refer to the influential effects from the genome of the dam (Willham, 1963; Meyer, 1992; Clément *et al.*, 2001; Varona *et al.*, 2015). On the other hand, maternal environmental effects refer to the influence of the dam by providing an environment that influences the phenotype of its offspring (Willham, 1972; Wolf & Wade, 2016). There is unfortunately no consensus on which is the most accurate model to disentangle maternal effects from the phenotypic variance. Developing a statistical model for maternally affected traits requires therefore, a careful balance between sufficient predictive ability and computational feasibility, which in turn is affected by the size of the dataset and potential biases in data recording (Eaglen *et al.,* 2012; David *et al*., 2015).

Such a model must both be reasonably accurate in describing the relevant biological aspects and yet simple enough to manipulate so that practical inferences can be made (Willham, 1972).

Generally, animal models with Restricted Maximum Likelihood (REML) method are favoured for genetic parameter estimation (Meyer, 1992; Kim *et al.*, 2006). The likelihood ratio test evaluates the significance of a model containing one or more additional parameters, compared with another identical model but with omission or addition of some parameters (Robinson, 1996). According to Eaglen *et al.* (2012), statistical models can account for direct and maternal effects in two ways i.e. (1) Animal models that fit calf and dam effects directly and (2) Sire-maternal grandsire (S-MGS) models that fit direct and maternal effects through the sire of the calf and that of the dam, respectively. The validity of any conclusions drawn from analyses performed using these models depends on whether the models used described the data accurately (Robinson, 1996).

2.5.1 Animal model

The animal model can be described as a biometrical model that combines the information on observed phenotypes of relatives to estimate a breeding value of an animal. The animal model usually incorporates an individual's 'breeding value' (or 'genetic merit') as an explanatory variable for a phenotypic trait of interest (Wilson *et al.*, 2010). Comparatively, the animal model is extensively used for predicting genetic values and estimating genetic parameters, because the optimum combined use of all relationships and performances tend to improve accuracy (Clément *et al.*, 2001). Animal models are often not too difficult to implement, given appropriate data, however, correctly specifying and interpreting their outputs remains quite complex (Wilson *et al.*, 2010).

2.5.2 Sire-maternal grandsire models

The S-MGS models partitions the direct and maternal effects through the sire of the calf and that of the dam (Eaglen *et al.,* 2012). Compared to sire models, S-MGS models employ the utilisation of relationships on the maternal side, accounting for non-additive genetic effects, at least partially (Parkkonen *et al.*, 2000; Kim *et al.*, 2006). As a result, more accurate (co)variance estimations and prediction of genetic values would likely be achieved with their use, given accurately detailed pedigree data. For instance, estimating genetic parameters for average daily gain and carcass traits, Kim *et al.* (2006) found that 6.25% of genetic variance was additionally explained with the S-MGS model. In contrast to animal models, S-MGS models are also often computationally manageable in analysing data from very large populations. In agreement, Eaglen *et al.* (2012) found that S-MGS models exceeded animal models in terms of practicality, as their robustness allowed the analysis of more data and the inclusion of more traits. However, a slight loss of accuracy is often observed when using the S-MGS models, particularly where too few sire-progeny data is available.

CHAPTER 3

VARIANCE COMPONENTS AND GENETIC PARAMETERS FOR GROWTH TRAITS

3.1 Introduction

Knowledge of the magnitude of the (co)variance components for traits of economic importance is critical for animal genetic evaluation and for development of sound breeding programs (Willham, 1980). This is firstly because, estimation of breed-specific components of variance for these traits provides knowledge of their heritability and the genetic correlations between them (Corbet *et al.*, 2006; Estrada-Leon *et al.*, 2014). Secondly, selection of animals requires more precise estimates of (co)variance components for the selection criteria, as they allow for the right prediction of the animals' genetic merit and the ranking of animals for each selection criterion (Araújo *et al.*, 2014). Furthermore, planning appropriate breeding programs requires knowledge of genetic parameters and the joint effect of genes for growth potential and for maternal ability (Baker, 1980). Incorrect (co)variance components can easily lead to biased breeding values, especially in multiple trait analysis of growth traits (Neser *et al.*, 2012). Knowledge of genetic parameters for growth traits is therefore crucial for accurate genetic evaluation programmes in animal breeding.

The most recent estimates of genetic parameters for growth traits of Afrikaner cattle in South Africa were reported by Groeneveld *et al.* (1998). The breeding strategy followed by the Afrikaner cattle breeders has on the other hand evolved, resulting in improvements in some growth traits, particularly weaning weights. For instance, Jordaan *et al.* (2014) observed genetic changes in estimated breeding values for direct weaning weight of the Afrikaner (from -0.36 to 6.34), which translated to a change of +6.7kg with no significant change in the breeding values of mature cow weight. This is not surprising considering that during the last decade, increased focus on more efficient selection programmes have accelerated genetic improvement in a number of breeds (Groeneveld *et al.*, 2010). There is therefore, a need for recent information on the genetic parameters for a full range of growth traits as well as their correlations, especially from large field data sets for the Afrikaner breed in South Africa.

In this chapter, the objective of the study was to estimate genetic variance-covariance components and genetic parameters for growth traits of Afrikaner cattle using different genetic models.

3.2 Materials and methods

Data description

Data used were sourced from the Integrated Recording and Genetic Information Systems (INTERGIS) as managed by the Agricultural Research Council of South Africa. The data originated from records collected between 1966 and 2017, from a population of 260 789 animals. A complete animal record consisted of its identity; pedigree information; dates of birth and weaning; dates at the age of 12 and 18 months; sex; herd of origin; supplementary feeding; weights recorded at birth, weaning, 12 months and at 18 months of age.

For the animal model, pedigree information consisted of 99 298 individual identities from pedigree data that were 10 generations deep. For WWT, individual identities were progeny of 2 570 sires, 597 sires of sire, 1 220 dams of sire, 30 492 dams, 1 752 sires of dam and 10 754 dams of dam. For all other weight traits, individual identities were progeny of 2 572 sires, 601 sires of sire, 1 230 dams of sire, 30 589 dams, 1 758 sires of dam and 10 829 dams of dam.

For the S-MGS model, pedigree information consisted of 19 150 individual identities from pedigree data that were four generations deep. The individual identities were progeny of 1 002 sires, 120 sires of sire, 35 dams of sire, 446 dams, 70 sires of dam and 21 dams of dam. Data with inconsistencies in the pedigree records, dates of birth and weight records were excluded from the analyses. All incomplete records, as well as records that exceeded four standard deviations from the mean for the metric traits, were disregarded. Contemporary groups with fewer than five records were also removed from the final data set used for analyses. Two distinct calving seasons were identified according to the dispersion of the dates of birth for the formation of contemporary groups: September to March was classified as summer calving season, whereas April to August was classified as winter calving season.

Contemporary groups were created by the concatenation of the herd, year and season of birth (HYS). For WWT, 6 453 HYS contemporary groups were identified from a data set consisting of weight records obtained from 98 832 animals. The data set for remainder of the traits had 6 502 HYS contemporary groups respectively from weight records obtained from 99 298 animals. For all models, HYS effects were also fitted as random. Sex was fitted as a fixed categorical effect; dam age was also fitted as a categorical effect with 5 classes: <2 yr. = 1; 2-4 yr. = 2; 4-5 yr. = 3; 5-10 yr. = 4 >10 yr.= 5. The dam age categories were based on the BIF guidelines of America (BIF, 2010). The selected animals were born between 1976 and 2017 and their summary statistics is presented in Table 3.1.

Table 3.1. Summary statistics for the traits analysed

Trait	n	Min	Mean	Max	SD
BWT	27633	24.00	32.60	40.00	2.98
WWT	70504	113.00	190.70	269.00	28.59
YWT	21624	103.00	224.90	347.00	43.17
EWT	23248	166.00	296.50	430.00	48.66

BWT = Birth weight, WWT = Weaning weight, YWT = Yearling weight, EWT = Eighteen months' weight, Min - Minimum and Max = maximum, SD = Standard deviation

Statistical analysis

Significant fixed effects to be included in the mixed model for each trait were identified in preliminary analyses conducted using the general linear model (GLM) procedure of SAS (2010). All growth data were analysed using linear univariate animal models. In addition, BWT and WWT data were also analysed using the sire-maternal grandsire Model. The reason for fitting the sire-maternal grandsire model for only BWT and WWT was because of the depth of available data for sufficient sire-maternal grandsire connections and also that these traits are expected to be highly influenced by maternal effects.

For the animal model, random effects were successively fitted to construct six alternative models (Models 1a to 6a) as described by Meyer (1992). The random effects fitted into this model were: direct animal genetic, maternal genetic and maternal permanent environmental effects, respectively. The comprehensive model (designated as model 5a) accounted for all sorts of maternally influenced effects. The five alternative models were constructed by either including or excluding the maternal effects.

For the S-MGS models, the (co)variance between direct- and maternal genetic effects was computed using all available pedigree information to construct two models (Models 1b and 2b). Sire and maternal grandsire (co)variances were fitted as random effects to account for direct and maternal genetic effects. Estimation of the correlation between sire and maternal grandsire effects were allowed by the model through the inclusion of the sire of the individual and maternal-grandsires. Model 2b was the most detailed model and accounted for all sorts of maternally influential effects, whilst model 1b alternatively ignored these effects.

The genetic models were compared for statistical goodness of fit to the data through the log likelihood ratio test. A model with an added random effect was considered to provide a significantly best fit, when twice the difference in the log likelihood ratio between the two models is larger than the Chi-square value at $P = 0.05$ with degrees of freedom equal to the difference in the number of parameters estimated.

