EVALUATION OF GENETIC RELATIONSHIP BETWEEN MILK YIELD AND WEANING WEIGHT IN NGUNI CATTLE

BY

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DECLARATION

I declare that the mini-dissertation hereby submitted to the University of Limpopo, for the degree of Master of Science in Agriculture (Animal Production) has not previously been submitted by me for a degree at this or any other university; that it is my work in design and in execution, and that all material contained herein has been duly acknowledged.

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Lucky Tendani Nesengani 05/05/2014

Abstract

Weaning weight and milk production are traits of economic importance in beef production and knowledge of their genetic relationship is of importance for genetic improvement. While indigenous cattle constitute a big percentage of the beef cattle population in South Africa, limited research has been done to investigate the genetic relationship between milk production and weaning weight in this type of cattle. The objective of this study was to estimate the genetic relationship between weaning weight and milk yield in Nguni cattle. Milk yield data (n = 125) were collected from 116 Nguni cows using the weigh-suckle-weigh technique from Mara Research Station located in Limpopo Province and Loskop South Farm located in Mpumalanga Province. Weaning weight data (n = 19,065) were obtained from stud Nguni cattle from 146 herds distributed throughout South Africa. Milk yield data was collected on average once per month from birth to weaning at about seven months. Editing of the data to remove observations beyond 3 standard deviations was conducted using Statistical Analysis Software. Estimates of (co)variance components for milk yield and weaning weight were calculated using PEST and VCE software. The average weaning weight, age of the calf at weaning and 24-h milk yield was 158.94 kg, 210 days and 5.25 kg/day respectively. Phenotypic variance for weaning weight and milk yield were 284.80 kg^2 and 2.33 kg^2 respectively. The phenotypic correlation between weaning weight and milk yield was 0.47 ± 0.025. Estimates of heritabilities from univariate analysis for milk yield, direct and maternal weaning weight were 0.16 ± 0.299, 0.48 ± 0.038 and 0.25 ± 0.025 respectively. Estimates of heritabilities from multivariate analysis for milk yield, direct and maternal weaning weight were 0.22 ± 0.238, 0.47 ± 0.039 and 0.25 ± 0.029 respectively. Estimates of genetic correlations for milk yield and maternal weaning weight, milk yield and direct weaning weight, direct and maternal weaning weight were 0.97 ± 0.063, -0.71 ± 0.416 and -0.56 ± 0.247 respectively. The results of the current study indicate that maternal weaning weight is genetically highly predictive of milk yield in Nguni cattle. It could be concluded that selection for milk production could be successfully achieved by selecting for maternal weaning weight since measuring milk yield directly could prove to be difficult under practical production setting.

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DEDICATION

This dissertation is dedicated to my parents, Mr. M.J. Nesengani and Mrs. M.E. Nesengani; Sisters (Nancy, Phumudzo and Memorancy); my Little Brother Shumani; My Uncle Mr. M.F. Mashamba and my family at large for their support through educating me and for never giving up on me. Lastly much appreciated words of encouragement from Carnatian Mashapa.

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CHAPTER 1

INTRODUCTION

1.1 Introduction

Milk production in beef cattle is generally considered the most significant component of the maternal effect on the growth of the calf from birth to weaning (Clutter and Nielsen, 1987; Gregory *et al*., 1992). Maternal effect for weaning weight has been used as an indicator for milk yield in beef cattle due to the positive genetic correlation between the two traits (Willham, 1972; Gregory and Cundiff, 1980). Thus, weaning weight reflects the expression of the genes for both the growth of the calf and the genes for milk production of the dam of the calf (Meyer *et al.,* 1994).

Several studies conducted to investigate the genetic relationship between weaning weight and milk production considered mostly European breeds and a positive genetic correlation between the two traits was reported (Mallinckrodt *et al*., 1993; Meyer *et al.,* 1994). Such genetic information is of importance for developing breeding objectives and selection programmes aimed at improving efficiency in beef production. However, there is greater paucity in the availability of genetic information necessary for use in breeding programmes to improve indigenous cattle breeds such as the Nguni.

1.2 Problem statement

Milk yield and weaning weight are traits of economic importance in beef production. The positive genetic relationship between the two traits has been and continues to be used as the main genetic information in developing appropriate selection programmes and breeding objectives aimed at improving beef production (Vaccaro *et al.,* 1996). However, it is not known if this high genetic correlation is also applicable to the indigenous cattle breeds found in the subtropical region such as the Nguni.

1.3 Motivation of the study

The lack of information on the magnitude of the genetic correlation between weaning weight and milk production in indigenous Nguni cattle is the major hindrance towards successful genetic improvement (Vaccaro *et al.,* 1996; Norris *et al.,* 2004). Such information has been used and still is of critical importance in developing selection programs and breeding objectives for genetic improvement in beef cattle (Miller and

Wilton, 1999). There is therefore a need for determining the magnitude of the genetic correlation between weaning weight and milk production in Nguni cattle to ensure that appropriate selection and breeding programmes are designed that would enhance efficiency of production in indigenous cattle.

