Variance component estimations for the South African Merino sheep breed for application in genetic and genomic evaluations

By

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Declaration

I, the undersigned, hereby declare that this thesis, submitted for the MSc(Agric) Animal Science: Animal Breeding and Genetics degree at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at any other University.

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Abstract

The estimation of genetic parameters allows for the accurate prediction of estimated breeding values (EBVs), which plays a crucial role in developing selection indices that can be used to generate genetic progress for economically important traits. This study aimed to estimate genetic parameters for the estimation of EBVs and genomically enhanced breeding values (GEBVs) for the South African Merino sheep breed for application in genetic and genomic evaluations. A population of 864 754 South African Merino sheep were included in this study. Variance components were estimated for all sheep born after 2009, consisting of 62 460 animals. A multi-trait animal model was used to estimate the variance components, using VCE6 statistical software (Groeneveld *et al*., 2010). The multi-trait animal model estimated the heritabilities and standard errors for seven traits: Direct weaning weight (0.25 ± 0.01), maternal weaning weight (0.20 ± 0.00), body weight at wool test (0.26 ± 0.01), clean fleece weight (0.33 ± 0.01), fibre diameter (0.63 ± 0.00), staple length (0.33 ± 0.00) and coefficient of variation of fibre diameter (0.43 ± 0.00). Conventional EBVs were obtained using PEST2 (Groeneveld et al., 2019), employing the same genetic models as used for variance component estimation. The genetic trends were determined by averaging the breeding values of measured animals per year of birth per trait and were plotted against the national trends provided by SA Stud Book. SNP data was incorporated for the estimation of GEBVs with Single-Step GBLUP methodology, using MIX99 (Lidauer *et al*., 2013), for a highly heritable (fibre diameter) and a lowly heritable (wean maternal) trait. The genetic trends for the GEBVs were determined by averaging the GEBVs per year of birth for measured animals per trait. The EBVs and GEBVs for all active, as well as for the genotyped animals were correlated to assess the effect of the inclusion of genomic information in EBV estimation on the ranking of the animals, as well as on the accuracy of estimation of the breeding values. The results indicated that including genomic information did not change the ranking of animals or the accuracy in which EBVs were estimated for fibre diameter. In contrast, for the lowly heritable trait, wean maternal, the inclusion of genomic information improved the accuracies of the EBVs, increasing from a range of 18% and 97% to a range of 37% and 97%.

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List of Abbreviations

ANOVA	Analysis of Variance
ATLAS	Automatic Tester for Length and Strength
AW	Adult Weight
BLUP	Best Linear Unbiased Prediction
BW	Birth Weight
BWW	Body Weight at Wool Test
CFW	Clean Fleece Weight
CVFD	Coefficient of Variation of Fibre Diameter
DALRRD	Department of Agriculture, Land Reform and Rural Development
Dir	Direct
EBV/s	Estimated Breeding Value/s
EL/EJ	Fertility
FD	Fibre Diameter
GBLUP	Genomic Best Linear Unbiased Prediction
GEBV/s	Genomically Enhanced Breeding Value/s
G/D	Growth Rate
GFW	Greasy Fleece Weight
h^2	Narrow Sense Heritability
INTERGIS	Integrated Registration and Genetic Information System
Mat	Maternal
Max	Maximum
Med	Median
Min	Minimum
ML	Maximum Likelihood Estimation
MME	Mixed Model Equations
MSE	Mean Square Error
NLB/EL	Number of lambs born/ewe lambing
NLB/EJ	Number of lambs born/ewe joined
NLW/EL	Number of lambs weaned/ewe lambing
NLW/EJ	Number of lambs weaned/ewe joined
NLB	Number of Lambs Born
NLW	Number of Lambs Weaned (Ewe Rearing Ability)
NSSIS	National Small Stock Improvement Scheme
NWGA of SA	National Woolgrowers Association of South Africa
OFDA	Optical Fibre Diameter Analysis
PEST	Parameter Estimation
PWW	Post Weaning Weight
QTL	Quantitative Trait Loci
REML	Restricted Maximum Likelihood

rg	Genetic Correlations
SA	South Africa
SC	Scrotal Circumference
SD	Standard Deviation
SDFD	Standard Deviation of Fibre Diameter
SE	Standard Error Values
SL	Staple Length
SNPs	Single Nucleotide Polymorphisms
SS	Staple Strength
ssGBLUP	Single Step Genomic Best Linear Unbiased Prediction
VCE6	Variance Component Estimation Version 6
WM	Wean Maternal
WW	Weaning Weight
WW/EL	Weight weaned/ewe lambing
WW/EJ	Weight weaned/ewe joined
YLD	Yield

Chapter 1 Introduction

1.1. Introduction

The Merino and Merino-derived sheep breeds are widely spread across the globe and represent an economically important genetic resource (Ciani *et al*., 2015). Although the origin of the Merino breed is ambiguous, historical Roman documentary evidence suggests that the dark-coated Iberian Black Merino is the ancestral origin of this breed (Granero *et al*., 2022). The Romans crossed the Iberian Black Merino with foreign animals from Northern Africa, known for their quality coat characteristics and ability to adapt to extreme weather conditions. During the second century, these crossbred individuals were further selected by the Romans to produce white wool, which marks the beginning of the modern Merino breed (Granero *et al*., 2022). The initial expansion of the Merino breed started across Northern Europe and then into other countries and continents, including South Africa (SA), Australia, and Northern America, through the use of direct selection and cross breeding with native sheep breeds (Diez-Tascon *et al.,* 2000). The South African Merino sheep breed originated from Spanish Merino sheep introduced to the Cape Colony in 1789. The initial flock consisted of two rams and four ewes gifted by the King of Spain to the Dutch government, and these sheep were kept at the Groenekloof experimental farm near Cape Town (Bath, 2023). Merino SA, established in 1937, was the South African organisation that represented all South African Merino sheep breeders and is still the official organisation for the management and communication of the Merino industry (Merino SA, 2023). The modern Merino is a dual-purpose breed, producing wool and mutton and is beneficial due to the breeds' ability to adapt to and produce in varying, harsh climates and weather conditions that is common to SA (Granero *et al*., 2022). It has also been used as the basis for the development of various composite SA breeds, including the Dormer and Dohne Merino (Ciani *et al*., 2015).

The SA national sheep population peaked in 2013 at 24.5 million sheep (Statista, 2023). However, the sheep population has generally followed a decreasing trend since 2010, declining by 500 000 heads from 22.09 million in 2019 to 21.6 million sheep in 2020 (Statista, 2023). Consequently, the number of South African Merino sheep have also decreased, declining from 9.9 million sheep in 2020 to 9.7 million sheep in 2021 (DAFF, 2022). The decreasing trend of the sheep population in SA is mainly due to ongoing drought, stock theft and predation (DALRRD, 2021). The South African sheep industry consists of a large range of breeds and production types (Van der Merwe *et al*., 2020). According to the National Small Stock Improvement Scheme (NSSIS), 49.7% of the data consists of the Merino and Dohne Merino breeds, the South African Mutton Merino contributes 18.1%, Dormer sheep 7.1%, Ile de France 2% and the Merino Landsheep, and Afrino breeds contribute less than 2% (Van der Merwe *et al*., 2020). The remainder of the national flock consists of breeds that are reared for meat production only (Van der Merwe *et al*., 2020). The small stock industry contributes 8 to 10% of total animal product income, with the bulk of the income derived from mutton and lamb and then wool (Zenda *et al*., 2023). Presently, SA is a net exporter of wool, however a net importer of mutton and lamb, indicating that local sheep consumption exceeds domestic production (Nyam *et al*., 2020). The total amount of mutton produced from the South African sheep population equated to 1.60 million tonnes in 2021, with total consumption equating to 1.66 million tonnes (DAFF, 2022). There is, however, pressure from the government to reduce imports of sheep products and to promote domestic production due to the increased pressure on foreign currency reserves (Nyam *et al*., 2020).

Sheep production in SA plays a key role in the livelihoods of rural communities as it provides food security, employment, a source of income and also is a cheap source of manure for crop production (Nyam *et al.,* 2020). There are roughly 8 000 commercial sheep farms and 5 800 communal farmers throughout South Africa (DALRRD, 2021). Sheep farming contributes to sustainable production in extensive pastoral areas, particularly where no alternative production can be practiced, an example is the vast, extreme climatic Karoo regions forming part of central SA (Cloete *et al*., 2014). The majority of Merino sheep farming in SA occurs in the dry western and central districts, consisting of mainly the Northern Cape, Free State, and Eastern Cape provinces (Cloete, 2010). The South African Merino breed plays a significant role in both the meat and wool industries due to the breeds' ability to thrive in a highly diverse and harsh environment (Granero *et al*., 2022). Historically, focus was primarily placed on wool production, however, due to the increase in the price of lamb and mutton, the Merino was developed into a more balanced, dual-purpose breed with meat production being considered along with wool traits (Cloete *et al*., 2004).

Small stock selection practices and improvement services have undergone several changes due to fluctuations in demand and the advancement of statistical methods and technological innovations. This progress includes the development of genomic selection, enhanced software tools for data analysis, and more efficient breeding programs (Schoeman et al., 2010). Significant improvements in data capturing, such as increased participation and the integration of automated data collection systems and real-time monitoring tools, have resulted in increasingly efficient and accurate genetic evaluations of the South African Merino. (Cloete et al., 2014). Continuous scientific and statistical developments are providing further advancements in animal breeding, including progress in estimating the true genetic merit of livestock with the use of Estimated Breeding Values (EBVs), as well as the introduction and use of genomic selection (Koopaee & Koshkoiyeh, 2014). Accurately estimating breeding values is imperative as it influences the response to selection, the potential genetic gain a breeding programme can achieve, and it reflects the risk of whether or not an EBV will change over time when more information becomes available (Bijma, 2012). In the future, sheep farming is expected to become an increasingly important meat industry due to increased population demand for livestock derived foods, as well as the ability of sheep to adapt to varying climates (Gowane *et al*., 2017). Therefore, in order to develop efficient breeding programmes that allow for rapid genetic progress, estimation of accurate genetic parameters and EBVs are essential (Safari *et al*., 2005).