Not all generic statistical software packages are able to fit the random effect structure associated with large pedigree information (Wilson *et al.*, 2010). Therefore, estimates of (co)variance components were obtained with the commonly used ASREML package (Gilmour *et al.*, 2009) due to its greater speed and superior flexibility to fit more complex models. Using linear models, direct and maternal genetic effects were incorporated by fitting genetic effects for calf and dam for the animal model, and sire and maternal grandsire for the S-MGS model as follows:

Animal model

Model 1a $Y = Xb + Z_1a + e$
Model 2a $Y = Xb + Z_1a + Z_2m + e$ $[\text{cov}(a,m) = 0]$
Model 3a $Y = Xb + Z_1a + Z_3c + e$
Model 4a $Y = Xb + Z_1a + Z_2m + e$ $[\text{cov}(a,m) = A\sigma_{am}]$
Model 5a $Y = Xb + Z_1a + Z_2m + Z_3c + e$ $[\text{cov}(a,m) = A\sigma_{am}]$
Model 6a $Y = Xb + Z_1a + Z_2m + Z_3c + e$ $[\text{cov}(a,m) = 0]$

Sire-maternal-grandsire model

Model 1b $Y = Xb + Z_s s + e$
Model 2b $Y = Xb + Z_s s + Z_{mgs} + e$ $[\text{cov}(s, mgs) = A\sigma_{s,\,mgs}]$

where, **y** is a vector of phenotypic observations (BWT, WWT, YWT, EWT), **b** is a vector of fixed effects, **a** is a vector of random direct genetic effects, **m** is a vector of random maternal genetic effects, **c** is a vector of permanent maternal environmental effects, **s** is a vector of sire genetic effect, **mgs** is a vector maternal grand-sire genetic effect, **e** is a vector of random residuals, **X** is the incidence matrix relating observations to fixed effects, Z_1, Z_2, Z_3, Z_s and Z_{mgs} are incidence matrices relating observations to random direct genetic, direct maternal, permanent maternal environmental, sire, and maternal grandsire effects, respectively.

Univariate analyses were conducted using each model to estimate the variance and covariance components. The (co)variance components obtained were used to calculate genetic parameters for the traits under study. In addition, the total heritable variance (σ^2_{TBV}) was computed using the formula of Eaglen and Bijma (2009):

$$\sigma^2_{TBV} = \sigma^2_a + 2\sigma_{am} + \sigma^2_m$$

Estimates of direct heritability (h^2_a), maternal heritability (h^2_m) and maternal permanent environmental effects (c^2) were calculated as ratios of the estimates of σ^2_a , σ^2_m and σ^2_c respectively, to the phenotypic variance. Where applied, total heritable variance as a ratio of the phenotypic variance (T^2) was computed as follows (Eaglen and Bijma, 2009):

$$T^2 = \frac{\sigma^2_{TBV}}{\sigma^2_P}$$

The correlation between direct- and maternal genetic effects (r_{am}) was calculated as the ratio of the estimates of σ_{am} to the product of the square roots of the estimates of σ^2_a and σ^2_m.

For the S-MGS model, estimates of σ^2_a , σ_{am} and σ^2_m were respectively computed by transforming σ^2_s, σ^2_{mgs} and $\sigma_{s\text{-}mgs}$ using the equations given by Eaglen and Bijma (2009):

$$\sigma^2_a = 4\sigma^2_s$$

$$\sigma_{am} = 4\sigma_{s\text{-}mgs} - 2\sigma^2_s$$

$$\sigma^2_m = 4\sigma^2_{mgs} + \sigma^2_s - 4\sigma_{s\text{-}mgs}$$

All heritability and genetic correlation estimates were considered significantly different form zero, when the estimated values were more than twice in magnitude to that of their respective standard errors. For a significant fixed effect, mean separation was conducted using Tukey's procedure and were considered significant when $P < 0.05$.

3.3 Results and discussion

3.3.1 (Co)variance components and genetic parameters for BWT, WWT, YWT and EWT using the Animal and Sire-maternal grandsire models

Estimates of genetic parameters for growth traits of Afrikaner cattle fitting several models to separate direct genetic, maternal genetic and maternal permanent environmental effects are presented in Tables 3.2 to 3.8. In all respects, models that accounted for maternal genetic and environmental effects in addition to accounting for a genetic correlation between direct- and maternal effects proved to fit the data better. Accounting for maternal effects is of importance in the estimation of genetic parameters (Meyer, 1992; Robinson, 1996). A full discussion of the results of the variance components for BWT, WWT, YWT and EWT is presented here after.

Estimates of (co)variance components and genetic parameters for BWT and WWT using the S-MGS model are presented in Tables 3.2. and 3.4, respectively. Model 2b, which was the most detailed model, resulted in a significantly better fit for the data in comparison to model 1b when judged by the Log likelihood (Log L) ratio. For both traits, Model 1b ignored the maternal grandsire effect and the correlation between sire and maternal grandsire effects. On the other hand, Model 2b accounted for sire and maternal grandsire effects as well as the correlations among these effects.

Using the Animal Model (AM), estimates of (co)variance components and genetic parameters for BWT, WWT, YWT and EWT are presented in Tables 3.3 to 3.8. Six different animal models were fitted for each trait, ranging from a simple model with the animal as the only random effect, to the most comprehensive model allowing for both genetic; permanent maternal environmental effects and a genetic covariance between direct and maternal effects.

3.3.1.1 Birth weight

Estimates of (co)variance components and genetic parameters for BWT of the Afrikaner cattle breed are presented in Table 3.2 (S-MGS) and Table 3.3 (AM).

Comparisons among results from different statistical models can be used to ascertain their strengths and weaknesses and to determine whether simpler computational models may be adequate (Ferreira *et al*., 1999). Using the S-MGS as opposed to the AM yielded increased additive genetic variance components. The largest increases were observed with maternal additive variances albeit with larger standard errors when compared to the animal model. The larger standard errors are however small enough relative to the estimated parameters, to consider this estimate as a reliable estimate of the population parameter. Direct additive genetic effects (σ^2_a) represented a higher proportion of total variation than maternal genetic effects (σ^2_m) throughout. The largest differences between σ^2_a and σ^2_m were observed with the AM (Table 3.3) resulting in a large range between the direct and maternal heritabilities. The S-MGS model presented marginal differences between σ^2_a and σ^2_m with a consequently smaller range between h^2_a and h^2_m. Furthermore, addition of the maternal grandsire effect had negligible or no effect on estimates of direct additive genetic variances which remained stable for BWT (1.72 to 1.71). This result reveals that for BWT, the inclusion of maternal grandsire effect did not cause any change in the estimated direct variance.

Table 3.2. (Co)variance components and genetic parameters with their respective standard errors for BWT using the S-MGS model, with the “best” model in bold

Parameter	Model 1b	**Model 2b**
σ^2_a	1.72 ± 0.18	**1.71** ± **0.18**
σ^2_m		**1.30** ± **0.26**
σ_{am}		**-0.42** ± **0.17**
σ^2_s	0.43 ± 0.045	**0.43** ± **0.045**
σ^2_{mgs}		**0.33** ± **0.062**
$\sigma_{s\text{-}mgs}$		**0.11** ± **0.042**
σ^2_e	4.90 ± 0.055	**4.83** ± **0.054**
σ^2_{TBV}		**2.17** ± **0.34**
σ^2_p	6.62 ± 0.18	**7.42** ± **0.28**
r_{am}		**-0.28** ± **0.10**
h^2_a	0.26 ± 0.02	**0.23** ± **0.02**
h^2_m		**0.18** ± **0.03**
T^2		**0.29** ± **0.04**
Log L	-3012.74	**-2955.39**

σ^2_a and σ^2_m are the direct additive and maternal additive genetic variances, respectively; σ_{am} is the direct- and maternal genetic covariance; σ^2_s is the sire variance; σ^2_{mgs} is the maternal grandsire (MGS) variance; $\sigma^2_{s\text{-}mgs}$ is the covariance between sire and MGS effects; σ^2_e is the residual variance; σ^2_{TBV} is the total additive variance = and σ^2_p is the phenotypic variance. r_{am} is the genetic correlation between direct additive and maternal additive effects; h^2_a and h^2_m are the direct additive and maternal additive heritabilities respectively and T^2 is the fraction of phenotypic variance due to total genetic variance (direct and maternal). Log L is the log likelihood value.

For the six animal models used, Model 5a resulted in a significantly better fit in comparison to the rest of the models. This appropriate Model (5a) included the direct- and maternal genetic covariance as well as the permanent maternal environmental effects. Accounting for the direct–maternal genetic covariance using the animal model (Models 4a & 5a) produced a better model fit for BWT than when this covariance was ignored. In addition, accounting for permanent maternal environmental effects (Model 6a) seemed to decrease direct genetic variations when direct–maternal genetic covariance was ignored. Accounting for both the direct–maternal genetic covariance and permanent maternal environmental effects resulted in the least residual variance, indicating better partitioning of the effects. However, fitting permanent maternal environmental effects (Model 6a) when the direct–maternal genetic covariance was ignored, notably increased the residual variance at the expense of the maternal additive genetic variance.

The best S-MGS model (Model 2b,) produced a moderate direct heritability estimate of 0.23 ± 0.02 for BWT. Corresponding direct heritability estimates of 0.21; 0.23 and 0.25, obtained using S-MGS, were reported by Burfening *et al*. (1981); Hetzel *et al*. (1990) and Bertrand & Benyshek (1987), respectively. Direct heritability estimates decreased by 3% (from 0.26 to 0.23) when the additive genetic effects were partitioned into sire and maternal grandsire components. Direct heritability can therefore be marginally overestimated by about 3% if maternal grandsire effects are ignored for evaluating BWT using S-MGS models. In corroboration of this result, Meyer (1992) concluded that ignoring maternal effects resulted in noticeable inflation of direct heritability estimates for growth traits in Australian beef cattle. This is in agreement with the findings of Ferreira *et al*. (1999) who found that including the covariance between direct and maternal effects decreased direct heritability of birth weight.