1.4 Objectives of the study

The objectives of this study were:

I. To estimate (co)variance components for weaning weight and milk yield in Nguni cattle.

II. To estimate the genetic correlation between weaning weight and milk yield in Nguni cattle.

CHAPTER 2

LITERATURE REVIEW

2.1 History of the Nguni cattle

The Nguni cattle have existed as long as there were people in Africa from about 8 000 years ago (Epstein, 1971; Ballard, 1986). The DNA evidence suggests that this breed descends from both *Bos Taurus* and *Bos indicus* cattle (Hanotte *et al.*, 2000). Since around 8 000 years ago, man's unquenchable appetite for more land and space for their livestock forced migration of man towards the southern part of the African continent (Schoeman, 1989). During the process of migration, the Nguni people were amongst the group of people who migrated towards the southern part of Africa from the North, Central and Eastern part during 590 and 700 AD with their then called Sanga cattle which currently are known as the Nguni cattle (Bergh and Gerhard, 1999). As the tribes settled into different areas with different agro-ecological regions, different Nguni ecotypes developed within the breed, with the six common ecotypes being the Makhathini, Venda, Pedi, Swazi, Sanga and Shangaan consisting of different colour patterns (Brown, 1959; Scholtz, 2010). These different ecotypes are still collectively called the Nguni cattle.

The Nguni breed is believed to have developed from natural selection and environmental interaction due to their ability to survive under several African harsh environments with their genetic potential to perform better in optimal production environment (Bester *et al.,* 2001; Collins-Lusweti, 2000). As a result, this indigenous breed is well-adapted to such harsh uncomfortable environment (Maree and Casey, 1993). The Nguni breed is characterised by a small body frame with the dams weighing 300 kg to 440 kg and the bulls weighing 500 kg to 650 kg. They also have a variety of colour patterns with excellent mothering ability as reported by Armstrong and Meyer (1986). The Nguni cattle also have excellent calving ability, with cows reported to have higher calving percentage (87%) compared to the Afrikaner and Bonsmara (69% and 70%) as observed by Collins-Lusweti (2000). An earlier study of Schoeman (1989) reported calving rate of 89.6% for the Nguni cattle as compared to the 77.4 % of the Drakensberger and Bonsmara. Furthermore, Schoeman (1989) observed that Nguni heifers reach puberty much earlier than Bonsmara and Drakensberger (349.9 days *vs* 419 and 407 days, respectively). This breed has been exposed to the extreme climatic and environmental conditions such as poor grazing , internal and external parasites which is believed to have been an important tool that resulted in the breed being resistant to some diseases and ticks (Schoeman, 1989). This indigenous breed is genetically adapted to harsh African environments than the European breeds requiring less input with high output (Pretorius, 2011).

In the mid-1930s indigenous cattle were regarded as inferior due to their small body frame. This perception led the then South African government to appoint officials to go around the communal areas to test bulls of the cattle belonging to communities and castrate those considered inferior (Scholtz, 2012). This act almost decimated the Nguni breed. Fortunately, some of the communal farmers decided to keep Nguni cattle despite the fact that it was classified as inferior. The villages remained the only source of the breed as it was later not available in commercial farms (Collins-Lusweti, 2000).

The interest in the Nguni breed was renewed after the demonstration of potential of the breed as a result of the introduction of beef cattle recording scheme around 1959 in South Africa (Scholtz *et al*., 2011). Data collected through the scheme led to the publication of research results on the Nguni breed during the early 1980's. The recording scheme provided information on the adaptability and ability of the Nguni to perform better in harsh environments as compared to European breeds. As a result, the breed was recognised as a source of genetic material suitable for farmers who require low input cattle with high productivity (Bester *et al*., 2001). The Nguni breed has been reported to be amongst the very fertile beef cattle breeds in South Africa and more likely to be amongst the most fertile cattle in the World (Scholtz *et al.,* 2011).

The interest in the Nguni breed started to advance during the early 1970's where the breed was only found in the remote areas where some of the Government officials didn't reach during the period they were eliminating the then said to be inferior animals (Scholtz, 2010). The interest in the breed by the commercial farmers further accelerated during the 1980's which resulted in the breed being recognised as one of the developing breed under the Livestock Improvement Act (No. 25 of 1977). Subsequently, the Nguni Cattle Breeder's Society was established in 1986. By then, there were only around 3 000 Nguni females in a few well-managed herds mainly belonging to the Government. The communal herds, on the other hand, were exposed to a threat of being crossbred to other breeds such as Bonsmara and Afrikaner (Scholtz *et al*., 2011).

The Nguni cattle breed currently has grown to be the second largest breed in the seed stock industry in South Africa with about 60 000 stud animals and approximately one million estimated Nguni animals in South Africa (Scholtz, 2010). The superior Nguni genetic material is disseminated throughout the population according to the gene flow pyramid. The seed stock (stud) produce and sell to commercial farmers, then commercial farmers sell breeding stock to the emerging farmers who then sell to subsistence or communal farmers (Scholtz *et al*., 2008).

2.2 Milk production in beef cattle

Milk production in beef cattle is important to sustain growth of the calf from birth to weaning (Beal *et al*., 1990; Theron *et al.,* 2011). Milk plays a major role in providing proper nutritional requirements for the calf. Thus, the difference in the growth of the calves from birth to weaning in different breeds is believed to be highly associated with the difference in milk production of their dams (Brown *et al*., 2010).