1.2 Aims and Objectives

The aim of this study was to estimate genetic parameters for implementation in the prediction of breeding values (EBVs) and genomically enhanced breeding values (GEBVs) for the South African Merino sheep breed.

In order to achieve this, the following objectives were set.

1. Estimate the genetic parameters for growth and wool traits using VCE6 (Variance Component Estimation version 6.0) (Groeneveld *et al.*, 2010).
2. Estimate breeding values for growth and wool traits using Parameter Estimation Version 2.0 (PEST2) (Groeneveld *et al.*, 2019).
3. Incorporate genotypic information to estimate GEBVs for a highly heritable (fibre diameter) and a lowly heritable (wean maternal) trait, using Single-Step GBLUP methodology with MIX99 software (Lidauer *et al.*, 2013).
4. Assess the effect on accuracy and ranking of animals using GEBVs *versus* EBVs for these two traits.

Chapter 2: Literature review

2.1 Introduction

Most traits of economic importance are classified as complex traits, in which the phenotype is continuously distributed and controlled by many genes, as well as environmental effects (Lush, 1949). The traditional method of improvement for these traits has relied on the use of phenotypic data and pedigrees of individuals and their relatives to estimate the combined effect of all genes on the breeding value of each animal (Goddard, 2012). Scientific and statistical breakthroughs have resulted in the estimation of estimated breeding values (EBVs) using Best Linear Unbiased Prediction (BLUP), which has increased the accuracy of estimating the genetic merit of an animal, thus improving the rate of genetic progress (Mofakkarul Islam *et al*., 2013). BLUP is a statistical approach that allows for the prediction of a non-observable random variable as the additive genetic value and is suitable for genetic evaluation in a variety of scenarios (Viana *et al.*, 2022). Advances made in molecular genetics have resulted in the development of DNA markers, the identification of many genes and quantitative trait loci (QTL) that affect quantitative traits, and this has further improved responses to selection (Koopaee & Koshkoiyeh, 2014). The development and introduction of genomic selection and the inclusion of genomic data in breeding programmes has changed how certain livestock species are selected and has substantially increased profitability and genetic gains per year due to the reduced generation interval and the decreased need for progeny testing (Meuwissen *et al*., 2016).

Accurately estimating genetic parameters such as heritabilities and repeatabilities, as well as genetic and phenotypic correlations, is imperative in animal breeding as it allows for the accurate prediction of EBVs (Hofer, 1998). Updating and re-estimating variance components must be done in order to ensure maximum accuracy in identifying the genetic component of the variance in the trait when estimating EBVs. The higher the accuracy value of estimation, the lower the likelihood of change in the animal's EBVs, as more information is analysed for that animal and its relatives' predictions (Bijma, 2012). Animal scientists routinely perform genetic evaluations and stud breeders rely on EBVs as a selection tool for accurate genetic improvement (Van Marle-Köster & Visser, 2018). Gene frequencies within a population change due to continuous selection, as well as mutations and migrations that might have occurred in the population. Genetic parameters therefore need to be re-estimated periodically to ensure accuracy (Mayo, 2008).

This literature review provides a brief background on variance component and breeding value estimations for the South African Merino sheep breed for application in genetic and genomic evaluations. It will highlight the statistical importance and development of animal models, discussing the progression from foundational models to more efficient computational methodologies. This review will focus exclusively on wool and growth traits as they are the main objectives of this study and will further discuss the incorporation of genotypic information in order to estimate genomically enhanced breeding values (GEBVs).

2.2 Small stock recording and genetic improvement in South Africa

Animal identification and recording are vital in breeding programmes and serves multiple purposes including managing inbreeding, pedigree verification, traceability, and performance recording (Mosconi, 2011). Methods of genetic evaluation, including BLUP, requires individual performance records, as well as detailed pedigrees of the animals' relatives in order to estimate genetic parameters. Repeatability and heritability values are needed to accurately determine EBVs for economically important traits (Greene, 2010). The data collected through performance recording aids in identifying best breeding strategies and is a powerful tool for generating genetic progress and livestock development (Mosconi, 2011). In order to achieve rapid, efficient genetic progress and improvement, genetic evaluations need to be conducted, which can only be done through the detailed and accurate recording of the animals' phenotypic data (Mosconi, 2011).

The South African wool industry consists of a long value chain, which includes producers, buyers, brokers, processors and the Wool Testing Bureau. The associations which provide services such as training, advisory consultations as well as development, include the National Woolgrowers Association of South Africa (NWGA of SA), as well as Wool South Africa (Zenda *et al*., 2023). Cape Wools South Africa, authorised by the Department of Agriculture, Land Reform and Rural Development, is the national body representing wool producers in South Africa and provides information regarding marketing and data of wool to relevant, related stakeholders (Zenda *et al*., 2023). Fleece testing has also been a pre-requisite for genetic improvement of SA small stock and has been present in some form since 1934. The National Fleece Testing Centre established in 1965 at the Grootfontein Experimental Farm as well as the Wool Testing Bureau in Port Elizabeth are both accredited fleece testing services (Cloete *et al*., 2014).

The South African National Small Stock Improvement Scheme (NSSIS) was established in 1964 and served as a basis for the accurate recording of economically important traits in various goat and sheep breeds and aimed to holistically, genetically improve traits while maintaining breed standards (Olivier, 2002). The NSSIS described five main elements that must be followed by every institute/production system that owns sheep in order to comply with National legislation, namely, registration, identification, movement, record-keeping and census (Department of Agriculture, Food and Marine, 2020). The NSSIS included the complete value chain of the sheep sector such as producers, exportation and abattoirs (Department of Agriculture, Food and Marine, 2020). The Scheme consisted of a pedigree and data recording system known as Integrated Registration and Genetic Information System or INTERGIS, which provides breeding values for economically important traits of participating breeds (Schoeman *et al*., 2010). INTERGIS, which is ICAR approved, is a collection of databases and programs that addresses animal recording needs in the livestock industry, including breeders of purebred and commercial animals, as well as registration authorities and other related industry organisations (National Small Stock Improvement Scheme, 2014). SA Stud Book, the official Registration Authority of stud animals in South Africa, established their own ICAR approved Performance Testing Scheme for beef, dairy, small stock and pig breeds in 2012. SA Stud Book became the official body for estimation of breeding values of small stock breeds in South Africa in 2016. Data collected by SA Stud Book is shared with the INTERGIS. The primary objective of Logix (SA Stud Book's Database) and the INTERGIS is to allow stakeholders to upload performance data of individual animals and the herd/flock to the National Animal Database. This is then converted into useful management information available in the form of reports and query facilities (National Small Stock Improvement Scheme, 2014). The top five most numerous sheep breeds participating in animal recording includes the Dohne Merino, SA Merino, SA Mutton Merino, Dormer and the Dorper (Figure 2.1) (SA Stud Book Annual Academic Report, 2022).

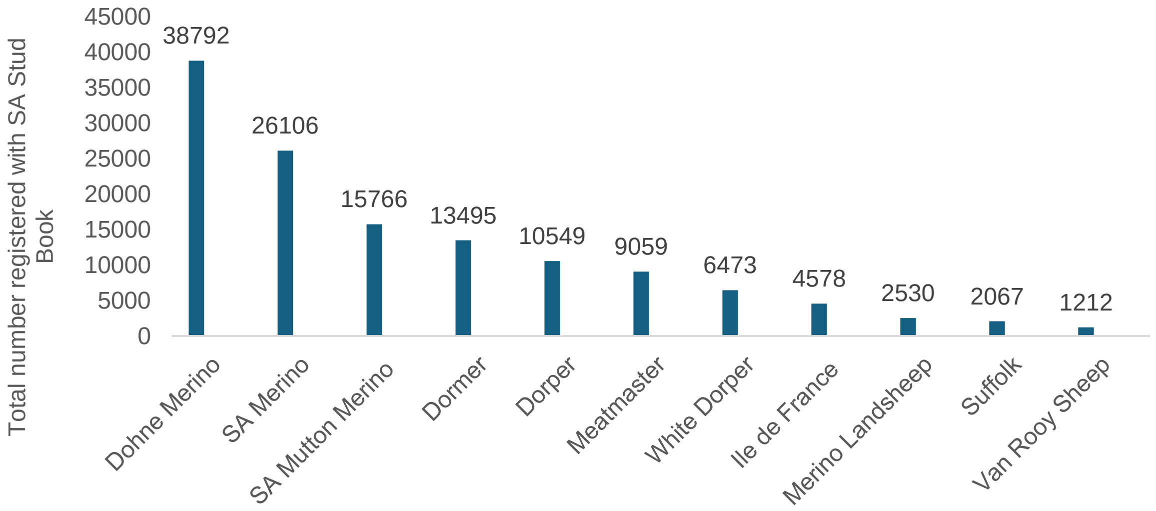


Figure 2.1 Registered South African sheep breeds that are participating in animal recording with SA Stud Book (SA Stud Book Annual Academic Report, 2022).

Currently, there are 67 South African Merino flocks registered with SA Stud Book. These flocks include a total of 26 106 registered SA Merino sheep, consisting of 14 146 males and 119 60 females. This indicates that the SA Merino has a strong participation in record-keeping and Animal Improvement Schemes (SA Stud Book Annual Academic Report, 2022). Genetic variation among economically important traits, as well as accurate heritability, repeatability and genetic correlation estimates are required in order to develop effective breeding objectives and efficient, long term genetic improvement programs (Mekuriaw & Haile, 2014).

2.3 Traits of economic importance

The success of sheep enterprises relies on how much wool and meat the flock produces, as well as their ability to reproduce effectively (Olivier, 2014). The genetic improvement of meat and wool sheep has typically focussed on economically important traits that are relatively easy and inexpensive to measure. This approach has been effective in some important traits of interest such as weaning weight, mature weight, fibre diameter and clean fleece weight, due to their relatively high heritability and easy measurability in both sexes (Daetwyler *et al*., 2010). However, the measurement and improvement of some economically important traits such as female fertility traits and parasitic resistance can be expensive and difficult to measure, which has ultimately resulted in slow genetic progress being made for these traits (Daetwyler *et al*., 2010). Fertility and growth traits have the largest influence on the profitability of a dual-purpose sheep enterprise as more than 70% of the total income of a sheep flock is generated from meat production, while 30% is generated from wool production (Olivier, 2014). To improve the overall efficiency of these sheep production systems, increases in production per animal need to occur and can be accomplished by selecting for a combination of an improved reproduction rate, a shorter production cycle and optimum fibre and wool production (Cloete *et al*., 2004).