Using the animal model, direct heritability estimates increased from 0.20 ± 0.015 to 0.28 ± 0.024 when the direct–maternal genetic covariance was accounted for (Table 3.3). A similar behaviour of genetic parameters for BWT has been observed in beef cattle (Abera *et al*., 2011). Model 5a (best) and model 4a (second best) identically produced a higher direct heritability estimate of 0.28 ± 0.024, respectively. Studying growth traits in Brahman cattle, Pico *et al*. (2004) observed a similar h_d^2 estimate (0.28) for BWT. Lower h_d^2 estimates ranging from 0.07 (Diop & Van Vleck, 1998) to 0.23 (Corbet *et al*., 2006) have been observed elsewhere for BWT using the animal model. The estimate observed in this study is however much lower than that of Groeneveld *et al.* (1998) who reported a direct heritability estimate of 0.52 for Afrikaner cattle. The large difference between direct heritability estimate for BWT in the current study and that of Groeneveld *et al.* (1998) could be due to a number of reasons. Factors such as, the model used as well as the effects fitted, or even the magnitude of connectedness of the few records (5 602) used by Groeneveld *et al.* (1998) as compared to 27 633 records used in this study could have contributed to the difference in the two estimates. According to Wilson *et al.* (2009) fewer individuals in a well-connected pedigree can be very informative. Nonetheless, the moderate h_d^2 estimates observed in this study indicate that there is sufficient direct genetic variation for BWT in the Afrikaner cattle population. The observed estimates in the current study remain well within reported literature values for beef cattle.

Using the S-MGS model, maternal heritability (h_m^2) estimate from the current study was 0.18 ± 0.03. Corresponding S-MGS model derived maternal heritability estimates of 0.19 (Baker, 1980); 0.17 and 0.20 (Trus & Wilton, 1988) have been reported elsewhere for beef cattle. This result suggests that maternal effects exist in this population. The estimated maternal heritability was higher than that estimated from the animal model, however this could also be attributed to difference in effects fitted using the animal vis-a-vis the S-MGS model. Nonetheless, the improvement in maternal heritability seems to be a reasonable compromise to the observed modest reduction in direct heritability as a result of using the S-MGS model.

On the other hand, estimates of maternal heritability that were obtained using the animal model were distinctively much smaller than direct heritabilities for all models, irrespective of the effects fitted. The observed estimates of maternal heritability ranged from 0.009 ± 0.007 to 0.080 ± 0.013 across models, which is much smaller than the estimate of h_m^2 obtained using the S-MGS model (Table 3.2). The best animal model (Model 5a) produced a low h_m^2 estimate of 0.05 ± 0.013 which is slightly lower albeit comparable to the estimate of (0.07) as reported by Groeneveld *et al*. (1998) for this same population. Comparatively, Diop & Van Vleck (1998) and Choi *et al*. (2000), respectively observed an even lower estimate of (0.04) for the same trait. However, Van Niekerk and Neser (2006) observed a corresponding h_m^2 estimate of 0.05 for Limousin cattle in corroboration with the results of this study.

The maternal heritability estimate in this study is well within range of literature values obtained using the animal model even though it is much lower than those reported by

Maiwashe *et al*. (2002) 0.13 in Bonsmara cattle as well as Beffa *et al*. (2009) 0.15 in a close bred herd of Afrikaner cattle. Maternal heritability estimates observed in this study from the S-MGS model were much higher than the animal model derived h_m^2 estimates and suggest that where grand-maternal effects exist, and are ignored in analyses, maternal heritability may well be underestimated.

Using the S-MGS model, the correlation between direct- and maternal genetic effects (r_{am}) was moderately negative (-0.28 ± 0.10) for BWT. Corresponding estimates ranging between -0.22 (Trus & Wilton, 1988) and -0.38 (Garrick *et al*., 1989) have been reported elsewhere for BWT. Estimates of direct- and maternal genetic correlations reported for pre-weaning weights using S-MGS models are limited in recent studies. However, the estimates found in this study are well within range of literature values varying from 0.55 to -0.44 as reported by Meyer (1992).

Judged against the AM, the S-MGS model successfully produced improved values for the covariance between direct- and maternal additive genetic effects. Accordingly, the correlation between direct- and maternal genetic effects improved by 0.36 from (-0.64 to -0.28). This notable improvement might suggest that the S-MGS model have a better potential to partition genetic variances for models that account for maternal effects. Evidence to advocate for similar conclusions has been observed by other workers (Meyer & Tier, 2012; Varona *et al.*, 2015) in recent years.

In general, Meyer (1992) presented ranges of S-MGS model derived literature estimates for genetic parameters due to direct- and maternal effects on growth traits in beef cattle. For BWT, the literature values varied from 0.16 to 0.44 for h_a^2 and 0.06 to 0.20 for h_m^2. By comparative deduction, estimates obtained in the current study for direct (0.23) and maternal (0.18) heritability are therefore well within range of similarly derived (S-MGS) estimates in the literature.

The animal model derived correlation between direct- and maternal genetic effects was strongly negative -0.64 ± 0.062. In corroboration however, corresponding estimates of -0.64 (Van Niekerk and Neser, 2006) and -0.68 (Araujo *et al*., 2014) have been reported for Limousin and Nellore cattle, respectively. In addition, poorer estimates of -0.76 for Horro (Abera *et al*., 2011) and -0.90 for Nellore cattle (Martínez *et al.,* 2010) have also been reported in the literature. In contrast, several authors (Meyer, 1992; Dodenhoff *et al*., 1998; Choi *et al*., 2000; Plasse *et al*., 2004) have found positive estimates of the correlation between direct- and maternal genetic effects for BWT. The negative direct-and maternal correlation observed in this study suggest that in this population, majority of animals that have a positive breeding value for direct effects are likely to have a negative breeding value for maternal effects or vice-versa. This suggestion implies that selection on solely either breeding value is not advisable since selecting individuals on direct performance may result in animals with poor maternal genetics.

The negative correlation between direct- and maternal genetic effects is a source of great controversy in studies estimating (co)variance components for growth traits using models that account for maternal effects (Meyer, 1997; Varona *et al.*, 2015). Generally, maternal effects appear to be statistically confounded with maternal inheritance (Willham, 1980; Baker, 1980; Roehe & Kennedy, 1993). This confounding creates difficulties in effectively disentangling all possible maternal influences of the parents on the progeny. In addition to the commonly proposed explanations for negative correlation between direct- and maternal genetic effects, recent studies (Meyer and Tier, 2012; Varona *et al.*, 2015) suggests that ignoring parent-of-origin effects may be one of the possible causes for the unexpectedly large negative estimates of the correlation between direct- and maternal genetic effects.

Estimates of maternal permanent environmental variance as a fraction of the phenotypic variance (c^2) ranged to between 0.03 ± 0.007 and 0.04 ± 0.008 for all models that accounted for maternal permanent environment. These estimates are on the lower side of literature values for c^2 which range from 0.00 (Corbet *et al.*, 2006) to 0.18 (Abera *et al.*, 2011). This result suggests that, for BWT in Afrikaner cattle, maternal permanent environmental effects contribute very little to the phenotypic variance. This is not surprising because BWT is measured within 72hrs of birth, and by this time the dam has not had enough opportunity to exert an environmental influence beyond that of the uterine conditions, on the phenotype of the calf.

Total heritability (T^2) mirrored h_a^2 when the direct- and maternal covariance was ignored (Table 3.3). When the same effect was fitted (best model), T^2 was reduced from 24 to 19%. This erosion of the T^2 estimate is mainly influenced by the negative magnitude of the direct- and maternal genetic covariance. Total heritability is the regression of an animal's total breeding value (direct and maternal) on its phenotype (Meyer, 1992) and can be useful in estimating response to selection based on phenotypic values (Abera *et al.*, 2011; Estrada-León *et al*., 2014).

Using the S-MGS model, a moderate estimate of total heritability (0.29 ± 0.04) as proportion of phenotypic variance due to total genetic variance was obtained for BWT. This estimate indicates that there is sufficient genetic variance to make genetic changes in BWT, should it be so desired.

Table 3.3. (Co)variance components and genetic parameters with their respective standard errors for BWT, and with the "best" model in bold

Parameter estimates	Model 1a	Model 2a	Model 3a	Model 4a	**Model 5a**	Model 6a
σ_a^2	1.23 ± 0.077	1.05 ± 0.083	1.07 ± 0.079	1.46 ± 0.133	**1.49 ± 0.134**	1.03 ± 0.082
σ_m^2		0.13 ± 0.033		0.39 ± 0.067	**0.26 ± 0.066**	0.04 ± 0.035
σ_{am}				-0.40 ± 5.03	**-0.40 ± 5.24**	
σ_c^2			0.18 ± 0.034		**0.19 ± 0.043**	0.15 ± 0.041
σ_e^2	3.99 ± 0.066	4.01 ± 0.064	3.94 ± 0.064	3.79 ± 0.083	**3.70 ± 0.085**	3.96 ± 0.065
σ_p^2	5.22 ± 0.051	5.19 ± 0.050	5.19 ± 0.050	5.24 ± 0.054	**5.24 ± 0.054**	5.19 ± 0.050
r_{am}				-0.53 ± 0.056	**-0.64 ± 0.062**	
h_a^2	0.24 ± 0.014	0.20 ± 0.015	0.21 ± 0.014	0.28 ± 0.024	**0.28 ± 0.024**	0.20 ± 0.015
h_m^2		0.03 ± 0.006		0.08 ± 0.013	**0.05 ± 0.013**	0.009 ± 0.007
c^2			0.03 ± 0.007		**0.04 ± 0.008**	0.03 ± 0.008
T^2	0.24	0.21	0.21	0.20	**0.19**	0.20
Log L	-4406.33	-4394.97	-4387.82	-4375.33	**-4364.07**	-4386.72

σ_c^2 is the permanent maternal environmental variance; and c^2 is the fraction of phenotypic variance due to permanent environment ($c^2 = \sigma_c^2/\sigma_p^2$.). See Table 3.2 for other abbreviations.

3.3.1.2 Weaning weight

Estimated (co)variance components and genetic parameters for WWT are presented in Tables 3.4 and 3.5. Using the S-MGS model (Table 3.4), Model 2b was the most detailed model, and resulted in a significantly better fit for the data in comparison to model 1b when judged by the Log likelihood ratio. From the AM, the best model was Model 5a. This model included the direct- and maternal genetic (co)variance as well as permanent maternal environmental effects and resulted in a significantly better fit for the data in comparison to the five alternative models.