It is notable that milk yield differ from breed to breed. The differences in milk yield have been reported across breeds of cattle with most of the work having been done in European breeds. Melton *et al*. (1967) evaluated milk production using the weigh-suckle-weigh technique over a period of 175 days in different breeds in the United States. They reported average milk production of 3.3 kg/day, 4.5 kg/day and 3.8 kg/day in Hereford, Charolais and Angus respectively. In Venezuela, Neidhardt *et al.* (1979) reported milk yield of 4.2 kg/day obtained through a hand milking procedure and a 5.9 kg/day milk yield measured by calf nursing (i.e. weigh-suckle-weigh technique) in the Brahman cattle. Brown *et al.* (1993) measured milk production using machine milking and reported an average milk yield of 5.6 kg/day and 5.5 kg/day in Angus and Brahman cattle respectively over a period of 3 years. Mallinckrodt *et al.* (1993) reported an average daily milk yield of 5.3 kg in Polled Hereford and 7.6 kg in Simmental cattle over a 205-d period. Research conducted at the Wokalup Research Station in southwestern Australia by Meyer *et al*. (1994) reported a 14-hour milk yield of 3.6 kg in Hereford and 4.9 kg in Wokalups cattle. Recently, a study conducted in Botswana by Chabo *et al*. (2003) reported an average daily milk yield of 12.5 kg/day in Tuli breed as compared to the 9.2 kg/day in Brahman cattle.

Nguni cattle have been reported to have low milk yield ranging from 2 - 5 kg/day (Musemwa *et al.*, 2008). The report by Musemwa *et al*. (2008) is in general agreement with the study conducted by Dugmore *et al*. (2004) in Kwazulu Natal, South Africa who reported milk production in Nguni cattle of 5.0 kg/day compared to the Jersey and Jersey*Nguni F_1 cross which produced 9.0 kg/day and 4.5 kg/day respectively under hot subtropics environment.

2.3 Genetic relationship between milk production and weaning weight

Genetic relationship or correlation refers to genetic influence that is shared in common between two traits (Theron *et al*., 2011). Knowledge of genetic relationship between traits is of paramount importance for use in developing sound selection and breeding programmes (Michael, 1999).

Several studies have been conducted to estimate genetic correlation between economic traits such as maternal weaning weight and milk yield in beef cattle. Most of the studies have reported positive relationship between weaning weight and milk yield (e.g. Beal *et al*., 1990).

A study by Marston *et al*. (1992) reported a genetic correlation between maternal weaning weight and milk yield of 0.3 in Angus and 0.47 in Simmental cattle respectively using machine milking. This report is in general agreement with the study by Mallinckrodt *et al*. (1993) who reported a correlation of the same magnitude of 0.4 in both the Polled Hereford and Simmental cattle. However, Meyer *et al*. (1994) conducted a study at Wokalup research station in the Southwest of Australia and reported a high genetic correlation of 0.8 in Polled Hereford and Wokalup breeds. The results of Meyer *et al*. (1994) are in general agreement with the report by Miller and Wilton (1999) who also reported a high positive genetic correlation of 0.76 between maternal weaning weight and milk yield in Simmental, Charolais, Maine-Anjou, Pinzgauer, Tarentaise, Angus, Hereford and Gelbvieh beef cattle.

Recently, a study conducted in Fort Keogh Livestock and Range Research Laboratory, Miles City, Montana, USA by MacNeil and Mott (2006) reported a positive genetic correlation of 0.80 between weaning weight and milk production in Line 1 Hereford cattle. The positive correlations provide evidence that the two traits are influenced by similar genes in the European breeds (Minick *et al.,* 2001).

2.4 Maternal influenced traits

A maternal effect refers to the environment which the dam provides for the calf, which is mainly through milk yield from birth to weaning (Willham, 1972; Totusek *et al*., 1973). Thus the performance of the calf from birth to weaning is highly influenced by the ability of the dam's genetic makeup to provide the environment which is suitable for the calf to grow during the pre-weaning stage (Trus and Wilton, 1988). Campêlo *et al*. (2004) stated that the growth of a mammalian during suckling is generally influenced by the rate at which milk is produced by the dam for the calf.

However, the dam also contributes to the performance of the calf through its direct genetic effect passed on to the progeny, in which the phenotypic expression of this trait in the calf is partly influenced by the genetic effects and partly by the environmental effects (Mrode, 2005). The current study investigated the genetic relationship between maternal weaning weight and milk yield in indigenous Nguni cattle.

CHAPTER 3

MATERIALS AND METHODS

3.1 Study site

The experiment to collect milk yield data was conducted at the Loskop South Farm and Mara Research Station located in Mpumalanga and Limpopo Province, respectively. The Loskop South Farm is situated 25° 18' S and 29° 20' E in a bushveld region, South-East of Groblersdal, with the annual rainfall ranging between 447 mm and 468 mm. Mara Research Station is located about 54 km west of Makhado (23^{o} 05´S, 29^{o} 25´E) under the arid sweet bushveld area. The mean annual rainfall at Mara is 452 mm and the mean daily maximum temperature varies from 23^{o}C in June to 30^{o}C in January. Weaning weight records from Nguni herds that participated in the National Beef Cattle Improvement Scheme were obtained from the Integrated Registration and Genetic Information System (INTERGIS).

3.2 Layout of the experiment

The Loskop South Farm has approximately 300 stud Nguni breeding cows. The herd has a long history of participation in the National Beef Cattle Improvement Scheme and is regarded as one of the elite Nguni herds in the country. Stud bulls bred from the Loskop herd have been used in many Nguni herds throughout the country and thus the herd is genetically well-connected to the national Nguni herd which makes it suitable for genetic analysis. The stud Nguni herd from Mara Research Station has been widely used in several studies for genetic analysis (e.g. Du Plessis *et al*., 2006). Animals bred in Mara Research Station have been used in many breeding herds across the country. The herd also has a long history of participation in the National Beef Cattle Improvement Scheme that makes it genetically connected to the national herd. Almost all cows considered in this study had pedigree records. The number of animals considered in this experiment was modest due to constraints imposed by the availability of labour since this research was labour intensive. A total of 55 Nguni cows from Loskop South Farm and 117 Nguni cows from Mara Research Station were chosen based on age to obtain a representative sample of the different age groups because milk production depends on age of the cow (Beal *et al*., 1990). Field data were considered for weaning weight whereby 28,893 animals from 146 herds distributed throughout the country were involved. These animals participated in the National Beef Cattle Improvement Scheme and the data were obtained from the INTERGIS.