Wool traits

Wool is a versatile product that is of great demand due to its durability, and textile attributes. However, wool yield and quality are affected by many factors including genetics, the environment as well as management practices and therefore routine evaluation and quantification of wool characteristics are vital (Holman & Malau-Aduli, 2012). Wool quality and production traits are used to determine the quality and grade of wool, therefore determining the economic value of wool (Wei *et al.,* 2020). Historically, the objective of South African wool producers was to increase the amount of wool produced, however this resulted in a reduced amount of finer wool being produced, resulting in decreased price premiums. Therefore, focus shifted to maintain a fine fibre while still producing a high wool yield (Zenda *et al*., 2023).

Although wool traits generally have remarkably high heritability estimates, it is important to estimate genetic parameters and correlations on a regular basis for the South African Merino sheep breed in order to develop efficient breeding programmes that account for all economically important traits and their interactions (Olivier, 2014). Table 2.1 shows a range of heritabilities (h^2) and their standard errors (SE) of the Merino for wool traits of interest, as reported in previous studies.

Table 2.1 Wool traits and their respective heritabilities (h^2) and standard errors (SE) for the Merino sheep breed (Adapted from Olivier, 2014).

Wool Traits	**Heritabilities and standard errors (h^2 ±SE)**	**References**
Greasy Fleece Weight (kg)	0.35 ± 0.02	(Brown *et al*., 2005)
	0.37 ± 0.02	(Safari *et al*., 2005)
	0.38 ± 0.03	(Safari *et al*., 2005)
	0.46 ± 0.01	(Safari *et al*., 2007)
	0.36 ± 0.05	(Matebesi *et al*., 2009a)
Clean Fleece Weight (kg)	0.28 ± 0.05	(Cloete *et al.,* 2005)
	0.36 ± 0.02	(Safari *et al*., 2005)
	0.51 ± 0.07	(Safari *et al.,* 2005
	0.44 ± 0.07	(Naidoo & Cloete, 2006)
	0.54 ± 0.04	(Olivier *et al*., 2006a)
	0.40 ± 0.05	(Matebesi *et al*., 2009a)
Fibre Diameter (μm)	0.59 ± 0.02	(Safari *et al*., 2005)
	0.57 ± 0.05	(Safari *et al*., 2005)
	0.68 ± 0.05	(Matebesi *et al*., 2009a)
	0.62 ± 0.03	(Brown *et al*., 2010)
Staple Length (mm)	0.46 ± 0.04	(Safari *et al.,* 2005)
	0.48 ± 0.03	(Safari *et al*., 2005)
	0.39 ± 0.08	(Cloete *et al*., 2006)
	0.37 ± 0.03	(Cloete *et al.,* 2006)
Standard Deviation of Fibre Diameter	0.58	(Ponzoni *et al*., 1995)
	0.35	(Swan *et al*., 1995)
	0.50 ± 0.03	(Li *et al*., 1999)
	0.57 ± 0.08	(Hill, 2001)
	0.52 ± 0.05	(Safari *et al*., 2005)
	0.61 ± 0.03	(Matebesi *et al*., 2009a)
Coefficient of Variation of Fibre Diameter (%)	0.60 ± 0.08	(Hill, 2001)
	0.60 ± 0.06	(Wuliji *et al*., 2001)
	0.37 ± 0.03	(Brown *et al*., 2002)
	0.52 ± 0.04	(Safari *et al.,* 2005)
	0.52 ± 0.06	(Cloete *et al*., 2006)
	0.61 ± 0.04	(Matebesi *et al*., 2009a)
Staple Strength (N/Ktex)	0.34 ± 0.03	(Safari *et al.,* 2005)
	0.23 ± 0.08	(Cloete *et al.,* 2006)
	0.20 ± 0.05	(Matebesi *et al.,* 2009a)
	0.39 ± 0.05	(Brown *et al*., 2010)
Crimp Frequency (cr/cm)	0.29	(Ponzoni *et al*., 1995)
	0.37 ± 0.10	(Taylor *et al*., 1997)
	0.54 ± 0.07	(Taylor *et al*., 1999)
	0.43 ± 0.05	(Hill, 2001)
	0.41 ± 0.03	(Safari *et al*., 2005)
	0.45 ± 0.11	(Wuliji *et al*., 2001)

Fibre diameter is the average width of a single cross section of wool fibre of a sheep and is the main factor determining trading price, processing performance, wool quality, as well as the end-use of wool (Qi *et al*., 1994). Fibre diameter is seen as the most important economic wool trait accounting for approximately 75% of the total price of raw wool. The trait indicates the fineness in which a yarn can be spun and consequently has a large influence on the post-processing wool value (Holman & Malau-Aduli, 2012). A low fibre diameter value, thus a fine, soft and light weight wool, is considered more desirable as it can be processed into high value textiles and end products and thus has a higher economic value (Khan, 2012). Contrary to this, wool that is coarser and has a larger fibre diameter, are less sought after due to their use in lower valued end products such as carpets and bedding (Qi *et al*., 1994). Fibre diameter is typically measured in microns (μm) and can be determined relatively quickly and cheaply using various instruments. The Laserscan is the most commonly used instrument and involves a laser which quantifies fibre diameter values (Holman & Malau-Aduli, 2012). Optical Fibre Diameter Analysis (OFDA) analyses the fibre diameter based on automatic image analysis technology and is measured using an automated scanning light microscope (Qi *et al*., 1994). Lastly, the Airflow instrument, although less commonly used, uses gravitational variation between wool fibres to determine the fibre diameter value (Holman & Malau-Aduli, 2012). The South African Merino has an average fibre diameter of 19.4 to 19.5 microns and is categorised as fine wool (Woods, 2023).

Staple length refers to individual fibre lengths and has become an increasingly important determinant of wool quality (Jamshed Khan, 2012). Measured in millimetres (mm), staple length determines the wool's processing performance. A longer staple length is more commercially desired and therefore has a greater economic value due to its tendency to spin more easily, have fewer stoppages and can form strong and more even yarns (Holman & Malau-Aduli, 2012). Shorter staple lengths cause piling and fibre loss, and this can be worsened due to mainstream processing techniques causing fibre breakages during the carding and scouring phases (Holman & Malau-Aduli, 2012). Staple length is measured using the CSIRO instrument known as the Automatic Tester for Length and strength (ATLAS), which is conveyed past photocells and assesses the length in millimetres (Thompson *et al.*, 2008). The average staple length of South African Merino wool is between 60 and 70 mm (Woods, 2023).

Staple strength is the ability of wool fibres to resist tension and is measured as the minimum amount of force needed in order to break a staple (Zenda *et al*., 2023). The degree of resistance indicates the wool's performance when undergoing processing and is therefore an important trait influencing wool quality (Zenda *et al*., 2023). Staple strength was traditionally measured using the "flick test" in which a wool handler would quantify the strength of the wool, however the ATLAS machine is now used in order to quantify staple strength in Newtons per kilotex (N/Ktex) (Holman & Malau-Aduli, 2012). Wool with a lower N/Ktex indicates a weaker strength and is more likely to break when force is applied. A higher staple strength is more desired as this indicates the wool is sound, will have fewer breakages under processing and therefore a higher economic value (Holman & Malau-Aduli, 2012). The average staple strength of South African Merino wool is between 20 and 40 N/Ktex (Woods, 2023).

Greasy fleece yield refers to the amount of wool produced prior to skirting and includes the combined weight of wax, dirt, clean fibre wool and other non-fibre components and contaminants, typically measured on a scale in the shearing shed (Schlink, 2009). Clean fleece weight (CFW) is the total greasy wool yield minus suint, dust, wax and other contamination matter and therefore refers to the total amount of usable wool fibres within the unprocessed fleece (Schlink, 2009). Clean fleece weight is an economically important trait as higher prices are offered for wools with a greater clean fleece yield and therefore is directly related to the commercial value of wool (Holman & Malau-Aduli, 2012). Clean fleece weight is measured by taking core samples from a wool bale which accurately indicates the amount of clean fleece yield (Holman & Malau-Aduli, 2012). The clean fleece yield produced on average for the South African Merino sheep ranges between 71% and 74% of the greasy fleece weight (Van der Merwe *et al*., 2020).

Fertility traits

The profitability of sheep production systems is largely determined by the improvement of fertility and fitness traits (Mekuriaw & Haile, 2014b). Although breeding objectives differ for different production systems, improving fertility traits of both male and female sheep should be a universal goal (Olivier *et al*., 1998). Reproductive performance is a key factor determining the efficiency of flock production and is affected by numerous factors including season, photoperiod, age, nutrition, management, behaviour as well as genetics (Ajafar *et al*., 2022). Selecting for and improving reproduction traits in sheep thus poses many difficulties, as most of these traits have low heritability estimates, reflecting small genetic variance. Depending on the reproductive trait, some traits such as inter-lambing period are also expressed later in life, are sex-limited and are time consuming to record (Bolormaa *et al*., 2017). The fertility traits that are recorded on-farm, are listed in Table 2.2.

Table 2.2 Description of fertility traits and their respective heritabilities (h^2) and standard errors (SE) for the Merino sheep breed (Adapted from Olivier, 2014).