Using the S-MGS model, addition of maternal grandsire effects had negligible influence on estimates of direct additive genetic variances, with only a maximum change of 2.5% (from 130.66 to 127.41). Using the AM, the σ^2_a and h^2_d estimates were higher and conspicuously biased upwards when maternal effects were ignored. However, fitting the maternal additive effects reduced the σ^2_a and h^2_d estimates by at least half from 161.12 to 78.30 and from 0.37 to 0.18, respectively, without much change to the standard errors. Likewise, failure to account for maternal permanent environmental effects resulted in higher maternal genetic variances (σ^2_m) and consequently, the corresponding h^2_m estimates. For instance, the exclusion of permanent maternal environmental effects (Model 4a) when direct- and maternal genetic covariance was already fitted, resulted in a 130% upward bias (from 52.40 to 120.66) on σ^2_m, resulting in a 16% (from 0.12 to 0.28) increase on h^2_m. It is therefore evident that the relative values of h^2_d and h^2_m were greatly influenced by the model used in the analysis.

Table 3.4. (Co)variance components and genetic parameters with their respective standard errors for WWT using the S-MGS model, and with the “best” model in bold

Parameter	Model 1b	**Model 2b**
σ^2_a	130.66 ± 14.02	**127.41 ± 13.79**
σ^2_m		**104.88 ± 21.57**
σ_{am}		**-33.50 ± 15.08**
σ^2_s	32.67 ± 3.50	**31.85 ± 3.45**
σ^2_{mgs}		**25.81 ± 4.93**
$\sigma_{s\text{-}mgs}$		**7.55 ± 3.63**
σ^2_e	370.98 ± 4.13	**365.22 ± 4.10**
σ^2_t		**165.30 ± 27.52**
σ^2_p	501.65 ± 14.21	**564.02 ± 22.21**
r_{am}		**-0.29 ± 0.12**
h^2_a	0.26 ± 0.02	**0.23 ± 0.02**
h^2_m		**0.19 ± 0.03**
T^2		**0.29 ± 0.04**
Log L	-9413.92	**-9369.25**

See Table 3.2 for abbreviations

The direct- and maternal genetic covariance was also exaggerated by 38% (from -38.33 to -53.00) when the permanent maternal environmental effects were ignored. Furthermore, fitting the permanent maternal environmental effects (Model 6a) when the direct–maternal genetic covariance was ignored increased the residual variance (from 3.70 to 3.96) at the expense of the additive genetic variances. This result suggests that, ignoring maternal effects significantly compromise genetic parameter estimates, particularly for weight at weaning in Afrikaner cattle.

Similar to BWT, direct heritability estimates that were derived using the S-MGS model decreased by 3% (from 0.26 to 0.23) when the additive genetic effects were partitioned into sire and maternal grandsire components. This further confirms a 3% overestimation of h_d^2 when maternal grandsire effects are ignored. The best (Model 2b) produced a moderate direct heritability estimate of 0.23 ± 0.02. Corresponding direct heritability estimates ranging from 0.20 (Hetzel *et al*., 1990) to 0.28 (Bertrand & Benyshek, 1987) have been reported elsewhere in the literature. In general, direct heritability estimates observed in this study for WWT are moderate and remain well within range of estimates reported in the literature.

Using the AM model, direct heritability estimates ranged from 0.18 ± 0.01 to 0.37 ± 0.01 across models. Model 5a (best) and model 4a (second best) identically produced a higher h_d^2 estimate of 0.27 ± 0.02, respectively. This estimate is comparable to estimates reported elsewhere in the literature for different beef breeds: 0.23 for Afrikaner (Groeneveld *et al*., 1998); 0.25 for Bonsmara (Maiwashe *et al*., 2002) and 0.29 for Nellore (Martínez *et al.,* 2010). In contrast, higher h_d^2 estimates of 0.53 for Horro (Abera *et al*., 2011) and 0.60 for Asturiana de los Valles cattle (Gutierrez *et al*., 1997) have been observed elsewhere. The moderate h_d^2 estimate of 0.27 observed in this study indicates sufficient direct genetic variation for WWT in the Afrikaner cattle population.

The S-MGS model produced a higher maternal heritability estimate of 0.19 ± 0.03. Corresponding S-MGS model derived maternal heritability estimates of 0.19 (Garrick *et al*., 1989) and 0.20 (Bertrand & Benyshek, 1987) have been reported in the literature. The maternal heritability estimate observed in this study corresponds closely to available literature values obtained using the S-MGS model. Similar to BWT, these results confirm the existence of maternal effects in this population. This magnitude of maternal effects suggests that improvement in these traits can also be efficiently achieved if selection is based on both the animal's direct and maternal genetic potential.

For the AM, maternal heritability estimates varied from 0.07 ± 0.007 when the maternal permanent environment effect was fitted, to 0.28 ± 0.01 when the same effect was ignored. The best model (Model 5a) produced a h_m^2 estimate of 0.12 ± 0.01 which is higher than the estimate of 0.04 as reported for Nellore cattle by Boligon *et al*., 2012. The estimate obtained in this study is in agreement to the estimates reported by Van Niekerk and Neser (2006) for Limousin cattle, by Meyer (1992) for Hereford and by Groeneveld *et al*. (1998) for Afrikaner cattle. Several other studies observed comparable but higher h_m^2 estimates of 0.14 (Plasse *et al.*, 2004; Wasike, 2006) and 0.15 (Raphaka, 2008). Maternal effects observed here are the highest of all other weight traits in this study. This means therefore that for Afrikaner cattle, maternal effects are more important for WWT than for any other weight trait in the growth path. This result is consistent with knowledge suggesting that maternal environment (mainly milk production) has important genetic components affecting growth in beef cattle (Martínez *et al.,* 2010).

Generally, direct- and maternal heritabilities were respectively similar in magnitude within each model that fitted either or both of the maternal effects whilst ignoring maternal permanent environmental effects (models 2a & 4a). Fitting maternal permanent environmental effects when direct–maternal genetic covariance was already fitted (Model 5a), reduced maternal heritability by more than half (from 0.28 to 0.12). This confirms that, ignoring maternal permanent environmental effects could overestimate maternal heritability by more than half of its relative estimate value when evaluating WWT.

Using a S-MGS model that accounted for direct- and maternal genetic effects (Model 2b), the correlation between direct- and maternal genetic effects was moderately negative (-0.29 ± 0.12). Corresponding estimates of between -0.29, -0.30 for Brangus and Limousin cattle respectively (Bertrand & Benyshek, 1987) and -0.36 for Angus cattle (Brown *et al*., 1990) have been reported. Large negative estimates of the correlation between direct- and maternal genetic effects are often reported, albeit mostly with the animal model.

Similar to BWT, the S-MGS model successfully produced improved values for the covariance between direct- and maternal additive genetic effects. Accordingly, the correlation between direct- and maternal genetic effects for WWT was improved by 0.20 from (-0.49 to -0.29). The correlation between direct- and maternal genetic effects may indeed be biased downward if grand-maternal effects are ignored in the model for weaning weights of beef cattle (Dodenhoff *et al*., 1999; Varona *et al*., 2015). The differences in the r_{am} from S-MGS model vis-a-vis the animal model as observed in this study, further verifies this view by presenting an improved direct- and maternal genetic correlation when maternal effects are estimated through the S-MGS model. This result further suggests that maternal effects could probably be statistically confounded with maternal inheritance.

On the other hand, the animal model derived r_{am} estimate of -0.49 ± 0.04 is slightly larger than that of -0.44 (Groeneveld *et al*., 1998) and -0.42 (Beffa *et al*., 2009) for

Afrikaner cattle. However, much larger estimates of -0.71 for Horro (Abera *et al*., 2011) and -0.90 for Nellore cattle (Martínez *et al.,* 2010) have also been reported in the literature. In contrast, several authors (Meyer, 1992; Plasse *et al*., 2004; Boligon *et al*., 2012) observed positive estimates of the correlation between direct- and maternal genetic effects for WWT.

In general, S-MGS model derived literature estimates for genetic parameters due to direct- and maternal effects on WWT in beef cattle varies from 0.10 to 0.36 (h_a^2), 0.08 to 0.19 (h_m^2) and 0.16 to -0.32 (r_{am}) Meyer (1992). Comparatively, heritability estimates obtained in the current study for direct (0.23) and maternal (0.19) heritability as well as the genetic correlation between direct- and maternal effects (-0.29) are well within range of similarly derived (S-MGS) estimates in the literature.

For growth traits of cattle in modern times, estimates of direct and maternal heritabilities as well as direct- and maternal genetic correlations have been mostly obtained using the animal model incorporating maternal effects, and as a result, no recent S-MGS model derived estimates for growth traits are known to the author.

From the AM, the proportional permanent maternal environmental effect (0.13 ± 0.007) was closely comparable to the observed maternal heritability of 0.12 albeit slightly higher. This result implies that for WWT, the contribution of permanent maternal environmental effects and maternal genetic effects are equally important. Similarly, several studies (Meyer, 1992; Corbet *et al*., 2006; Van Niekerk & Neser, 2006; Wasike, 2006; Beffa *et al.,* 2009; Boligon *et al*., 2012) observed a similar trend where c^2 estimates were similar and even higher than h_m^2 for WWT. For WWT, h_m^2 and c^2 estimates found in this study are generally within expected range of literature values for beef cattle. According to Robinson (1996), estimates of c^2 tends to be higher in most studies using field data, as is the case in this study. Relatively strong c^2 estimates for WWT can also be a reflection of differences in the rearing abilities of the dams.

Specifically, this result showed that the permanent maternal environmental effects are most evident at weaning as compared to other land mark ages in the growth trajectory of Afrikaner cattle. For instance, the exclusion of the permanent maternal environmental effects when maternal effects are accounted for (Models 2a & 4a) increased maternal genetic variance to even above the direct genetic variance. This behaviour of the estimate is however only observed for WWT, confirming the pronounced existence of permanent maternal environmental influence for this trait in Afrikaner cattle. The results for WWT in this study suggest that permanent maternal environment has important components affecting growth traits in Afrikaner cattle. Maternal environmental effects in this case seem to complicate our ability to estimate the genetic basis of the trait, suggesting therefore that it should be included in a model that estimates direct and maternal breeding values for WWT. Greater response to selection for maternal ability around weaning age can therefore be expected if the selection aspiration is as such.