3.3 Data collection

Traits measured in the current study include milk yield estimated using the weigh-suckle-weigh technique (Totusek *et al*., 1973; Williams *et al.,* 1978; Beal *et al*., 1990; Lee and Pollak, 2002; McNeil and Mott, 2006) and weaning weight. Milk yield data was collected at least once per month from birth to weaning at about seven months for the period of two years (i.e. 2011 and 2012). Weaning weight data was collected by the research technicians from ARC-API following the National Beef Cattle Improvement Scheme guidelines. All animals in a contemporary group were weaned on the same day. Weaning weight data included observations from 1989 through 2012. The number of records collected for milk yield was 1,941 repeated observations and 28,893 records for weaning weight.

3.3.1 Weigh-suckle-weigh technique

Milk yield was measured using the weigh-suckle-weigh technique. The weigh-suckle-weigh technique could be described as follows. Cows were separated from their calves at 15h00 and re-united at 18h00, allowed to suckle for about 30 minutes to ensure that all cows are milked out before the trial; cows were then separated from the calves at 18h30 to 06h00 the following morning. In the morning of the trial, calves were quickly weighed before they were re-united with their dams. Calves were allowed to suckle their dams for about 30 minutes and then re-weighed as soon as possible. The difference between the weight of the calf before and after suckling was assumed to reflect milk yield produced during the 12 hour period. The 12-hour milk yield was multiplied by 2 to obtain 24-hour milk yield [(milk yield/12)*24]. The weigh-suckle-weigh technique was used successfully to measure milk yield in beef cattle in several experiments (e.g. MacNeil and Mott, 2006).

3.4 Data editing

Few negative estimates of milk yield were observed in this study. This could be calves that did not suckle much from their dams and had exhibited a lot of physical activity. These were considered an anomaly and these records were excluded from further analyses. Several estimates of milk yield per cow per lactation were obtained. These estimates were averaged per cow to obtain a more accurate measure of daily milk yield per cow. Milk yield records which were beyond 3 standard deviations from the mean were removed. After editing, there were 125 observations for milk yield available for analysis distributed over 3 contemporary groups which was defined as a concatenation of herd-year. Weaning weight data was also edited to remove extreme weights i.e. weights beyond 3 standard deviations from the mean. After editing, there were 19,065 weaning weight observations remaining. These records were distributed over 990 contemporary groups defined as herd-year-season. The calves were progeny of 8,749 dams and 862 sires from 146 herds.

The pedigree data of the animals used in the current study was traced as far back as the early 1960s. The pedigree file was created using a bash script. The number of base animals was 4507.

3.5 Data analysis.

The Generalised Linear Model (GLM) procedure of Statistical Analysis System (2012) was used to test the significance of fixed effects i.e. contemporary group; sex of the calf; age of the dam and age of the calf. The fixed effects model for milk yield was:

$$\mathbf{y}_1 = \mathbf{X}_1\mathbf{b}_1 + \mathbf{e}_1$$

$\mathbf{y}_1$ – a vector of observations for milk yield i.e. average daily milk yield

$\mathbf{X_1}$ – a design matrix linking fixed effects with milk yield observations

$\mathbf{b}_1$ – a vector of fixed effect parameters for contemporary group, sex of the calf and age of the dam (fitted with the following classes: ≤3, 4, 5, 6, 7, 8+ years)

$\mathbf{e}_1$ – a vector of residual effects assumed to be identically, independently and normally distributed ($\mathbf{e}$ ~ N (0, $\mathbf{I}\sigma^2_e$)).

The fixed effects model for weaning weight was:

$$\mathbf{y}_2 = \mathbf{X}_2\mathbf{b}_2 + \mathbf{e}_2$$

$\mathbf{y}_2$ – a vector of observations for weaning weight

$\mathbf{X_2}$ – a design matrix linking fixed effects with weaning weight observations

$\mathbf{b}_2$ – a vector of fixed effect parameters for contemporary group, sex of the calf, age of the calf (fitted as linear and quadratic) and age of the dam (fitted with the following classes: ≤3, 4, 5, 6, 7, 8+ years)

$\mathbf{e}_2$ – a vector of residual effects assumed to be identically, independently and normally distributed ($\mathbf{e}$ ~ N (0, $\mathbf{I}\sigma^2_e$)). The $\mathbf{I}$ is an identity matrix and σ^2_e is the residual variance.

Two sets of analyses were conducted to estimate (co)-variance components and genetic parameters for milk yield and weaning weight. In the first analysis, univariate linear mixed animal models were fitted for milk yield and weaning weight. In the second analyses, a bivariate linear mixed animal model was used to estimate the genetic correlation between milk yield and weaning weight. The PEST and VCE software were used to estimate (co)-variance components (Groeneveld, 1998).

The following linear mixed animal model was used for the univariate analysis of milk yield:

$$\mathbf{y_1} = \mathbf{X}_1\mathbf{b}_1 + \mathbf{Z}_1\mathbf{u}_1 + \mathbf{e}_1$$

$\mathbf{y_1}$, $\mathbf{X}_1$, $\mathbf{b}_1$ and e_1 are as defined previously.