Fertility Traits	**Description**	**Heritabilities and standard errors (h^2 ±SE)**	**References**
Lambing Rate (Number of lambs born)	Percentage of ewes that birthed a live lamb (Hall & Paruelo, 2006)	0.05 ± 0.03	(Woolaston *et al.*, 1995)
		0.23 ± 0.05	(Olivier *et al.*, 2001)
		0.19 ± 0.04	(Olivier *et al.*, 2001)
		0.13 ± 0.01	(Safari *et al.*, 2005)
		0.10 ± 0.01	(Vatankhah & Talebi, 2008)
		0.10 ± 0.01	(Zishiri *et al.*, 2013)
Number of Lambs weaned per lambing	Number of lambs weaned in a 12-month period divided by the number of lambing's in the same 12-month period (Ontario sheep health programme, 2014).	0.05 ± 0.01	(Safari *et al.*, 2007a)
		0.05 ± 0.01	(Safari *et al.*, 2005)
		0.11	(Notter, 2008)
		0.10 ± 0.01	(Vatankhah & Talebi, 2008)
		0.09 ± 0.01	(Zishiri *et al.*, 2013)
Total Weight of Lamb Weaned (kg)	Depends on the ewes ovulation rate, mothering ability, as well as the viability and growth rate of the lamb (Duguma *et al.*, 2002)	0.19 ± 0.04	(Olivier *et al.*, 2001)
		0.21 ± 0.05	(Olivier *et al.*, 2001)
		0.15 ± 0.04	(Cloete *et al.*, 2004)
		0.13 ± 0.03	(Safari *et al.,* 2005)
		0.12 ± 0.01	(Vatankhah & Talebi, 2008
Age at First Lambing (months)	The difference between the birthdate of the ewe and the date of her first lambing (SA Studbook Annual Academic Report, 2022).		
Inter-lambing Period (days)	Calculated as the difference between the ewes most recent date of lambing and the date of lambing of her previous lamb (SA Studbook Annual Academic Report, 2022).		
Scrotal Circumference (SC) (cm)	Measured using a scrotal tape around the widest part of the scrotum when the testicles are fully extended. A larger SC indicates a higher daily sperm count production (Duguma et al., 2002).	0.29 ± 0.04	(Duguma *et al.*, 2002)
		0.40 ± 0.05	(Duguma *et al.*, 2002)
		0.21 ± 0.06	(Safari *et al.*, 2005)

Growth traits

Growth traits are generally defined as the weight of the animal at various ages in its life, including birth weight, weaning weight (usually taken between 3 to 5 months of age), post-weaning weight (generally up to 12 months of age), as well as adult/mature weight (taken after 12 months of age) (Safari *et al*., 2005). Weights at different ages are measured and recorded on the farm by the breeder and then adjusted for sex, rearing status (weaning weight), age at measurement and age of the dam differences within the same management and environmental contemporary groups when processed by SA Stud Book, to determine the phenotypic indices for the traits (SA Stud Book Annual Academic Report, 2022). Body weight and rate of gain are the most economically important and easily measurable traits of sheep, allowing for rapid genetic progress to be made (Mekuriaw & Haile, 2014b).

In this study only weaning weight and body weight at wool test (mature weight) will be considered. Weaning weight is important to measure as it not only gives an indication of the mothering ability and efficiency of the ewe but also indicates the growth potential and growth rate of lambs (SA Stud Book Performance Recording, 2015). Weaning weights are typically recorded between 60 and 150 days of age, with the average weaning weight of Merino’s ranging between 30kg and 33kg (SA Stud Book Annual Academic Report, 2022). Weaning weight is economically important as it is used to determine the true genetic growth potential of the animal and influences the total weight weaned per ewe per production year, which considers the quality of lambs produced (SA Stud Book Performance Recording, 2015). The most important growth traits to be recorded on-farm, are listed in Table 2.3.

Table 2.3 Description of growth traits and their respective heritabilities (h^2) and standard errors (SE) for the Merino sheep breed (Adapted from Olivier, 2014).

Growth Traits (kg)	**Description**	**Heritabilities and standard errors (h^2 ±SE)**	**References**
Birth Weight	Measured within 3 days of birth.	0.29 ± 0.04	(Vaez Torshizi *et al*., 1996)
		0.05 ± 0.04	(Annalla & Serradilla, 1998)
		0.35 ± 0.08	(Wuliji *et al*., 2001)
		0.19	(Duguma *et al*., 2002)
		0.21 ± 0.03	(Safari *et al*., 2005)
		0.19 ± 0.02	(Safari *et al*., 2005)
		0.15 ± 0.02	(Safari *et al*., 2005)
		0.18 ± 0.01	(Safari *et al*., 2007b)
Pre-Weaning Weight (42 Days)	Measured at 6 weeks (42 d); Accepted: 20-80d	0.08 ± 0.04	(Annalla & Serradilla, 1998)
		0.13 ± 0.05	(Annalla & Serradilla, 1998)
		0.34 ± 0.08	(Wuliji *et al*., 2001)
Weaning Weight (100 Days)	Measured at just over 3 months (100 d); Accepted: 30-150d	0.37 ± 0.08	(Lewer *et al*., 1994)
		0.27 ± 0.03	(Mortimer & Atkins, 1995)
		0.27 ± 0.04	(Vaez Torshizi *et al*., 1996)
		0.23 ± 0.02	(Safari *et al*., 2005)
		0.18 ± 0.02	(Safari *et al*., 2005)
		0.18 ± 0.04	(Safari *et al*., 2005)
Post-Weaning Weight (270 Days)	Measured at approximately 9m	0.18 ± 0.04	(Snyman *et al*., 1996)
		0.44 ± 0.09	(Wuliji *et al*., 2001)
		0.28 ± 0.08	(Ingham *et al*., 2003)
		0.33 ± 0.02	(Safari *et al*., 2005)
		0.29 ± 0.03	(Safari *et al*., 2005)
		0.21 ± 0.01	(Safari *et al*., 2005)
Mature Weight (365 Days)	Measured at 12 m; Accepted: 320 to 540d	0.25 ± 0.10	(Woolaston *et al*., 1995)
		0.33 ± 0.15	(Brown *et al*., 2002a)
		0.35 ± 0.02	(Clarke *et al*., 2003)
		0.41 ± 0.02	(Safari *et al*., 2005)
		0.31 ± 0.03	(Safari *et al*., 2005)

2.4 Genetic Correlations

In selecting for multiple traits, it is important for breeders and animal scientists to take into consideration that traits of interest might have relationships and interact with one another. Genetic correlations indicate that the genetic potential for performance in one trait can be estimated from the performance in another correlated trait (Taylor, 2013). Therefore, when creating a selection index and breeding program with the aim to genetically improve economically important traits, genetic and phenotypic correlations must be accounted for (Oldenbroek & van der Waaij, 2014).

Economically, the most important wool traits influencing the profit of a wool enterprise are clean fleece weight (CFW) and fibre diameter (FD) (Holman & Malau-Aduli, 2012). These traits largely influence the property of fabrics, processing performance, softness and price per kilogram (Doyle *et al*., 2021). Due to their economic importance, it is vital that when selecting for these traits, correlations between these traits are considered. Sheep with a high clean fleece yield, generally have a coarser fibre diameter, indicating a positive, undesirable correlation (Safari *et al*., 2005). This is shown in multiple studies including Olivier (2014), where a genetic correlation (r_g) of 0.36 ± 0.04 was estimated, as well as in Safari *et al*., (2005) that reported a r_g of 0.28. The relationship between fibre diameter and clean fleece weight is, however, highly variable and there is opportunity to identify and select sheep which have a low fibre diameter with a relatively high clean fleece weight (Doyle *et al*., 2021).

Clean fleece weight is generally positively genetically correlated with other wool traits including favourable genetic correlations with staple strength and staple length (Olivier, 2014). However, selecting for CFW can result in excessive wool oil yield, as suggested by the significantly unfavourable, positive genetic correlation of 0.28 between CFW and wool oil (Matebesi *et al*., 2009a). Bodyweight at wool testing generally also has positive, favourable correlations with CFW and staple length and unfavourable correlations with fibre diameter and coefficient of variation of fibre diameter (CVFD) (Matebesi *et al.,* 2009a). This indicates that a heavier body weight will yield more clean fleece, however, will also result in a larger, and more variable fibre diameter (Holman & Malau-Aduli, 2012). Table 2.4 lists genetic and phenotypic correlations for wool traits of economic importance.

Table 2.4. Weighted means of literature estimates for genetic (below diagonal) and phenotypic (above diagonal) correlations for economically important wool traits (Safari *et al*., 2005).

Trait	GFW	CFW	FD	CVFD	SDFD	SL	SS	YLD
GFW	-	0.90	0.31	0.36	0.15	0.32	0.19	-0.04
CFW	0.86	-	0.25	-0.04	0.10	0.33	0.18	0.37
FD	0.36	0.28	-	-0.09	0.40	0.19	0.23	0.01
CVFD	0.09	0.19	-0.10	-	0.82	-0.12	-0.38	-0.13
SDFD	0.25	0.22	0.43	0.76	-	-	-	-0.13
SL	0.44	0.36	0.19	-0.06	-	-	0.07	0.19
SS	0.16	0.20	0.37	-0.52	-	0.05	-	0.15
YLD	-0.14	0.38	0.04	-0.08	-0.10	0.25	0.35	-

[1] GFW: greasy fleece weight; CFW: clean fleece weight; FD: fibre diameter; CVFD: coefficient of variation of fibre diameter; SL: staple length; SS: staple strength; YLD: yield

Generally, the sale of mutton and lamb contributes the most to the profitability of a sheep enterprise, therefore it is vital to achieve efficient growth rates in order to maximise income and profits (McGovern *et al*., 2020). The commercial value of sheep and lamb carcasses are determined by their weight and quality. Liveweights, including birth weight and weaning weight, allow farmers the ability to predict and assess these attributes early in the season and therefore offer substantial value to sheep producers (Jones *et al*., 2020). Live weights, which affect meat yield, is a key indicator of flock productivity and animal performance and thus poor growth rates can result in higher maintenance costs and an overall reduction in production efficiency (McGovern *et al*., 2020). Therefore, liveweights are used to achieve a fast and efficient growth rate (Atac & Altincekic, 2023).

An optimal birth weight is one where there are no complications during delivery and the survival of the offspring is maximised, typically averaging 4.2 kg for SA Merino sheep (Gardner *et al*., 2007). Birth weight also has a positive, favourable correlation on growth rate, particularly in the first, early stages of the sheep's life (Sveinbjörnsson *et al*., 2021). Weaning weight largely influences an animal's mature weight and production efficiency. Generally, lambs with a heavier weaning weight experienced faster growth rates post-weaning than lambs with a lighter weaning weight (Sveinbjörnsson *et al*., 2021). Jones *et al.* (2020), further showed that lambs with a heavier weaning weight were more likely to have leaner, muscular compositions and therefore produce more economically valuable carcasses. Therefore, a heavier weaning weight can result in a faster growth rate and more desirable carcass composition. Weaning weight, however, has a positive, unfavourable correlation with birth weight, which can result in dystocia (Jones *et al*., 2020). Table 2.5 lists genetic and phenotypic correlations for growth traits of economic importance.