As a useful yard stick for estimating response to selection based on phenotypic values, total heritability ranged from 0.20 when maternal effects were fitted to 0.37 when the same effects were ignored.

Table 3.5. (Co)variance components and genetic parameters with their respective standard errors for WWT, and with the "best" model in bold

Parameter estimates	Model 1a	Model 2a	Model 3a	Model 4a	**Model 5a**	Model 6a
σ^2_a	161.12 ± 4.80	78.30 ± 4.38	92.48 ± 4.51	115.69 ± 7.00	**114.89** ± **6.88**	82.80 ± 4.47
σ^2_m		80.73 ± 2.71		120.66 ± 4.87	**52.40** ± **4.88**	27.51 ± 3.06
σ_{am}				-53.00 ± 10.20	**-38.33** ± **8.37**	
σ^2_c			73.79 ± 2.24		**53.06** ± **3.06**	52.02 ± 2.91
σ^2_e	271.91 ± 3.41	270.50 ± 3.05	254.64 ± 3.11	249.68 ± 4.16	**241.84** ± **4.09**	258.83 ± 3.11
σ^2_p	433.03 ± 2.92	429.52 ± 2.90	420.91 ± 2.79	433.03 ± 3.06	**423.85** ± **2.93**	421.15 ± 2.80
r_{am}				-0.45 ± 0.03	**-0.49** ± **0.04**	
h^2_a	0.37 ± 0.01	0.18 ± 0.01	0.22 ± 0.01	0.27 ± 0.02	**0.27** ± **0.02**	0.20 ± 0.01
h^2_m		0.19 ± 0.006		0.28 ± 0.01	**0.12** ± **0.01**	0.07 ± 0.007
c^2			0.18 ± 0.005		**0.13** ± **0.007**	0.12 ± 0.007
T^2	0.37	0.28	0.22	0.22	**0.20**	0.23
Log L	-9414.81	-8693.60	-8602.27	1364.27	**-8475.64**	-8518.87

See Tables 3.2 and 3.3 for abbreviations

3.3.1.3 Yearling weight

Estimates of (co)variance components along with genetic parameters for YWT using six different models are presented in Table 3.6. Similar to BWT and WWT, Model 5a proved to be the best model for evaluating YWT. Contrary to WWT, estimates of maternal heritability were much smaller than direct heritabilities for models that ignored the permanent maternal environmental effects, indicating a reduced influence of these effects at this age.

Direct heritability estimates ranged from 0.22 ± 0.02 to 0.34 ± 0.02 across models. Model 5a (best) produced a moderate direct heritability estimate of 0.24 ± 0.03 which is higher than the estimates reported by Groeneveld *et al*. (1998) 0.17 and Pico *et al*. (2004) 0.13. This estimate is equal to, and comparable to estimates reported elsewhere in the literature: 0.24 (Martínez *et al.,* 2010) and 0.26 (Corbet *et al*., 2006). Higher h_d^2 estimates of 0.31 (Boligon *et al*., 2009); 0.34 (Araujo *et al*., 2014) up to 0.49 (MacNeil, 2003) have been observed elsewhere in recent years. Nonetheless, the moderate h_d^2 estimates observed in this study demonstrate that a considerable part of the total variability for YWT is due to additive genetic action.

The correlation between direct- and maternal genetic effects was -0.22 ± 0.09. This estimate is slightly better than that of -0.46 (Beffa *et al*., 2009) and. -0.41 (Groeneveld *et al*., 1998) as observed for Afrikaner cattle. Larger negative estimates of -0.86 for Nellore cattle (Martínez *et al.,* 2010) have been reported in the literature. In contrast, some authors (Meyer, 1992; Corbet *et al*., 2006) found positive estimates of the correlation between direct- and maternal genetic effects for YWT. For this population, the least negative estimates of direct- and maternal genetic correlations are evident at yearling age.

A maternal heritability estimate of 0.10 ± 0.02 was observed for YWT. Comparable YWT maternal heritability estimates of 0.11 (Meyer, 1992) and 0.10 (Chin-Colli *et al*., 2016) have been reported for Hereford and Brown Swiss cattle, respectively. In contrast, lower estimates ranging from 0.04 to 0.08 (Meyer, 1992; Pico *et al*., 2004; Groeneveld *et al*., 1998 and Corbet *et al*., 2006) and higher estimates ranging from 0.15 to 0.22 (Martínez *et al.*, 2010; Beffa *et al*., 2009 and Wasike 2006) have been reported in the literature. According to Eler *et al*. (1995), the time between weaning and yearling is not enough to clear up maternal effects on growth. This could therefore explain the observed closeness of maternal heritability for YWT (0.10) to that of WWT (0.12) in this population. The existence of maternal genetic influence on YWT indicate that this source of variation has a noteworthy contribution to the observed phenotypic variance among animals and should therefore not be ignored in models designed to estimate breeding values for this trait.

The proportional permanent maternal environmental effect was 0.04 ± 0.01, and was comparable to the estimate of 0.04 by Wasike (2006) for Boran cattle. Similarly, several studies (Meyer, 1992; Pico *et al*., 2004; Corbet *et al*., 2006) observed comparable c^2 estimates ranging from 0.03 to 0.05. In contrast, higher estimates of 0.16 (Plasse *et al*., 2002) and 0.25 (Beffa *et al*., 2009) have been reported in the literature. Nonetheless, YWT c^2 estimates found in this study are generally within expected range of literature values for beef cattle. This result implies that for YWT, the contributions of permanent maternal environmental effects are least important.

Total heritability estimates for YWT were closely comparable to the direct additive heritabilities across all models. However, fitting maternal effects when the direct- and maternal covariance was ignored (models 2a and 6a) slightly overestimated T^2 in comparison to direct additive heritabilities. This result demonstrates the disadvantage of ignoring maternal effects and their covariance with respect to T^2.

Table 3.6. (Co)variance components and genetic parameters with their respective standard errors for YWT, and with the "best" model in bold

Parameter estimates	Model 1a	Model 2a	Model 3a	Model 4a	**Model 5a**	Model 6a
σ^2_a	228.18 ± 14.27	144.80 ± 14.10	171.22 ± 14.08	161.08 ± 17.60	**162.66 ± 17.66**	146.33 ± 14.11
σ^2_m		72.13 ± 7.46		90.48 ± 11.84	**65.13 ± 13.03**	49.78 ± 9.52
σ_{am}				-24.95 ± 2.07	**-22.88 ± 2.00**	
σ^2_c			63.95 ± 6.91		**28.01 ± 9.07**	27.44 ± 8.88
σ^2_e	452.59 ± 11.01	455.07 ± 10.13	435.17 ± 10.53	446.21 ± 11.64	**437.70 ± 11.97**	446.30 ± 10.55
σ^2_p	680.77 ± 8.03	672.00 ± 7.76	670.34 ± 7.76	672.81 ± 7.85	**670.63 ± 7.82**	669.84 ± 7.72
r_{am}				-0.21 ± 0.08	**-0.22 ± 0.09**	
h^2_a	0.34 ± 0.02	0.22 ± 0.02	0.26 ± 0.02	0.24 ± 0.02	**0.24 ± 0.03**	0.22 ± 0.02
h^2_m		0.11 ± 0.01		0.13 ± 0.02	**0.10 ± 0.02**	0.07 ± 0.01
c^2			0.10 ± 0.01		**0.04 ± 0.01**	0.04 ± 0.01
T^2	0.34	0.27	0.26	0.25	**0.24**	0.26
Log L	-3630.94	-3569.30	-3583.26	-3567.24	**-3562.70**	-3564.70

See Tables 3.2 and 3.3 for abbreviations

3.3.1.4 Eighteen months' weight

Estimates of (co)variance and genetic parameters for EWT using six models are presented in Table 3.7. For EWT in this study, Model 4a described the data better, with less parameters. The direct additive genetic variance remained similar and stable irrespective of the inclusion or exclusion of the permanent maternal environmental effect as long as the direct–maternal genetic covariance was fitted.

Direct heritability estimates ranged from 0.31 ± 0.02 to 0.37 ± 0.02 across models. Model 4a (best) produced a moderate direct heritability estimate of 0.35 ± 0.03 which is higher than the estimates of 0.17 as reported by Groeneveld *et al*. (1998) and 0.20 as reported by Beffa *et al*., (2009). The estimate observed in this study is comparable to estimate of 0.31 as observed by Raphaka (2008) for Tswana cattle in Botswana. On the other hand, Corbet *et al*. (2006) reported a higher estimate of 0.42 for South African Bonsmara and Belmont Red cattle. The EWT h_d^2 estimate of 0.35 in this population is in the higher range of literature estimates that vary from 0.13 (Plasse *et al*., 2002) to 0.42 (Corbet *et al*., 2006). The moderately high h_d^2 estimates observed in this study indicate sufficient direct genetic variation for EWT in the Afrikaner cattle population.

The observed maternal heritability estimate in this study was 0.08 ± 0.02. Plasse *et al*. (2002) reported a similar estimate of 0.08 for Brahman cattle in Venezuela. However, lower estimates of 0.03 (Groeneveld *et al*., 1998; Pico *et al*., 2004) were also observed elsewhere for beef cattle. Similarly, higher estimates ranging from 0.11 to 0.16 have been reported for beef cattle (Beffa *et al*., 2009; Corbet *et al*., 2006 and Diop & Van Vleck, 1998). In general, the maternal heritability estimates for EWT are within the parameter range described in the literature, which vary from 0.03 (Groeneveld *et al*., 1998; Pico *et al*., 2004) to 0.16 (Diop & Van Vleck, 1998).