$\mathbf{Z}_1$ – is an incidence matrix linking random direct additive genetic effects with observations

$\mathbf{u}_1$ – is a vector of random direct additive genetic effects assumed to be normally distributed as follows: $\mathbf{u}_1$ ~ N (0, $\mathbf{A}\sigma^2_{u1}$). $\mathbf{A}$ is a numerator relationship matrix and σ^2_{u1} is the direct additive genetic variance. The $\mathbf{u}_1$ and $\mathbf{e}_1$ are assumed to be uncorrelated.

The linear mixed animal model used for univariate analysis of weaning weight was as follows:

$$\mathbf{y_2} = \mathbf{X}_2\mathbf{b}_2 + \mathbf{Z}_2\mathbf{u}_2 + \mathbf{Z}_2\mathbf{m} + \mathbf{Wc} + \mathbf{e}_2$$

$\mathbf{y}_2$, $\mathbf{X}_2$, $\mathbf{b}_2$, and $\mathbf{e}_2$ are as defined previously.

$\mathbf{Z}_2$ – is an incidence matrix linking random direct additive genetic effects and maternal additive genetic effects with observations

W – is an incidence matrix linking permanent environmental effects of the dam with observations

$\mathbf{u}_2$ – is a vector of random direct additive genetic effects

m – is a vector of random maternal additive genetic effects

c – is a vector of random permanent environmental effects of the dam

The first and second moments of the random effects were as follows:

E ($\mathbf{y}_2$) = $\mathbf{X}_2\mathbf{b}_2$; E ($\mathbf{u}_2$) = **0**; E (**m**) = **0**; and E (**c**) = **0;** E (e) = **0**

and

$$var\begin{bmatrix}\boldsymbol{u_2}\\ \boldsymbol{m}\\ \boldsymbol{c}\\ \boldsymbol{e}\end{bmatrix} = \begin{bmatrix}\boldsymbol{A}\sigma_{u2}^2 & \boldsymbol{A}\sigma_{u2,m} & \mathbf{0} & \mathbf{0}\\ & \boldsymbol{A}\sigma_m^2 & \mathbf{0} & \mathbf{0}\\ & & \boldsymbol{I}\sigma_c^2 & \mathbf{0}\\ symmetric & & & \boldsymbol{I}\sigma_{e2}^2\end{bmatrix}$$

The following bivariate animal model was fitted to estimate (co)variance components for milk yield and weaning weight:

$$\begin{bmatrix}\boldsymbol{y}_1\\ \boldsymbol{y}_2\end{bmatrix} = \begin{bmatrix}\boldsymbol{X}_1 & 0\\ 0 & \boldsymbol{X}_2\end{bmatrix}\begin{bmatrix}\boldsymbol{b}_1\\ \boldsymbol{b}_2\end{bmatrix} + \begin{bmatrix}\boldsymbol{Z}_1 & \mathbf{0}\\ \mathbf{0} & \boldsymbol{Z}_2\end{bmatrix}\begin{bmatrix}\boldsymbol{u}_1\\ \boldsymbol{u}_2\end{bmatrix} + \begin{bmatrix}\mathbf{0} & \mathbf{0}\\ \mathbf{0} & \boldsymbol{Z}_2\end{bmatrix}\begin{bmatrix}\mathbf{0}\\ \boldsymbol{m}\end{bmatrix} + \begin{bmatrix}\mathbf{0} & \mathbf{0}\\ \mathbf{0} & \boldsymbol{W}\end{bmatrix}\begin{bmatrix}\mathbf{0}\\ \boldsymbol{c}\end{bmatrix} + \begin{bmatrix}\boldsymbol{e}_1\\ \boldsymbol{e}_2\end{bmatrix}$$

The following covariance structure was assumed for the random effects:

The (co)variance of u, m, e, were assumed as follows;

$$var\begin{bmatrix}\boldsymbol{u}_1\\ \boldsymbol{u}_2\\ \boldsymbol{m}\\ \boldsymbol{c}\\ \boldsymbol{e}_1\\ \boldsymbol{e}_2\end{bmatrix} = \begin{bmatrix}\boldsymbol{A}\sigma_{u1}^2 & \boldsymbol{A}\sigma_{u1,u2} & A\sigma_{u1,m} & 0 & 0 & 0\\ & \boldsymbol{A}\sigma_{u2}^2 & A\sigma_{u2,m} & 0 & 0 & 0\\ & & \boldsymbol{A}\sigma_m^2 & 0 & 0 & 0\\ & & & \boldsymbol{I}\sigma_c^2 & 0 & 0\\ & symmetric & & & \boldsymbol{I}\sigma_{e1}^2 & I\sigma_{e1,e2}\\ & & & & & \boldsymbol{I}\sigma_{e2}^2\end{bmatrix}$$

The $\sigma_{u1,u2}$ is the additive genetic covariance between milk yield and weaning weight; $\sigma_{u1,m}$ is the genetic covariance between direct genetic effect for milk yield and maternal genetic effect for weaning weight; $\sigma_{u2,m}$ is the genetic covariance between direct and maternal genetic effects for weaning weight; $\sigma_{e1,e2}$ is the residual covariance between milk yield and weaning weight. All the other terms are as defined before.

CHAPTER 4

RESULTS

4.1. Summary statistics of the data

Descriptive statistics for weaning weight, milk yield and age of the calf at weaning are presented in Table 4.1. The average milk production in Nguni cows was 5.25 kg/day with a minimum of 1.13 kg/day and a maximum of 9.91 kg/day. The average weaning weight was 158.94 kg with a minimum of 86 kg and a maximum of 220 kg and the average age at weaning was 210 days with a minimum of 100 days and a maximum of 298 days.