Table 2.5 Weighted means of literature estimates for genetic (below diagonal) and phenotypic (above diagonal) correlations for economically important growth traits (Safari *et al*., 2005).

Traits	BW	WW	PWW	AW	G/D
BW	-	0.37	0.32	0.26	0.13
WW	0.47	-	0.70	0.56	0.16
PWW	0.29	0.85	-	0.74	-
AW	0.22	0.75	0.93	-	0.34
G/D	0.27	0.79	0.19	0.78	-

[2] BW: birth weight; WW: weaning weight; PWW: post weaning weight; AW: adult weight; G/D: growth rate

The genetic improvement of reproductive traits is essential in improving the overall production efficiency and profitability of a sheep enterprise (Bolormaa *et al*., 2017). Due to reproductive traits having generally low heritability estimates (due to a greater influence of environmental effects), reproductive traits are more difficult to genetically improve (Rosati *et al*., 2002). Table 2.6 lists genetic and phenotypic correlations for reproduction traits of economic importance.

Table 2.6 Weighted means of literature estimates for genetic (below diagonal) and phenotypic (above diagonal) correlations for economically important reproduction traits (Safari *et al*., 2005).

Traits	NLW/EJ	NLB/EJ	WW/EJ	NLW/EL	NLB/EL	WW/EL	EL/EJ	NLW/NLB
NLW/EJ	-	0.73	0.93	-	0.46	-	0.54	0.76
NLB/EJ	0.84	-	0.59	-	0.80	0.78	0.72	-0.09
WW/EJ	0.80	0.60	-	-	0.13	-	0.68	0.64
NLW/EL	-0.04	0.00	0.10	-	0.23	-	-	-
NLB/EL	0.62	0.89	0.05	0.70	-	0.23	0.03	-0.13
WW/EL	0.16	0.84	0.09	0.89	0.57	-	-	-
EL/EJ	0.73	0.79	0.70	0.42	0.44	0.32	-	0.04
NLW/NLB	0.63	0.52	0.41	0.55	-0.14	0.14	0.44	-

[3] NLW/EJ: number of lambs weaned/ewe joined; NLB/EJ: number of lambs born/ewe joined; WW/EJ: weight weaned/ewe joined; NLW/EL: number of lambs weaned/ewe lambing; NLB/EL: number of lambs born/ewe lambing; WW/EL: weight weaned/ewe lambing; EL/EJ: fertility; NLW/NLB: ewe rearing ability

2.5 Variance component estimation and genetic evaluation

2.5.1 Methods of genetic parameter estimation

In animal breeding, knowledge of genetic parameters of economically important traits is the main requirement in developing a selection programme (Meyer, 1989b). Estimation of genetic parameters involves breaking down the shared phenotypic covariances among relatives into distinct components. These components include variances attributed to additive genetic effects, dominance, epistasis, as well as permanent and temporary environmental effects (Thompson *et al*., 2005). This approach therefore relies on the known degree of relationship between animals and the resulting predicted covariances between them (Thompson *et al*., 2005). The various methodologies, approaches and progress in which population genetic parameters are calculated, are discussed below.

Analysis of variance (ANOVA) methodology

The estimation of variance components was developed from Fisher's analysis of variance table in 1925 and is a well-established summary for testing hypotheses using ratios of mean squares (Lee, 2000). Under normality assumptions, the ANOVA has an F-distribution which was initially developed for models with fixed effects, in which the F-statistics were best suited to testing hypotheses for different levels of factors which had equal effects (Searle, 1995). Traditionally the phenotypic covariances between relatives have been estimated using ANOVA or analogous procedures and require individuals to be assigned to groups with the same degree of relationship with all members. The most considered family structures include paternal half-sib groups, parents, and their offspring (Meyer, 1989b).

ANOVA determines the covariance among relatives by partitioning the sum of squared observations due to different sources of variation in the model of analysis, such as groups of relatives and equating the corresponding mean squares (derived as the sum of squared observations divided by the associated degrees of freedom) (Meyer, 1989). For balanced data, the partial sum of squared observations is orthogonal, and their expected values are simple linear combinations of the variance components between groups so that calculations are straightforward, even for multiple cross classifications (Thompson *et al.,* 2005). ANOVA allows for the identification of environmental effects that influence traits of economic importance for the construction of contemporary groups. ANOVA is used to test which factors significantly influence traits of interest. Different fixed effects are added to the ANOVA model in order to increase the amount of variance explained, as well as to avoid biased EBVs.

The ANOVA method has the following model (Searle, 1995):

$$Y_{ijk} = \mu + \alpha_i + \beta_j + y_{ij} + e_{ijk}$$

Where:

Y_{ijk} = economic trait of interest
μ = mean of the trait
α_i, β_j, y_{ij} = unknown fixed effects
e_{ijk} = random error terms

The ANOVA method offers various advantages, such as its ease of calculation and interpretation. This method has only a few basic assumptions, including that the resulting estimators are unbiased, as well as the estimators have the property of being minimum variance quadratic unbiased (Searle, 1995). Disadvantages of the ANOVA method, however, include producing estimates that can be negative and containing distributions that are unknown. Additionally, sampling variances involve complicated functions of the numbers of observations in subclasses of the data (Searle, 1995). Therefore, analytic comparison of different applications of the ANOVA method is impossible and arithmetic comparison cannot produce satisfactory and informative results. Due to the shortcomings of the ANOVA method, the Maximum Likelihood estimation was developed to be used for especially unbalanced data and for many cases of balanced data (Meyer, 1989).

Maximum Likelihood Methodology

The methodology of Maximum Likelihood estimation (ML) was developed by R.A. Fisher in the 1920’s (Searle, 1995). The ML method differs from ANOVA as the ANOVA method of analysis is based on the assumption of random sampling, resulting in estimates that are biased by selection, whereas the ML method however, takes into account that data and records in animal breeding which originate from field records and therefore account for genetic selection (Meyer, 1989). The ML methodology is beneficial, as all information which has contributed to selection decisions are included in the analysis and thus results in less bias by selection compared to the ANOVA method (Meyer and Thompson, 1984). The ML estimation requires assumptions about the distribution of the data in order to calculate the likelihood of particular numeric values of genetic parameters (Thompson *et al.,* 2005). The ML estimation depicts how likely it is that the data has been sampled from a population with these parameter values and is, by definition, the parameter values for which the likelihood is maximized (Searle, 1995). In estimating variance components by ML, data is generally assumed to have a multivariate normal distribution, as the multivariate normal distribution is exploited in order to yield unbiased estimates (Meyer, 1989).

Advantages of the ML method include that it produces consistent, and asymptotically normal estimates, produces non-negative estimates, and all information that is available is utilised in an efficient manner. Additionally, the ML method better suits scenarios which cannot be accommodated by standard ANOVA methods (Meyer, 1989). Although the ML method is generally beneficial, a major disadvantage is that the fixed effects in a mixed model are treated as known effects, therefore the loss in the degrees of freedom due to fitting these effects are ignored (Thompson *et al.,* 2005). If the model of analysis comprises of many fixed effects, which is most common when using performance data in animal breeding, this can produce biased estimates, in which the residual variances are severely underestimated (Searle, 1995).

Restricted Maximum Likelihood (REML) Methodology

Due to the continuous development of technology and computational output, as well as the development of specialised algorithms, Restricted Maximum Likelihood (REML) became a main method of variance component estimation in animal breeding, using quantitative livestock data (Meyer, 1986). The REML method is based on maximising the likelihood on the error contrasts that have not contributed any information on fixed effects rather than all of the contrasts, as done by the ML Methodology (Thompson *et al*., 2005). The REML method overcame the ML drawback that fixed effects are treated as known by maximizing only the part of the likelihood which is independent of the fixed effects (Meyer, 1986).

The implementation of REML depends on the mixed model equations (MME) introduced by Henderson (1973) in order to construct Best Linear Unbiased Predictors (BLUP) (Thompson *et al*., 2005). To allow for the accurate prediction of breeding values, it is important to consider the genetic relationships between all animals (Searle, 1995). The Animal Model has largely influenced the use of mixed model methodology in the statistical analysis of data and typically includes a random effect for the breeding value of each animal, including animals with records and animals which are parents only, in which all known relationship information must be incorporated in the analysis (Kruuk, 2004). Animal Models can account for changes in genetic means and variances and therefore allows an optimal analysis of data involving multiple generations (Meyer, 1986). Using the Animal Model, covariances between random effects for relatives are also considered by specifying the variance matrix of random effects. Non-additive genetic components can be estimated by fitting a corresponding random effect, such as a dominance or maternal genetic effect, for each animal (Kruuk, 2004).

Although the REML method has the limitation of containing no information about estimating the fixed effects, it does offer various advantages over the Maximum Likelihood method. Advantages include that REML produces solutions that are identical to the ANOVA method for balanced data, REML estimators take into account the degrees of freedom associated with the fixed effects in the model, and it effectively eliminates bias in variance estimation due to not knowing the fixed effects (Searle, 1995). The use of REML methodology had the limitation of requiring complex, heavy computational software and therefore was not widely accessible and available, however due to the development of statistical packages (Searle, 1995), REML is now the most used and preferred method to estimate variance components.

Bayesian approach

Bayesian estimation refers to the estimation of genetic parameters through the use of inverse probability (Blasco, 2001). The Bayesian method obtains the probability density function of the genetic parameter of interest for a dataset. This density function is then used to obtain the most probable value of the parameter, or the probability that the parameter resides within certain limits (Blasco, 2001). The Bayesian approach is largely advocated for, as it allows for the use of prior knowledge in order to make informed decisions. If significant prior information exists and can be used, ignoring this information can be seen as wasteful. A difficulty in using prior information is accurately specifying and convincing others that this information is reasonable and therefore it is recommended to use prior information sparingly for inference problems (Thompson *et al*., 2005). There are typically two types of prior information that exists: Data based and non-data based (Gianola & Fernando, 1986). Data based prior information refers to information that is collected from past data, in a scientific manner, which is relevant to the current dataset, whereby non-data based prior information is the information resulting from theoretical considerations. The use of priors based on data or on theoretical grounds, as opposed to personal priors, is of general acceptance in statistical practice (Gianola & Fernando, 1986).