Compared to pre-weaning weights in beef cattle, estimates of (co)variance and genetic parameters for EWT or the so-called Final Weight are not commonly estimated. EWT is generally measured approximately 11 months after the individual calf has been weaned from its dam. This means therefore that for EWT, the animal would have been isolated from any maternal environmental influence for about 11 months at the time of observation. Maternal effects are however astonishingly found to persist up to the age of 18 months. This is rather surprising, as maternal effects are expected to fade out because the individual animal is independent of its dam. The presence of maternal effects at this age represents at least 8% of the variation due to maternal genetic effects and should be considered in the genetic evaluation of this population. At this age the maternal genetic effects are independent of additive genetic effects, but prove to have noteworthy existence for consideration.

Total heritability estimates were relatively close across models and ranged from 0.32 to 0.37. The computational formula for T^2 makes this estimate relatively sensitive to the magnitude of the direct- and maternal covariance. For instance, the least negative direct- and maternal covariance in this study (YWT) produced T^2 estimates that were equivalent to h_d^2 estimates. Similarly, the inverse was noticeable with (BWT) where the largest variation between T^2 and h_d^2 was evident as a result of the large negative magnitude of the direct- and maternal covariance for that trait.

In general, models ignoring maternal genetic effects consistently yielded higher heritability estimates, implying that some of the variance due to maternal genetic effects will be mistakenly assigned to additive genetic variance.

Table 3.7. (Co)variance components and genetic parameters with their respective standard errors for EWT, and with the "best" model in bold

Parameter estimates	Model 1a	Model 2a	Model 3a	**Model 4a**	Model 5a	Model 6a
σ_a^2	310.96 ± 17.48	260.36 ± 18.89	283.21 ± 18.03	**293.03 ± 25.31**	293.94 ± 25.32	260.75 ± 18.83
σ_m^2		45.45 ± 8.45		**71.47 ± 13.38**	60.22 ± 14.76	36.55 ± 10.38
σ_{am}				**-38.30 ± 2.58**	-37.32 ± 2.57	
σ_c^2			36.11 ± 8.10)		13.32 ± 10.40	12.38 ± 10.07
σ_e^2	532.59 ± 13.20	532.38 ± 12.85	519.09 ± 13.32	**514.52 ± 15.63**	509.73 ± 16.22	527.71 ± 13.53
σ_p^2	843.55 ± 9.72	838.19 ± 9.60	838.41 ± 9.64	**840.72 ± 9.87**	839.89 ± 9.86	837.38 ± 9.60
r_{am}				**-0.26 ± 0.08**	-0.28 ± 0.08	
h_a^2	0.37 ± 0.02	0.31 ± 0.02	0.34 ± 0.02	**0.35 ± 0.03**	0.35 ± 0.03	0.31 ± 0.02
h_m^2		0.05 ± 0.01		**0.08 ± 0.02**	0.07 ± 0.02	0.04 ± 0.01
c^2			0.04 ± 0.01		0.02 ± 0.01	0.01 ± 0.01
T^2	0.37	0.34	0.34	**0.32**	0.32	0.33
Log L	-956.822	-940.334	-946.948	**-937.314**	-936.584	-939.646

See Table 3.2 and 3.3 for abbreviations

3.3.2 Genetic and phenotypic correlations among weight traits

The estimates of genetic and phenotypic correlations between the traits studied, and their respective standard errors are presented in Table 3.8.

Table 3.8. Estimates of genetic correlations (above diagonal) and phenotypic correlations (below diagonal) with their respective standard errors for growth traits studied among Afrikaner cattle using a bivariate model

Traits[1]	BWT	WWT	YWT	EWT
BWT	–	0.30 ± 0.037	0.27 ± 0.051	0.35 ± 0.047
WWT	0.17 ± 0.008	–	0.89 ± 0.014	0.85 ± 0.016
YWT	0.14 ± 0.012	0.66 ± 0.004	–	0.88 ± 0.016
EWT	0.14 ± 0.013	0.59 ± 0.0050	0.74 ± 0.004	–

[1] BWT = Birth weight; WWT = Weaning weight; YWT = Yearling weight; EWT = Eighteen months' weight

Genetic correlation between traits is a measure of the association between breeding values of the one trait and that of the other trait. In this study, genetic correlations between BWT and weights at other ages were of low magnitude, ranging from 0.27 to 0.35, indicating a weak genetic relationship between BWT and weights at other ages. These genetic correlation values are in close agreement with those obtained by Araujo *et al*. (2014) for Nellore cattle, ranging from 0.22 to 0.34. Slightly higher (ranging from 0.33 to 0.41) but comparable estimates of genetic correlations between BWT and weights at other ages were reported by Van Niekerk and Neser (2006) for Limousin cattle. In contrast, much higher estimates of genetic correlations between BWT and the weights at other ages were reported by Neser *et al.* (2012) for South African Brangus cattle (ranging from 0.57 to 0.78) and by Boligon *et al*. (2009) for Nellore cattle in Brazil (ranging from 0.61 to 0.81). In this study, the observed correlation between BWT and weights at other ages was not too strong. This result suggests that, selection for weights at later ages might not result in a correlated response in BWT as the low positive correlation between BWT and weights at other ages suggests.

Phenotypic correlation is a measure of the strength of the association between performance in one trait and that of the other trait (Bourdon, 2000). In this study, phenotypic correlations between BWT and weights at other ages were of low magnitude, ranging between 0.14 and 0.17, indicating a weak observable relationship between BWT and weights at other ages in the growth trajectory of Afrikaner cattle. Comparable phenotypic correlation estimates of 0.08; 0.14 and 0.016 (BWT – WWT, YWT and EWT) were observed by Van Niekerk and Neser (2006) for Limousin cattle. Studying correlations between weights from birth to maturity in Nellore cattle, Boligon *et al*. (2009) found much higher phenotypic correlations ranging from 0.27 to 0.41.

The genetic correlation estimate between WWT and YWT was quite large (0.89 ± 0.014), indicating that genetically heavier animals at weaning responded with greater weights at yearling. Corresponding genetic correlation estimates of 0.86 ± 0.052 and 0.88 ± 0.04 were reported by Neser *et al.* (2012) for Brangus cattle and by Pico (2004) for Brahman cattle in South Africa, respectively. The current result is slightly higher than the mean genetic correlation of 0.81 reported for these traits in the review of literature by Koots *et al*. (1994b). Higher genetic correlation estimates of 0.99 ± 0.03 were observed by Van Niekerk and Neser (2006).

The phenotypic correlation between WWT and YWT was moderately strong (0.66 ± 0.004) and higher than the estimates of 0.57 ± 0.005 as reported by Pico (2004) for Brahman cattle. This result indicates that animals with heavier observable weight at weaning will tend to have heavier weights at yearling age, and this can be observed with a moderate consistency.

The genetic correlation estimate between WWT and EWT was large and positive (0.85 ± 0.016), indicating that genetically heavier animals at weaning responded with greater weights at eighteen months of age. Higher genetic correlation estimates of 0.91 ± 0.04 and 0.99 ± 0.043 were reported by Pico (2004) for Brahman cattle and by Neser *et al.* (2012) for Brangus cattle in South Africa, respectively.

The phenotypic correlation between WWT and EWT was 0.59 ± 0.005. Higher phenotypic correlation estimates of 0.64 and 0.699 were reported by Plasse *et al*. (2002) for Brahman cattle in Venezuela and by Meyer *et al*. (1993) for the Australian Wokalup cattle, respectively.

The genetic correlation estimate between YWT and EWT was also large (0.88 ± 0.016), and slightly higher than the estimate of 0.83 obtained by Pico (2004) for Brahman cattle. Corresponding estimates of 0.85 ± 0.048 and 0.92 ± 0.040 were respectively reported by Neser *et al.* (2012) and Van Niekerk and Neser (2006). Higher estimates of 1.0 were observed by Meyer *et al*. (1993) for both the Australian Hereford and Wokalup cattle, respectively.

The phenotypic correlation between YWT and EWT was 0.74 ± 0.005. Studying genetic parameters for growth traits of Australian beef cattle, Meyer *et al*. (1993) reported a similar phenotypic correlation estimate of 0.74 for Wokalup cattle and a comparable estimate of 0.72 for Hereford cattle. The correlation values found in this study indicate a strong positive relationship between YWT and EWT, and this finding is consistent with the report by Van Niekerk and Neser (2006).

In general, strong positive genetic correlations between any two weight traits in this study means that animals with a high estimated breeding value for one trait would also have high estimated breeding value for the other correlated trait. This implies that animals with low breeding values for one trait would also have low estimated breeding value for the other correlated trait. In other words, direct selection to improve one growth trait would result in a correlated selection response on the other trait. According to Bourdon (2000), genetic correlation between traits emanate from two genetic mechanisms: 1) Linkage – that is when the genes influencing the two traits are located in close proximity on a chromosome and are therefore inherited together causing a short-term correlation between traits until the linkage breaks by meiotic crossover. 2) From pleiotropic influences – that is the same set of genes influencing or affecting more than one trait, and causing long term genetic correlation between the affected traits. For the studied traits in this population, given the depth of the pedigree data, the observed correlations can confidently be expected to be due to pleiotropic influences.

3.4 Conclusions

Excluding the maternal genetic effect from the analysis model, particularly for maternally influenced early growth traits, exaggerated estimates of genetic variance upwards. This exclusion resulted in some loss of genetic variance since not all of it was taken up by direct additive genetic variance. This indicates the extent to which estimates of h_a^2 can be biased if maternal effects, either genetic or environmental, are ignored. Maternal additive variance and the corresponding heritability estimates were lowest at birth. The highest maternal heritability estimate was obtained for weaning weight. Similarly, the contribution of permanent maternal environmental variance to the phenotypic variation was large at weaning.

The covariances between direct- and maternal additive genetic effects for weights at birth to 18 months of age were intermediate and negative for all the traits analysed. Consequently, direct- and maternal genetic correlations were negative for all growth traits. However, fitting of the S-MGS models successfully moderated the genetic covariance between direct- and maternal additive genetic effects.