Table 4.1. Descriptive statistics for weaning weight, milk yield and age of the calf at weaning in Nguni cattle.

Item	N	Minimum	Maximum	Mean	STD Dev.
Milk yield (kg/d)	125	1.13	9.91	5.25	1.68
Weaning weight (kg)	19 063	86.00	220.00	158.94	26.89
Age at weaning (d)	19 063	100.00	298.00	210.00	31.48

4.2. Analyses of variance for fixed effects

Contemporary group, sex of the calf, age of the calf and age of the dam at weaning had significant (P < 0.001) effect on weaning weight (Table 4.2).

Table 4.2. ANOVA results for weaning weight

Source	**DF**	**Mean Square**	**F Value**	**Pr > F**
Contemporary group	990	5379.41	16.84	<.0001
Sex	1	477674.84	1495.28	<.0001
Age at weaning	1	1546246.33	4840.25	<.0001
Age of dam	5	126027.28	394.51	<.0001

Contemporary group and age of the cow had significant (P<0.05) effect on milk yield while sex of the calf slightly showing to be less significant (P>0.05). Table 4.3 shows the ANOVA results for milk yield.

Table 4.3. ANOVA results for milk yield

Source	**DF**	**Mean Square**	**F Value**	**Pr > F**
Contemporary group	2	23.50	10.42	<.0001
Sex	1	6.67	2.96	0.0882
Age of dam	5	7.01	3.11	0.0114

The least square means for sex and age of the dam for milk yield and weaning weight are presented in Table 4.4.

Table 4.4. Least square means and their respective standard errors for age of the dam and sex of the calf for milk yield and weaning weight in Nguni cattle.

Item	**Milk Yield (kg/d)**			**Weaning weight (kg)**		
	N	LS Mean	SE	N	LS Mean	SE
Sex						
Male	58	5.54	0.24	9136	163.21	0.34
Female	67	5.15	0.23	9929	151.47	0.33
Age of Dam (years)						
≤ 3	18	4.37	0.38	4912	145.77	0.38
4	20	6.06	0.37	2825	155.64	0.45
5	17	4.83	0.41	2475	159.10	0.47
6	18	5.55	0.38	2082	160.49	0.49
7	11	5.43	0.49	1579	161.90	0.54
8	41	5.82	0.26	5192	161.27	0.38

As illustrated in Table 4.4, there was a tendency for cows that had male calves to produce more milk (5.54 kg/day) than cows with female calves (5.15 kg/day). Male calves were heavier at weaning (163.21 kg) than female calves (151.47 kg). Milk yield depended on the age of the cow. That is, 3 and 5 year-old cows produced less milk compared to 4 year-old cows (6.06). Milk yield was similar for cows aged 6, 7 and 8 years. Age of the dam had a significant effect ($P < 0.01$) on the weaning weight. Weaning weight increased with age of the dam.

4.3. Estimates of (co)variance components and genetic parameters from univariate analyses

Estimates of (co)variance components and genetic parameters from univariate analyses are presented in Table 4.5. The heritability estimate for milk yield from univariate analysis was 0.16 ± 0.299. The standard error is high possibly due to the small sample size considered in the current study. The heritability estimate for weaning weight direct from the univariate analysis was 0.48 ± 0.038 and the estimate for maternal heritability of 0.25 ± 0.025. The genetic correlation between direct and maternal additive effects was -0.55 ± 0.053.

Table 4.5. (Co) variance components and variance ratios for direct (a) and maternal genetic (m), permanent environmental effect, residual and their respective ratios for milk yield (MY) and weaning weight (WW) in Nguni cattle

Item	**MY**	**WW**
σ^2_a	0.36	135.74
σ^2_m	-	69.80
σ_{am}	-	-53.87
σ^2_c	-	45.48
σ^2_e	1.90	142.08
σ^2_p	2.26	285.37
h^2_a	0.16 ± 0.299	0.48 ± 0.038
h^2_m	-	0.25 ± 0.025
c^2	-	0.15 ± 0.017
r_{am}	-	-0.55 ± 0.053

σ^2_a - direct additive genetic variance; σ^2_m - maternal additive genetic variance; σ^2_c - permanent environmental variance; σ^2_e - residual or error variance; σ^2_p - phenotypic variance; σ_{am} - covariance between direct and maternal additive genetic effects; r_{am} - genetic correlation between direct and maternal additive effects; h^2_a - direct additive heritability; h^2_m - maternal additive heritability; c^2 - the ratio of permanent environmental variance to phenotypic variance.

4.4. Estimates of (co) variance components and genetic parameters from multivariate analyses.

Estimates for (co)variance components and genetic parameters from the multivariate analyses slightly differ from the estimates of univariate analysis. This is due to the advantage that the multivariate analyses holds of analyzing two traits simultaneous which increases the accuracy of estimates (Mrode, 2006). The heritability for milk yield (h^2 = 0.22 ± 0.238) observed in multivariate analysis was higher than the corresponding estimate from univariate analysis (h^2= 0.16 ± 0.299). The heritability estimates for weaning weight (direct, h^2 = 0.47 ± 0.039 and maternal, h^2 = 0.25 ± 0.029) observed in multivariate analysis was of the same magnitude with the heritabilities observed in univariate analysis (direct, h^2 = 0.48 ± 0.038 and maternal, h^2= 0.25 ± 0.025). The number of observations considered in the univariate and multivariate analyses for weaning weight was virtually the same.