Statisticians were reluctant to use Bayesian methods in order to estimate genetic parameters due to the difficulties found in the use of prior information inherent to the Bayesian paradigm (Blasco, 2001). Another disadvantage of the Bayesian approach is that it tends to give estimates of zero for between group variance components (Blasco, 2001).

2.5.2 History of statistical genetic models

Quantitative traits are based on models in which many genes influence a trait and where non-genetic factors play a crucial role (Hill, 2010). Due to the genetic and environmental interactions, it is difficult to determine the influence of individual genes and how they affect a trait. Statistical methods were therefore developed to partition phenotypic variation and describe the resemblance between relatives (Hill, 2010). Statistical methodology and its continuous development have played a crucial role in animal breeding from foundational models that include the Infinitesimal model, the Sire and Maternal Grandsire Model, the Animal Model and Random Regression Models, to more efficient computational methodologies including BLUP, REML and genomic selection (Gianola & Rosa, 2015).

Statistical models used in animal breeding and genetics consists of a mathematical function that relates observations to random effects. This includes assumptions regarding the distribution of the observations and the random effects, including additive genetic values, dominance and epistasis, as well as components of variance and covariance (Gianola, 2000). The most widely accepted assumption is the assumption of normality. A reason for this assumption is due to many traits having many genes acting additively, with infinitesimally small substitution effects (Gianola & Rosa, 2015). Both traditional methods, as well as more recent and efficient computational methodologies of models used for variance component estimation, are discussed below.

Sire and Maternal Grandsire Models

The Sire Model is a statistical model typically used in dairy systems and assumes sires are unrelated to each other and that random mating occurs between sires and dams, resulting in the sire breeding values being regressed toward the population mean (Weigel *et al.*, 2017). The Sire Model contains a random sire effect within a fixed group effect and when BLUP methods are used, a set of mixed model equations are solved and an evaluation results in a group and sire solution (Quaas & Pollak, 1981). Sire evaluation for models represent an alternative approach to mixed model equations. In this modified system, sire evaluations serve as solutions, unlike regular mixed model equations where evaluations depend linearly on group and sire solutions (Quaas & Pollak, 1981).

The common matrix notation for sire evaluation is (Quaas & Pollak, 1981):

$$y = Xh + ZQg + Zs + e$$

Where:

h = fixed herd-year-season effects
X = incidence matrix relating herd-year-season to records
g = fixed group effects
ZQ = incidence matrix relating group of sire to daughters' records
s = random vector of sire effects
Z = incidence matrix relating sires to daughters’ records
e = random vector of errors

The assumption that sires are unrelated to each other, however, is highly unrealistic due to continual advancements being made with regards to artificial insemination and embryo transfer, which leads to large families of paternal half-siblings and small families of full-siblings (Weigel *et al.*, 2017). The Maternal Grandsire Model was introduced in order to address and combat this unrealistic assumption (Weigel *et al.*, 2017). The Maternal Grandsire Model incorporates an extra random effect which represents the additive merit of the maternal grandsire and a fixed effect which represents the genetic group of the maternal grandsire (Weigel *et al.*, 2017). Disadvantages of this model include that the maternal relationships between dams are not accounted for, and the model does not add value in cases where the maternal grandsire was unknown (Weigel *et al.*, 2017).

The Animal Model

Methodology for the estimation of breeding values was developed by the statistician C. R. Henderson (1911 – 1989), which enabled the ranking of animals according to their estimated genetic potential, which further resulted in more accurate genetic selection and thus faster genetic improvement (Oldenbroek & van der Waaij, 2014). In 1948, Henderson developed the mixed model of random and fixed effects which had been proven to give the same results as a selection index model while having fewer algorithms (Hunlun, 1989). Henderson then improved the accuracy with which breeding values are estimated by deriving BLUP in 1950 (Mofakkarul Islam *et al*., 2013). The accuracy of the breeding value depends on the amount and the type of information that can be used in a statistical model (Hunlun, 1989). Henderson further suggested the integration of full pedigrees to include genetic relationships between all individuals so that the performance data of relatives can be included in the estimation of breeding values, which brought about the practical implementation of the Animal Model in the 1980's (Oldenbroek & van der Waaij, 2014). In the development of statistical methodology, the next phase was developing the mixed, linear model which typically follows the form of fixed genetic groups, fixed contemporary groups, random additive effects and a residual effect, to large datasets (Ronnegard & Lee, 2013).

The Animal Model has become the global standard for genetic evaluation of livestock animals as it accounts for non-random mating and places greater emphasis on dams, which the Sire and Maternal Grandsire Models were unable to do (Kruuk, 2004). The Animal Model provides further advantages including the accurate assessment of the genetic quality of mates and provides a consistent framework for evaluating both males and females simultaneously (Gianola & Rosa, 2015).

The mixed linear Animal Model generally follows the form of (Gianola & Rosa, 2015):

$$y = Xb + Za + e$$

Where:

y = n x 1 vector of observations
n = number of records
b = p x 1 vector of fixed effects
p = number of levels for fixed effects
a = q x 1 vector of random animal effects
q = number of levels for random effects
e = n x 1 vector of random residual effects
X = design matrix of order n x p, which relates records to fixed effects
Z = design matrix of order n x q , which relates records to random animal effects

Random Regression Models

Random Regression Models were first introduced by Henderson, Laird and Ware around 1982, with their first application in dairy cattle breeding for the analysis of test-day production records occurring in 1994 (Schaeffer, 2004). The linear Random Regression Model was developed due to increasing focus on the treatment of repeated measurements, as well as to address scenarios in which successive records follow a time series with some trajectory, such as the growth curve (Gianola & Rosa, 2015). These models are therefore used for the analysis of repeated records where the observations for a trait are collected several times over the course of an animal's life such as periodic body weights (Schaeffer, 2004). These models also provide estimates of the genetic, permanent environmental and residual variances, as well as some population genetic parameters such as heritabilities and repeatabilities (Weigel *et al*., 2017). Typically, each individual is measured longitudinally, with the number of measurements per individual varying, which results in longitudinal unbalancedness (Gianola & Rosa, 2015). A mathematical formula which describes the expected trajectory of an animal, and a residual that indicates observations that vary or depart from the expected described trajectory, marks the first stage of the Random Regression Model (Gianola & Rosa, 2015). The second stage describes variation between individuals where the residual reflects the inability of the model to completely explain the variation of the parameters. Any additional stages needed in order to explain uncertainty about all population parameters can be imposed in a Bayesian context (Gianola & Rosa, 2015).

The Random Regression Model is beneficial as it can provide valuable insight about the trajectory of biological processes such as body fat deposition (Weigel *et al*., 2017). These models also provide information about correlated responses to selection for traits expressed over time. The results of Random Regression Models are used to facilitate the development of efficient data collection protocols that aim to maximize genetic progress (Weigel *et al*., 2017). Disadvantages of the Random Regression Model include that it is computationally demanding as well as that it requires the trajectories of the additive genetic, permanent environment, and temporary environment effects to be properly modelled (Weigel *et al*., 2017). Random Regression Models have been applied in various aspects of animal breeding and production systems, this includes its use in feed intake monitoring, body condition scores, conformation traits, heart girth in dairy cattle, weights and back fat thickness of swine and beef cattle as well as litter size in swine (Schaeffer, 2004). This model has various potential applications, including predicting wool yield in sheep, assessing the quantity and quality of sperm production in male livestock species, is able to analyse interactions between the genotype and environment, and can be used to conduct survival analysis (Schaeffer, 2004).

The simplified form of a Random Regression Model for a single trait is (Schaeffer, 2004):

$$y_{ijkn:t} = F_i + g(t)_j + r(a, x, m1)_k + r(pe, x,m2)_k + e_{ijkn:t}$$

Where:

$y_{ijkn:t}$ = n^{th} observation on the k^{th} animal at time t belonging to the i^{th} fixed factor and the j^{th} group
F_i = fixed effect that is independent of the time scale for the observations
$g(t)_j$ = function that accounts for the phenotypic trajectory of the average observations across all animals belonging to the j^{th} group
$r(a, x, m1)_k$ = notation adopted for a random regression function, where a denotes the additive genetic effects of the k^{th} animal
x = vector of time covariates
m1 = the order of the regression function
$e_{ijkn:t}$ = a random residual effect

Non-linear models: Threshold traits and Survival analysis

Threshold Models, first introduced by Gianola and Foulley in 1983, allow for the proper modelling of binary or categorical traits, such as stillbirth or dystocia (Weigel *et al*., 2017). The Threshold Model does not follow the assumption of normality; however, it has a link function which matches observed binary phenotypes with sire breeding values on an underlying “liability” scale (Weigel *et al*., 2017). If liability falls between two consecutive thresholds, it is treated as equivalent to an observation in the corresponding response category (Gianola & Rosa, 2015). In general, Threshold Models result in more accurate estimated breeding values than when fitting binary phenotypes with a conventional linear model (Weigel *et al*., 2017). Threshold Models are generally used in conjunction with maternal effects models, and their application is generally limited to Sire Models, rather than Animal Models (Weigel *et al*., 2017). Survival analysis is used primarily on functional traits such as longevity or length of productive life in which proportional hazard models are employed in order to determine population parameters (Gianola & Rosa, 2015). This model includes random additive genetic effects and relationships, which allow for the computation of sire breeding values for survival (Weigel *et al*., 2017).

2.6 Comparing pre- and post-genomic genetics

The development and introduction of genomic data is providing new opportunities that aid in increasing the selection accuracy and efficiency of livestock production (Goddard, 2012). Genomic prediction and selection are an approach that is being increasingly applied in animal breeding and refers to methodologies where all DNA markers are simultaneously used in a statistical model to predict the genetic merit or breeding value of an animal (Meuwissen *et al*., 2001). The genomic era of genetics has allowed for further gains in animal breeding to be made due to the additional advantage of being able to improve the accuracy of predicting EBVs through the inclusion of many DNA markers, specifically the use of Single Nucleotide Polymorphisms (SNPs), which are genotyped in a single assay (Hayes & Goddard, 2010). Genomic information allows breeders the opportunity to increase the rate of genetic progress due to the ability to accurately select animals at an earlier age, select for traits that are difficult and costly to measure, as well as for genetic improvement of traits with low heritability values (Swan *et al.,* 2012).