The estimates of direct and maternal heritability in this study indicate that the genotype of the calf was more important than the genotype of the dam in determining the weight of the calf at all ages using the either the animal or S-MGS model. However, estimates from both the animal and S-MGS models indicate that the maternal effects on early growth traits are also important contributors to the phenotypic variance. Therefore, ignoring maternal effects for early growth traits will inflate or bias direct additive genetic variance and the corresponding heritability estimates. As noted in other studies as well, direct heritability estimates increased with age and the highest estimate was recorded for 18 months' weight. The implication of this is that, should farmers decide to practice mass selection based on animal performance within a herd, use of later age weights is more reliable than weights at early ages.

Estimates of direct genetic and phenotypic correlations between BWT and weights at later ages were all favourable and below 35%, and suggests a possibility of increasing weights at later ages without adverse effects on birth weight. Estimates of direct genetic correlations between and among weights at weaning and subsequent ages were all above 85% and close to unity. The implication of this is that WWT could be used as a reliable indicator trait for weights at later ages.

The strong genetic correlations estimated in this study are consistently associated with the period from weaning to later ages, and indicates that the genes responsible for greater weights at these ages are most probably the same. Consequently, if care is not taken through manipulation of selection intensities for male and female breeding animals, the strong positive correlations poses a potential risk of correlated increases in mature weight of breeding females and subsequently increases in maintenance requirements that could decrease production efficiency. On the other hand, for traits with genetic correlations closer to unity as observed in this study, performance measurement of similarly influenced traits might not be necessary if the desired direction of genetic change is similar for both traits.

CHAPTER 4

VARIANCE COMPONENTS AND GENETIC PARAMETERS FOR REPRODUCTIVE TRAITS IN AFRIKANER CATTLE

4.1 Introduction

Variance components can change as the trait changes over the lifetime of an animal or over time within a population as allele frequencies change as a result of influences such as inbreeding, selection, migration and mutation (Berry *et al*., 2014). It is therefore imperative to conduct periodic estimation of variance components and genetic parameters for traits of economic importance. Reproductive traits are however generally considered lowly heritable (Minick Bormann and Wilson, 2010), resulting in little emphasis on them in genetic improvement programs. Nonetheless, knowledge of direct and/or associative genetic parameters for reproductive traits remains an important component in evaluating the potential for genetic improvement of reproductive performance of beef cattle. In support, Lôbo *et al*. (2011) noted that genetic evaluation programs have significantly increased the productivity of animals and the quality as well as yield of beef products throughout the world. However, little or no emphasis has been given to improving reproductive traits.

Fertility is among the most difficult physiological events to define because of the intricacies of reproduction, yet it remains an important factor influencing beef cow herd profitability (Cammack *et al.*, 2009). Excellent reproductive performance is of critical importance to profitable beef production systems (Berry and Evans, 2014). This is more so for breed types where heifers often take longer to reach puberty (Eler *et al*., 2014; Jones *et al*., 2018) and the Afrikaner cattle breed is no exception.

Studies that reported on genetic parameters for reproductive traits in Afrikaner cattle in recent years are rather scanty (see Rust & Groeneveld, 2001; Rust & Groeneveld, 2002; Rust *et al.*, 2009). There is therefore, a need for recent information on the genetic parameters for reproductive traits as well as their correlation with other easily measurable production traits in the Afrikaner cattle breed.

In this chapter, the objective of the study was to estimate (co)variance components and genetic parameters for selected reproductive and productive traits in Afrikaner cattle.

Genetic and phenotypic correlations between reproductive as well as lifetime production traits were also estimated.

4.2 Materials and methods

Data description and trait definition

The source and origin of data is described under Chapter 3. For reproductive traits, the used pedigree information consisted of 56 980 individual identities from pedigree data that were nine generations deep. These individuals were progeny of 3 513 sires, 25 501 dams, 2 425 sires of dam and 11 289 dams of dam. The number of records remaining, and included in the analysis of each of the fertility traits are presented in Table 4.1.

Table 4.1. Summary statistics for the reproductive traits analysed

Trait	n	min	mean	max	SD	CV %
AFC	45819	24	41.6	72.0	9.6	23.2
CI	21695	365	531.648	1439.5	123.0	23.1
ACP	15157	1.68	80.0	293.0	43.9	54.9

AFC = Age at first calving; CI = Calving Interval; ACP = Accumulated Productivity; Min = Minimum; Max = Maximum, SD = Standard deviation; CV % = coefficient of variation

The traits included in this study were age at first calving in months (AFC), calving interval (CI) in days, average calving interval (ACI) in days, and accumulated productivity (ACP) in kilograms.

For this study, AFC was defined as the number of months from birth to first calving, and only age at first calving records between 24 and 72 months were considered. Calving interval was defined as the difference in days, between two consecutive calving events within the same dam and only calving interval records between 365 and 1460d were retained. Subsequently, average CI was computed as the mean value of all parities of an individual dam.

On the other hand, ACP indicates the productivity of the dam, expressed in kilograms of calf weaned per year, and also approximates the reproductive precocity and periodicity of these same dams, as well as their maternal abilities to wean heavier calves (Grossi *et al.*, 2008; Carvalho & Bittencourt, 2015). The ACP is directly dependant on the age at first calving, the calving intervals, as well as the average body mass of the progenies weaned in the dam's life time (Lôbo *et al*., 2011). As a result, ACP was calculated as an index using the following equation (Lôbo *et al*., 2000):

$$\mathrm{ACP} = \frac{W_p \times n_p \times 365}{\mathrm{ADC}_n - 550}$$

where $\mathbf{W_p}$ is the average weaning weight of all progeny adjusted to 205 days of age, $\mathbf{n_p}$ is the total number of calves produced per dam, **365** is a constant equal to 365d as a production basis that allows fertility to be expressed on an annual basis. $\mathbf{ADC_n}$ is the dam's age at last calving, and **550** refers to the minimum age in days possible for beef cattle at first breeding when considering a minimum age at first calving of 30 months (Lôbo et al., 2000).

Statistical Analysis

Age at first calving and accumulated productivity were estimated using a basic animal model with only additive animal genetic effect as random, CI was estimated by using a repeatability model, where animal genetic and permanent environmental effects were fitted as random (Table 4.2). Furthermore, CI was analysed in two ways, first as a repeated trait considering individual parities and secondly, using the mean value of all parities of the same dam to compute an average calving interval.

Accumulated productivity (ACP) was calculated in an attempt to account for the total kilograms of live weight produced per dam per year over the dams' lifetime.

Table 4.2. Summary of fixed and random effects that were fitted for the different reproductive traits

Effects	AFC	CI	ACI	ACP
Fixed				
Parity		✓		
Birth year	✓			
Birth Season	✓			
Calving Year		✓		
Calving Season		✓		
Herd	✓	✓	✓	✓
Random				
Animal	✓	✓	✓	✓
Permanent Environment		✓		

AFC = Age at first calving; CI = Calving Interval; ACI = Average calving interval; ACP = Accumulated Productivity

To determine which fixed effects should be included in the model, a preliminary analysis was carried out using the general linear model (GLM) procedure of SAS (2010). Significant (*P* <0.05) fixed effects that were subsequently incorporated into the final model for genetic analysis are presented in Table 4.2 for each trait studied.

Subsequently, contemporary groups were defined separately for each trait based on the results of analysis performed using the GLM procedure of SAS (2010). Estimates of (co)variance components were obtained with the commonly used ASREML package (Gilmour *et al.*, 2009) using linear univariate and bivariate models.

Age at first calving, average calving interval and accumulated productivity were analysed using the animal model containing only animal additive genetic effect, while CI was analysed using repeatability model having the following structure:

$$y = Xb + Z_1a + Z_2c + e$$

in which $\boldsymbol{y}$ is the vector for phenotypic records, $\boldsymbol{b}$ is the vector of the solutions for fixed effects, $\boldsymbol{a}$ is the vector of solutions for the random additive genetic effects, $\boldsymbol{c}$ is a vector for permanent environmental effects, $\boldsymbol{e}$ is the vector for the random residuals, $\boldsymbol{X}$ is the incidence matrix relating records to fixed effects, and $\boldsymbol{Z_1}$ and $\boldsymbol{Z_2}$ are the incidence matrices relating performance records to random effects of $\boldsymbol{a}$ and $\boldsymbol{c}$, respectively.

4.3 Results and discussion

General

The overall least square means, and standard deviations (with coefficients of variation) of traits evaluated in this study, in relation to the reproductive performance of the animals, are presented in Table 4.1. Similarly, components of additive genetic variance (σ^2_a), environmental variance (σ^2_e), permanent environmental variance (σ^2_{pe}), phenotypic variance (σ^2_p) and heritability estimates (h^2) for AFC, CI and ACP for Afrikaner cattle are shown in Table 4.3.

The least square mean for age at first calving was 41.6 months. This result is comparable to the AFC value of 41.5 months reported for Drakensberger cattle (Rust, 2007) and 41.8 months for Boran cattle (Haile-Mariam & Kassa-Mersha, 1994). The observed mean AFC in this study corresponds to the minimum production requirement (on or before 42 months) as set out by the Afrikaner Cattle Breeders' Society of South Africa (ACBS, 2018). The observed AFC mean in this study is considered an improvement to the mean of 42.6 months that was reported by Rust (2007) for the same breed.

For calving interval, the least square mean observed was 531.648 days. The present study result is considered inferior to the report (442 days) of Haile-Mariam & Kassa-Mersha (1994) for naturally bred Boran cattle. This estimate is however within the approximated calving interval for tropically raised zebu type cattle, ranging from 12.2 to 26.6 months (Mukasa-Mugerwa, 1989). In addition, the observed mean corresponds to the average production requirement for calving interval (<660 d) as set out by the Afrikaner Cattle Breeders' Society of South Africa (ACBS, 2018).

In general, for all reproductive traits, a large portion of the phenotypic variance was accounted for by environmental variance. Consequently, additive genetic variance accounted for the least variation particularly for AFC and CI, resulting in low heritability estimates for these traits.