The estimates of genetic correlation for milk yield and weaning weight are presented in Table 4.6. The genetic correlation between weaning weight direct and maternal was moderate (-0.56 ± 0.247) and high between wean direct and milk yield (-0.71 ± 0.416). Milk yield and weaning weight maternal were genetically almost the same trait (0.97 ± 0.063).

Table 4.6. Estimates of the (co)variance components (on and above diagonal), genetic correlations (below diagonal) and heritability for milk yield (MY_a), weaning weight direct (WW_a) and maternal (WW_m)

Item	MY_a	WW_a	WW_m	h^2
MY_a	0.510	-5.904	5.900	0.22 ± 0.238
WW_a	-0.71 ± 0.416	134.824	-55.096	0.47 ± 0.039
WW_m	0.97 ± 0.063	-0.56 ± 0.247	72.376	0.25 ± 0.029

The estimates of the (co)variance components for temporary (residual) and permanent environmental effects, correlation and the ratio of residual variance to phenotypic variance (e^2) for milk yield (MY) and weaning weight (WW) are presented in Table 4.7. The residual environmental effect accounted for more variation in milk yield (0.78 ± 0.238) than in weaning weight (0.50 ± 0.038). The residual correlation between milk yield and weaning weight was high (0.75 ± 0.409).

Table 4.7. Estimates of the (co)variance components for temporary (residual) and permanent environmental affects (on and above diagonal), correlation (below diagonal) and the ratio of residual variance to phenotypic variance (e^2) for milk yield (MY) and weaning weight (WW).

Item	**MY**	**WW**	**e^2 / c^2**
Temporary / residual			
MY	1.83	12.15	0.78 ± 0.238
WW	0.75 ± 0.409	143.27	0.50 ± 0.038
Permanent			
WW		44.52	0.16 ± 0.044

The results of the phenotypic correlation between milk yield and weaning weight are shown in Table 4.8. The phenotypic correlation between weaning weight and milk yield was 0.47 ± 0.025.

Table 4.8. Estimates of the phenotypic (co)variance components (on and above diagonal) and phenotypic correlation (below diagonal) for milk yield (MY) and weaning weight (WW).

Item	**MY**	**WW**
MY	2.33	12.15
WW	0.47 ± 0.025	284.80

CHAPTER 5
DISCUSSION AND CONCLUSIONS

5.1. Discussion

The average weaning weight observed in the current study (158.94 kg) was higher than that reported by Collins-Lusweti (2000), who reported average weaning weight in Nguni cattle of 135.6 kg. Collins-Lusweti study was based on weaning weights collected during a drought period. Similar to the results obtained in the current study, Kars *et al*. (1994) reported an average weaning weight of 152.98 kg in Nguni cattle. Carvalheira *et al*. (1995) reported an average weaning weight of 149.5 kg in Landim cattle which are also known as Nguni cattle in Mozambique. It should be noted that Carvalheira *et al*. (1995) study was based on the data collected from 1968 through 1981. High average weaning weight (183 kg) corrected to 205-d was observed in Nguni cattle by Scholtz and Theunissen (2010) based on the data which was collected on a period of 3 years. Both genetic and environmental factors could have contributed to the differences observed in average weaning weight of Nguni cattle in different studies.

The average daily milk yield observed in the current study (5.25 kg/day) was of the same magnitude with that observed by Maiwashe *et al*. (2013) who reported milk yield in Nguni cattle of 6 kg/day. Similar observations of daily milk yield in beef cattle have been made in several studies. Meyer *et al*. (1994) reported 14-h milk yield of 3.6 kg/day and 4.9 kg/day for Hereford and Wokalups cattle respectively. Melton *et al*. (1967) reported mean daily milk yield of 3.79 kg, 4.48 kg and 3.32 kg collected over 175-d period for Angus, Charolais and Hereford cattle respectively. Maiwashe *et al.* (2013) also reported milk yield in Bonsmara cattle of 8.50 kg/day. It must also be noted that Maiwashe *et al*. (2013)'s measurements for milk yield were based on the weigh-suckle-weigh technique following the 12-h separation of calves. Meyer *et al*. (1994) measurements for milk yield were based on the weigh-suckle-weigh method following a 14-h separation of the calves. Melton *et al*. (1967) measurements for milk yield were based on weigh-suckle-weigh method following 12-h removal of the calf. Since milk yield is prominently influenced by the environment and the genotype, the variance in milk yield can be greatly explained by the difference in environment and genotype.

Heritability (0.47) for weaning weight direct observed in the current study was slightly higher compared to other findings. For example, Van Niekerk *et al*. (2004) observed a heritability of 0.17 for direct weaning weight in Nguni cattle and Norris *et al*. (2004) reported a heritability of about 0.29 for direct weaning weight in the Nguni breed. Neser *et al*. (2012) reported heritability for weaning weight direct of 0.23 in Brangus cattle while Van Niekerk and Neser (2006) reported heritability of 0.19 for South African Limousin cattle. In other breeds from other countries, Ndofor-Foleng *et al*. (2012) reported a heritability of 0.25 in Gudali beef cattle while Wasike *et al*. (2009) reported the direct heritability for weaning weight of around 0.62 from 4 496 observations and heritability of 0.32 from 2 026 observations respectively.

The heritability (0.25) for maternal weaning weight observed in the current study was the same from the univariate and the multivariate analyses. The maternal heritability observed in the current study is similar to literature reports. Wasike *et al*. (2009) reported a maternal heritability for weaning weight of 0.26 in Kenyan Boran cattle.