It was predicted that the inclusion of marker information together with phenotypic data when estimating breeding values could result in an increase in genetic gain of between 8% and 38% (Meuwissen & Goddard, 1996). However, including marker information when predicting breeding values could not be implemented at the time due to genomic selection requiring a large number of SNPs and it being too expensive to genotype a sufficient number of animals (Meuwissen *et al*., 2001). Genomic selection has, however, become more affordable and accessible due to the large-scale sequencing of livestock genomes which has resulted in the required SNPs being commercially available for livestock species (Matukumalli *et al*., 2009). Genomic selection is considered continuous with traditional selective breeding as it still relies on selecting parents based on predicting how their offspring will perform (Kramer & Meijboom, 2022). Genomic selection, however, differs from other marker-based strategies which mostly focus on individual markers that have strong statistical evidence for significant phenotypic effects (Meuwissen *et al*., 2001) and does not require the identification of the genes or sites causing variation in the trait (Goddard, 2012). The accuracy of genomic selection is affected by many factors, including the statistical models used, the size of the sample data, the heritability of the trait, as well as the degree of linkage disequilibrium (Muir, 2007).

Two statistical methods that can be used for genomic selection include genomic best linear unbiased prediction (GBLUP) and the non-linear Bayesian approach (Meuwissen *et al*., 2016). The linear Single Step GBLUP approach uses genomic information in the form of a genomic relationship matrix that defines the additive genetic covariance between individuals (Clark, 2013). GBLUP estimates the genomic relationship coefficients with greater accuracy than when using pedigree-based information, as the genomic information can capture Mendelian sampling across the genome (Nishio & Satoh, 2014). Genomic selection based on GEBVs requires dense markers that are spread evenly across the genome in order to take advantage of all the available genetic variation (Muir, 2007).

The statistical model for the GBLUP method is (Nishio & Satoh, 2015):

$$y = X\beta + Zaa + Zdd + Zii + e$$

Where:

y = vector of the phenotypes
β = vector of the fixed effects
a, d, and i = vectors of α, δ, and ε terms, respectively
X, Za, Zd, and Zi = are incidence matrices linking the phenotypes to β, a, d, and i, respectively
e = vector of errors

The non-linear, Bayesian approach assumes that some SNPs have an effect, but others do not, resulting in Bayesian methods having a higher accuracy than the GBLUP method when computer simulations are used instead of real data (Meuwissen & Goddard, 2010). BayesC assumes that the SNPs with effects are normally distributed, therefore is nearest to SNP-BLUP, BayesB uses the t-distribution allowing for some SNPs to have very big effects, while BayesR assumes a mixture of normal distributions, which allows for some SNPs with very big effects (Meuwissen *et al*., 2016). Table 2.7 summarises the linear and non-linear statistical approaches used in genomic selection.

Table 2.7 Summary of statistical approaches to genomic selection (Goddard, 2012; Meuwissen *et al*., 2016).

Method	Assumption	Use	Population	Examples
GBLUP (Linear)	All SNPs have small effects	Large number of QTL with small effects	Within breed	G-BLUP, ssGBLUP
Bayesian (Non-linear)	Only a fraction of the SNPs has an effect	Small number of QTL with large effects	Across breeds	BayesR, BayesC, BayesB

Genomic selection increases the accuracy of genetic selection and therefore rate of genetic gain as it provides breeders with the ability to select animals with a high genetic potential at an earlier age, thereby shortening the generation interval, as well as decreasing costs as it eliminates the need for progeny testing (Goddard, 2012). Genomic selection is further beneficial as it is not sex limited, therefore extends to all traits recorded in a reference population, aids in the selection of young animals with no phenotypic data available, as well as allows for genetic improvement for traits that are difficult and costly to measure (Zhang *et al*., 2013). Typically, the expected benefits of genomic selection for sheep breeding are less than that for cattle breeding (15% and 40% for wool and meat sheep respectively) and primarily relate to the opportunities of more accurate selection at an early age (Stock & Reents, 2013). The benefit of genomic selection is generally smaller in sheep as several important traits have high heritability, and there is less information available to derive accurate prediction equations as there are fewer progeny tested sires (Van Der Werf, 2009). Other challenges when implementing genomic selection in sheep breeding includes the cost of maintaining reference populations due to a higher genetic diversity within and between sheep breeds, as well as the limited ability of individual breeders to invest in genotyping (Van Der Werf, 2014). The sustainable use and implementation of genomic selection in sheep breeding requires low density genotyping of large numbers of animals with the imputation to high density information in order to provide predictability of breeding values that extend across the breed (Van Der Werf, 2014).

2.7 Conclusion

Stud breeders and animal scientists rely on population genetic parameters such as heritability, repeatability and genetic correlations, as well as EBVs for accurate genetic selection and improvement. The South African Merino sheep breed is of interest due to its dual-purpose nature, ability to adapt and produce in varying, harsh climates, as well as due to the breed’s efficient and accurate history of data collection and recording. Updating and re-estimating variance components must be done in order to ensure maximum accuracy when estimating EBVs. The incorporation of genotypic information to estimate GEBVs will aid in the genetic improvement of difficult to measure traits and therefore provides many benefits including increasing the accuracy with which breeding values are estimated of especially young animals, therefore increasing the rate of genetic gain. As this study will result in the genetic parameters of the SA Merino population to be updated, estimated breeding values will be based on more representative population parameters, resulting in faster genetic progress and improvement.

Chapter 3: Materials and Methods

3.1 Introduction

In this study, the variance components and breeding values (EBVs) for the South African Merino sheep breed for application in genetic and genomic evaluations were estimated. Routine updating and re-estimation of variance components should be performed at least once per generation to ensure the application of representative genetic parameters for the population in the estimation of EBVs. As the current generation's measurements will also be included, it is important to capture genetic changes that might have occurred in the population due to natural and artificial selection, mutations and migration. This study further incorporated genotypic information in order to estimate genomically enhanced breeding values (GEBVs) for more accurate prediction of breeding values of especially the young, unmeasured animals of the population. Pedigree and performance data of the South African Merino sheep breed was obtained from SA Stud Book with the required consent from the SA Merino Breeders Association. The data included a selection of routinely recorded traits to represent both growth and wool traits such as weaning weight (kg), body weight at wool test (kg), clean fleece weight (kg), fibre diameter (μm), coefficient of variation of fibre diameter (%) and staple length (mm). The data was obtained from official wool tests, analysed by the Wool Testing Buro in Gqeberha. Ethical approval for the use of secondary data was obtained from the Ethics Committee of the Faculty of Natural and Agricultural Sciences at the University of Pretoria (Reference number: NAS144/2023).

3.2 Materials

3.2.1 Population and distribution of the SA Merino sheep included in the study

The population of South African Merino sheep included in the current study consisted of 864 754 sheep, of which 457 757 (52.94%) animals were females and 406 996 (47.06%) were males. The pedigree information included animals born from 1919-07-20 to 2023-05-29, of which the birthdate was unknown for one animal. Dams were known for 658 787 animals (76.18%), and sires were known for 603 605 (69.80%) animals. Both parents (sire and dam) were known for 578 839 (66.94%) animals, while both parents were unknown for 181 201 (20.95%) animals. The sheep used in this study originated from 298 breeders.

Figure 3.1 contains information of South African Merino sheep from every province in South Africa. Figure 3.1 depicts the number of Merino's in the dataset born per province, with most Merino's born in the southern parts of the country (Eastern Cape: 340 862 animals and Western Cape: 265 741 animals) and the least born in Gauteng (245) over all the birth years.

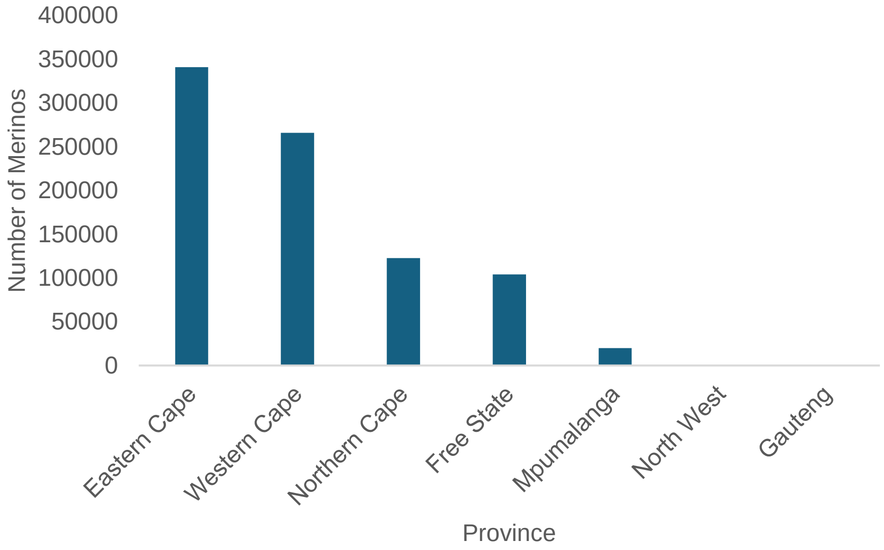


Figure 3.1 The distribution of the Merino sheep breed per province in South Africa over all the birth years.

3.2.2 Phenotypic data

Traits for which variance components were estimated, were weaning weight (kg), body weight at wool test (kg), staple length (mm), clean fleece weight (kg), fibre diameter (μm) and coefficient of variation of fibre diameter (%). The number of records, unique dams and sires, as well as the number of keepers for weight traits and flocks for wool traits are depicted in Table 3.1 for all the different traits. Unique dams and sires refers to the individual parent animals that were counted once for each specific trait, ensuring that there were no duplications in the data.

Table 3.1 demonstrates the unedited data available for the various traits measured for the South African Merino sheep breed. Weaning weight had the highest number of records at 581,242, indicating extensive data collection for this trait over many years.

Table 3.1 The number of records, unique dams and sires, as well as keepers/flocks for each trait of the South African Merino sheep breed.