Heritability estimates for the reproductive traits were of low magnitude for both the AFC 0.093 ± 0.01 as well as the CI 0.096 ± 0.03. This could be attributable to the high phenotypic variances arising from high environmental influences on these traits. The AFC estimate obtained in this study is in agreement to the estimate of 0.09 by Bernardes *et al.* (2015) for Tabapuã cattle. This result is comparable to the estimates of 0.10 by Cavani *et al.* (2015) for Brahman cattle and 0.11 by Lôbo *et al*. (2011) for Nellore cattle. In contrast, higher AFC heritability estimates ranging from 0.13 for Mpwapwa cattle (Chawala *et al*., 2017) up to 0.40 for crossbred beef cattle (Van der Westhuizen *et al.*, 2001, Martinez-Velazquez *et al*., 2003) have also been reported in the literature.

For CI, the estimate of 0.096 ± 0.03 as observed in this study is in agreement to the estimates of 0.09 and 0.10 by Santana *et al*. (2015) for Nellore cattle and Chawala *et al*. (2017) for Mpwapwa cattle, respectively. Rizzo *et al*. (2015) found a comparable estimate of 0.11 for Nellore cattle. In contrast, lower estimates ranging from 0.01 for South African and Irish crossbred cattle (Van der Westhuizen *et al.*, 2001 and Berry and Evans, 2014) respectively, to 0.08 for Tabapuã cattle in Brazil (Bernardes *et al.,* 2015) have also been reported in the literature. The current results are however within range of heritability estimates for beef cattle calving intervals ranging from 0.01 (Van der Westhuizen *et al*., 2001) to 0.125 (Gutierrez *et al*., 2002). The low heritability estimate observed here suggests that direct selection for calving interval may not yield the desired response for improving female reproduction in Afrikaner cattle.

The heritability estimate for ACP was of moderate magnitude 0.39 ± 0.02. The magnitude of the estimated heritability for ACP in this study is higher than those reported by several authors (ranging between 011 and 0.24) (Schwengber *et al*., 2001; Grossi *et al*., 2008; Duitama *et al*., 2013; Chud *et al*., 2014; Bernardes *et al*., 2015; Grossi *et al*., 2016; Schmidt *et al*., 2017). This result indicates the existence of sufficient additive genetic variability for ACP, suggesting that ACP could therefore, respond favourably to selection for genetic improvement when included in a selection program for the Afrikaner cattle breed. In support, several studies (Schwengber *et al*., 2001; Grossi *et al*., 2008; Chud *et al*., 2014; Bernardes *et al*., 2015; Grossi *et al*., 2016) concluded that the use of ACP in selection programs could be advantageous when used as a substitute for reproductive traits with low heritability.

Table 4.3. Components of additive genetic variance (σ_a^2), environmental variance (σ_e^2), permanent environmental variance (σ_{pe}^2), phenotypic variance (σ_p^2), and heritability estimates (h^2) with their respective standard errors for reproductive traits of Afrikaner cattle

Traits	AFC	CI	ACP
Parameters			
σ_a^2	4.29 ± 0.47	3068.9 ± 100.8	443 ± 22
σ_e^2	41.85 ± 0.49	28974.4 ± 143.4	683 ± 18
σ_{pe}^2	-	0.011 ± 0.0	-
σ_p^2	46.13 ± 0.33	32043 ± 147.5	1126 ± 14
h^2	0.093 ± 0.01	0.096 ± 0.03	0.39 ± 0.02

AFC = Age at first calving; CI = Calving Interval; ACP = Accumulated Productivity

The observed low heritability estimates for AFC and CI in this study are consistent with several other published reports on these traits in beef cattle. The current results indicate that, for the Afrikaner cattle population, only a small percentage of the phenotypic variance of these traits may be explained by genetic variance. Based on this fact and considering the same generation interval, selection based on these traits will yield low genetic gains in Afrikaner cattle. Therefore, selection of female breeding stock will be difficult in that many other variables influence the ability of the animal to conceive and to be productive over her lifetime. Even though heritability estimates for reproductive traits were low, their consideration in multitrait selection is still important and necessary for improving overall reproduction and profitability. This is so because the prediction equations from multi-trait selection benefit from phenotypic and genetic correlations among traits.

Correlations are measures of the strength of the relationship between two variables, with high correlation values implying a strong relationship between variables and vice versa (Bourdon, 2000). The genetic correlation between AFC and CI (Table 4.4) was positive and low 0.079 ± 0.059, indicating a positive but low genetic association between the two traits. This result is within range of reported genetic associations between AFC and CI ranging from 0.0 (Chawala *et al*., 2017) to 0.70 ± 0.34 (Bernardes *et al*., 2015) for different tropically adapted beef breeds. Despite being low, the positive genetic association between AFC and CI is suggestive of existence of genes in common that influences both traits.

Table 4.4. Estimates of genetic correlations (above diagonal) and phenotypic correlations (below diagonal) with their respective standard errors for reproductive and lifetime production traits of Afrikaner cattle using a bivariate model

Traits[1]	AFC	CI	ACP
AFC	-	0.079 ± 0.059	-0.409 ± 0.055
CI	-0.040 ± 0.008	-	-0.5242 ± 0.0313
ACP	-0.176 ± 0.009	-0.370 ± 0.008	-

[1] AFC = Age at first calving; CI = Calving Interval; ACP = Accumulated Productivity

The estimates of genetic correlations between ACP and other reproductive traits (AFC, CI) were moderate and negative (Table 4.4). The current results are within range of reported genetic associations between ACP and AFC ranging from -0.33 ± 0.04 (Grossi *et al*., 2008) to -0.76 ± 0.04 (Duitama *et al*., 2013) for tropically adapted beef breeds. Correlations aid in the prediction of response to selection in one trait due to selection in another. As noted by Grossi *et al*. (2015), the negative genetic correlation between ACP and CI in this study indicate that cows with lower CI are producing more kilogram of calf weaned per year, and could therefore yield favourable improvement in overall cow productivity. In agreement, Bernardes *et al*. (2015) postulated that, when the ACP presents a higher heritability estimate than CI as observed in this study (Table 4.3), and a negative genetic correlation with CI as presented in Table 4.4, the use of ACP in the selection criteria could assist in attaining improved reproductive precocity.

In the current study, the coefficients of phenotypic correlations arose from the net cumulative correlations of genetic and environmental effects of the traits involved. The estimates of phenotypic correlations between reproductive traits were negative and ranged from weak to moderate.

4.4 Conclusions

The estimates of (co)variance components for reproductive traits were low and followed the general pattern observed in many other previous studies in beef cattle. On the other hand, the ACP index which combines both reproductive and productive performance, indicates the existence of genetic variability as demonstrated by a moderate heritability estimate. This implies that genetic improvement could be achieved by considering ACP in the selection criteria for Afrikaner cattle breeding programmes. Furthermore, the negative genetic correlations between ACP and CI in this study indicate that cows with lower CI are producing more kilogram of calf weaned per year, and could therefore yield favourable improvement in overall cow productivity.

CHAPTER 5

GENERAL CONCLUSIONS AND RECOMMENDATIONS

Performance evaluation for genetic improvement is breed specific and requires knowledge of relevant genetic parameters estimates for economically important traits. These genetic parameter estimates are needed for accurate and unbiased prediction of breeding values as well as direct and correlated selection responses. The resultant outcomes of such predictions are then utilised in: designing breeding objectives; implementation of breeding programmes; evaluation of progress made regarding genetic improvement as well as for developing appropriate selection criteria. In line with the above, the objective of this study was to estimate genetic parameters for growth and reproductive traits using different genetic models after accounting for known systematic non-genetic effects. Analyses were performed using these models, with every effort to ensure that the models accurately describe the data.

For growth traits, the estimates of direct and maternal heritability in this study revealed that the genotype of the calf was more important than the genotype of the dam in determining the weight of the calf at all ages irrespective of the model used. As noted in other studies as well, direct heritability estimates increased with age and the highest estimate was recorded for 18 months' weight. The implication of this is that, should farmers decide to practice mass selection based on animal performance within a herd, use of later age weights is more reliable than weights at early ages.

The results further revealed that, excluding maternal genetic effects from the analysis model, particularly for maternally influenced early growth traits, estimates of genetic variance were exaggerated upwards. This exclusion resulted in some loss of genetic variance since not all of the variance was absorbed by direct additive genetic variance. As a consequence, the results demonstrated that estimates of direct heritability can be biased if maternal effects, either genetic or environmental, are ignored. In addition, estimates from both the animal and S-MGS models indicate that maternal effects on early growth traits are also important contributors to the phenotypic variance.

Comparisons among results from different statistical models represent a useful measure to ascertain models' strengths and weaknesses. Compared to the animal model, the S-MGS model accounted for more additive genetic variance particularly for maternal effects, resulting in improved maternal heritability. Furthermore, the covariances between direct- and maternal additive genetic effects for weights at birth to 18 months of age were intermediately negative for all the traits analysed using the AM. However, estimating maternal effects through the sire-maternal grandsire model successfully moderated the genetic covariance between direct- and maternal additive genetic effects. Finally, the consequential improvement on direct- and maternal genetic correlation thus suggests that, maternal effects could probably be statistically confounded with maternal inheritance and not entirely biological.

In general, considering that the estimates of direct genetic correlations between and among weights at ages later than weaning were positive and strong, care should be taken through manipulation of selection intensities for male and female breeding animals to avoid the potential risk of correlated increases in mature weight of breeding females. This will also assist in averting the possible increase in maintenance requirements that could decrease production efficiency.

Reproductive performance is a complex trait with many components. In general, for all reproductive traits, a large portion of the phenotypic variance was accounted for by environmental variance. For AFC and CI, heritability estimates were low and resembled the general pattern observed in many other studies on beef cattle. For these traits, only a small percentage of the phenotypic variance could be explained by genetic variance. Based on this fact and considering the same generation interval, selection based on these traits will yield low genetic gains in Afrikaner cattle. Despite low heritabilities, the observed positive genetic association between AFC and CI is still suggestive of existence of genes in common that influence both traits. Therefore, their consideration in multitrait selection is still important and necessary for improving overall profitability. On the other hand, the ACP index produced a larger heritability estimate, explaining up to 39% of phenotypic variance due to genetic variability of this trait in Afrikaner cattle. Therefore, genetic improvement could be achieved by considering ACP in the selection criteria for Afrikaner cattle breeding programmes.

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