In contrast to results obtained in the current study, Wasike *et al*. (2009) reported maternal heritability for weaning weight of 0.14 in Boran cattle in Kenya. Norris *et al*. (2004) also observed a lower maternal heritability of about 0.16 in Nguni cattle. Furthermore, Ndofor-Foleng *et al*. (2012) reported a maternal heritability of about 0.11 in Gudali beef cattle. Meyer *et al*. (1994) also reported the weaning weight heritability of the same low magnitude in Wokalups breed of about 0.11 using a model that did not include milk production of the dam and heritability of 0.08 in a model that included milk production of the dam respectively. They further observed maternal heritability of weaning weight of about 0.19 in Hereford cattle in a model that did not include milk production of the dam and heritability of 0.15 in a model that included milk production of the dam respectively. It must be further noted that other studies observed different heritabilities in estimates that included milk yield and estimates that did not include milk yield which in the current study was not the case. The moderate heritability for maternal weaning weight was also confirmed by Van Niekerk and Neser (2006) who reported the maternal heritability of 0.19 for South African Limousin cattle. Recently, Neser *et al*. (2012) reported maternal heritability for weaning weight of 0.11 in Brangus cattle.

The current estimates for maternal heritability and the genetic correlation between the direct and maternal components for weaning weight provides evidence that response can be obtained if both the direct and maternal breeding values are considered in a breeding Programme. The current results also provide useful information for developing dam lines based on the maternal abilities. However, it must be noted that the environment effects still have a major effect. The response to selection would be slow due to the moderate maternal heritability.

The positive genetic correlation between maternal weaning weight and milk yield (0.97) observed in the current study is higher than the estimates of 0.80 from MacNeil and Mott (2006) for Line1 Hereford cattle; 0.80 from Meyer *et al*. (1994) for Hereford and Wokalups and 0.76 from Miller and Wilton (1999) for Hereford and multibreed rotational cross cattle. However, it must be noted that estimates from MacNeil and Mott (2006) was calculated on an adjusted age at weaning of 180-d from the data which was measured from 1994 through 2005 using the weigh-suckle-weigh technique. An estimate from Meyer *et al*. (1994) was calculated from single observation per lactation which was obtained using the weigh-suckle-weigh technique. It is also important to note that different method to measure milk yield was used in a study by Miller and Wilton (1999) who used 2 to 4 records from machine milking after the oxytocin injection after a 6 hour calf removal to estimate 200-d milk yield. Mallinckrodt *et al*. (1993) reported a low correlation between maternal weaning weight and milk yield (0.4) for Polled Hereford and Simmental cattle. The results of Mallinckrodt *et al*. (1993) were based on 163 and 154 observations from Polled Hereford and Simmental cattle respectively in which the cows received supplementation feeding during winter. Greater variation in estimates of the correlation across studies might be explained by the different techniques used in measuring milk yield. However, the positive relationship between the maternal weaning weight and milk yield as observed in different studies using different protocols is evidence that the two traits are influenced by the same genes; this phenomenon has been explained in several papers (e.g. Miller and Wilton 1999). As suggested by MacNeil and Mott (2006) selection for milk production using maternal weaning weight as an indicator trait in Line 1 Hereford would be as effective as mass selection. The current estimate explains the very same phenomenon of maternal weaning weight as an effective indicator for milk yield in Nguni cattle. Thus, selection for milk yield in Nguni cattle using maternal weaning weight would also be as effective as direct selection for milk yield.

The negative genetic correlation estimated between direct and the maternal effects is largely an indication of the genetic antagonism between the genes that influence the two traits (Lee and Pollack, 2002; Norris *et al*., 2004; Van Niekerk *et al*., 2004). The negative correlation between the direct and maternal effect for weaning weight observed in the current study was also observed in other several studies. Norris *et al.* (2004) reported a negative genetic correlation between direct weaning weight and maternal weaning weight of -0.52 in Nguni cattle. Similarly, Meyer *et al.* (1994) observed a correlation of -0.57 and -0.17 in Hereford and Wokalups cattle respectively. Recently, a moderate genetic correlation was observed by Ndofor-Foleng *et al*. (2012) who reported a negative correlation of -0.42 between direct weaning weight and maternal effects in Gudali beef cattle. A slightly lower genetic correlation of -0.32 was reported for Nelore beef cattle by Eler *et al*. (1995). A weak genetic correlation (-0.18) was reported for crossbred animals by Splan *et al*. (2002).

The negative genetic correlation between direct weaning weight and milk yield observed in the current study was much higher than the estimates observed by Lee and Pollack (2002) who observed a correlation of −0.04 to −0.21 for weaning weight and milk yield in Korean Hanwoo beef cattle using the weigh-suckle-weigh method. It is also of interest to note that MacNeil and Mott (2006) observed a very low positive genetic correction of 0.18 between pre-wean direct and milk yield in Line 1 Hereford beef cattle using the weigh-suckle-weigh method.

5.2. Conclusions

The results from the current study indicate that milk yield is heritable and genetically strongly correlated with maternal weaning weight. This knowledge has been successfully utilized in other beef cattle breeds in which the evidence has been documented. The current results motivate for inclusion of maternal breeding value for weaning weight as an indicator trait for milk yield in Nguni cattle breeding Programme. Furthermore, more studies are necessary to strengthen the current results and to provide greater knowledge on the milk yield potential of Nguni cattle.

CHAPTER 6

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