Trait	Number of records	Number of Dams	Number of Sires	Number of Keeper/flocks
Weaning weight (kg)	581 242	175 629	6 874	175
Body weight at wool test (kg)	457 233	27 171	2 818	91
Clean fleece weight (kg)	517 319	27 115	2 790	92
Fibre diameter (μm)	471 941	27 264	2 837	93
Coefficient of variation of fibre diameter (%)	458 303	25 043	2 350	87
Staple length (mm)	459 303	27 181	2 739	92

3.3 Methodology

3.3.1 Data cleaning and initial analysis

Datasets containing records for weaning weight and wool trait information of interest for the South African Merino sheep breed were received in a csv format from SA Stud Book. The datasets were imported into the statistical R Studio software program (RStudio Team, 2020) for data editing, manipulation and statistical analyses. Using R, data description was done for all traits, with regards to the number of records, animals, sires, dams, and herds involved. Before editing and cleaning of the imported files, simple statistics on both datasets were done including calculating the minimum, 1st quartile, median, mean, 3rd quartile, maximum, standard deviation, kurtosis and skewness values. Table 3.2 shows the descriptive statistics of the unedited data.

Table 3.2 Descriptive statistics of the unedited data including mean, median, standard deviation, first and third quartiles and minimum and maximum values of weight and wool traits of the SA Merino population.

Trait	**Min**	**1st**	**Med**	**Mean**	**3rd**	**Max**	**SD**
Weaning Weight (kg)	0.40	23.00	27.50	27.94	32.50	106.00	8.07
Body Weight at Wool test (kg)	2.00	88.00	98.00	84.20	105.00	1097.00	37.74
Staple Length (mm)	34.00	91.70	105.30	90.54	119.00	166.00	38.07
Clean Fleece Weight (kg)	0.02	2.26	3.10	3.15	3.99	1499.00	8.86
Fibre Diameter (μm)	15.30	16.60	17.70	17.33	18.80	29.25	3.38
Coefficient of variation of fibre diameter (%)	10.50	15.50	17.00	16.62	18.80	37.30	4.49

[1] Min: minimum; 1st: first quartile; Med: median; 3rd: third quartile; Max: maximum; SD: standard deviation

Table 3.2 highlights the importance of editing the data prior to analysis, as evidenced by the presence of implausible and unrealistic values shown per trait. Therefore, the data was extensively edited and cleaned allowing for the removal of any errors. Edited data ensures accurate and reliable results and avoids erroneous analyses. The dataset containing weaning weight information was filtered to exclude all animals with no weaning weight measurements or incomplete records (all animals with a measurement of '0', 'NA' or 'null' or with unknown weigh dates were excluded). Records with unknown dams, animals that were hand reared (indicated by a rearing status of 9), embryo lambs (indicated by animals with a service code of 3 on Logix and 4 on farm software), were all removed and excluded from the analysis. The dataset was then cleaned by checking for and removing any duplicated records. Using the accepted production norms for the South African Merino sheep breed, which are applied in the Logix National Genetic Evaluation of SA Stud Book (*i.e.* 10 – 80 kg for weaning weight, 30 - 150 days for age at weaning and 10 – 96 months for age of dam), the biological limits of these traits were assessed for implementation in editing of the data for this study's genetic evaluation. The confidence intervals (at a 95% level) were determined. The standard deviation was then used to determine realistic biological limits on the data (typically basing it around 2 standard deviations from the mean). Adjusting to 2 standard deviations from the mean, animals which had a weaning weight outside the range of 10 – 65kg were removed, animals outside the range of 35 – 182 days for age at weaning were removed. Finally, for the age of dam at birth of the lamb, records where dams had ages outside the range of 19 – 71 months, were removed.

This process was then repeated on the dataset containing the wool information. The dataset containing wool traits analysed in this study were filtered to exclude all animals with no dam records, as well as records with unknown measurements (all animals with a measurement of ‘0’, ‘NA’ or ‘null’ were excluded). The dataset was then cleaned by checking for and removing any duplicated animals and measurements. The accepted production norms for the South African Merino sheep breed applied in the Logix National Genetic Evaluation of SA Stud Book (*i.e.* 50 - 160 for body weight phenotypic indices at wool test, 45 – 170 for clean fleece weight phenotypic indices, 60 – 140 for fibre diameter phenotypic indices, 50 – 170 for staple length, phenotypic indices and 260 – 900 days for age at shearing, as well as 150 – 540 days for length of test) were used.

Simple statistics on both edited datasets were then determined including calculating the minimum, 1st quartile, median, mean, 3rd quartile, maximum, standard deviation and kurtosis and skewness values. This aided in comparing the unedited data with the edited, clean data statistics. The spread of the data was also assessed with the aid of distribution graphs, such as boxplots, bar graphs and line graphs.

3.3.2 Analysis of Variance (ANOVA)

Environmental effects that significantly influence the traits of interest were identified in order to construct contemporary groups and to allow for the adjustment for differences of these effects in the model when estimating the variance components of the traits. This was done by analyses of variance (ANOVA), using R at a significance level of 0.05.

The following model was used:

y = intercept + significant fixed effects + significant covariate functions + error

Where:

y = economic trait of interest
fixed effects = categorical effects such as sex and breeder
covariate functions = continuous functions such as age at weighing

ANOVA tests for both growth and wool traits started with testing of different levels for the categorical effect of number of seasons, namely two *versus* three seasons per year. These tests were conducted to determine whether two or three seasons explained more of the environmental variance of the traits in the model. The seasons were defined based on Figure 3.2, which depicts the number of Merino's born per month of the year over all the years available.

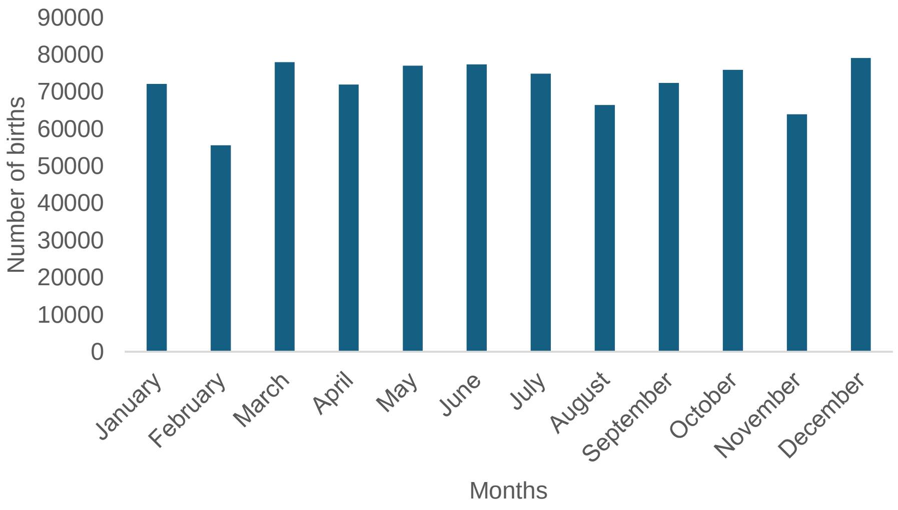


Figure 3.2 Distribution of births per month of the year for the SA Merino population

Most lambs were born in December (79 112), March (78 017) and June (77 367) and the least number of lambs were born in February (55 628) and November (63 970). For both growth and wool traits ANOVA tests were conducted to compare results using different seasons. Initially the months of the year were grouped into two seasons; March to August (Season 1) and September to February (Season 2). ANOVAs were then tested using three seasons: December to March (Season 1), April to July (Season 2) and August to November (Season 3).

For weaning weight, the environmental effects tested for in the ANOVA model included keeper (farm where animal was weaned), year of weaning, sex of the animal, birth status (born as a single, twin, triplet or quadruplet lamb), rearing status (reared as a single, twin, triplet or quadruplet lamb), age of the animal at weaning in days (tested for as linear and quadratic regressions), age of the dam as a categorical trait (3 levels: 1 = younger than 30 months; 2 = 30-60 months; 3 = > 60 months) or age of dam in months tested as a linear or quadratic regression. Environmental code as allocated by the keeper to indicate pasture/feeding difference amongst lambs weaned in the same contemporary group, management group, also allocated by the keeper to indicate differences in management amongst the lambs weaned in the same contemporary group, season (2 or 3 seasons per year) and reference number, which is the number of the weaning test in which the lamb was measured for weaning weight. These effects were added to the model in order to explain as much environmental variance as possible, to enable the estimation of unbiased EBVs in the genetic evaluation.

For weaning weight, the age of the dam included as a categorical effect *versus* a continuous effect was tested to determine which effect resulted in a higher R^2 and lower MSE value, and whether the effect should be included as a regression or a class effect. The results indicated that for weaning weight, the age of the dam fitted as a continuous variable achieved a higher R^2 value than the dam age code, which is a class effect. The construction of the contemporary groups was performed as follows: As the reference number of the weaning test already indicates which lambs were weighed together, it was concatenated with the keeper to ensure that the reference number is linked to the relevant keeper. Furthermore, the environmental code, as well as management codes were also included in the concatenation, so that the contemporary group then included all lambs that were reared together in the same environment and that were subjected to the same management procedures.

For wool traits, *i.e.* staple length (mm), fibre diameter (μm), coefficient of variation of fibre diameter (%), clean fleece weight (kg) and body weight at wool test (kg) (body weight at wool test is grouped with the wool traits as it is measured during wool testing), the environmental effects tested for significance with ANOVA included keeper, year of measurement, age at wool test (in months as linear or quadratic regressions), age of the dam as a categorical effect (3 levels: 1 = younger than 30 months; 2 = 30-60 months; 3 >60 months) or age of dam in months as a continuous variable, rearing status (animal reared as a single, twin, triplet or quadruplet). Environmental code as allocated by the keeper for animals within the same contemporary groups being subjected to different pasture/feeding regimes, season (defined similarly as for weaning weight: two or three seasons), reference number of the wool test and group number, as allocated by the keeper to indicate different treatments for animals tested in the same wool test. As rams and ewes always participate in different wool tests, sex need not be tested as a possible environmental effect that influences the traits significantly.

3.3.3 Estimating Variance Components

Variance components were estimated using multi-trait animal models that included the environmental effects that significantly influenced the data as fixed or continuous effects, as well as random permanent environmental and sire x herd effects, depending on the trait. With regards to the genetic effects, a direct as well as maternal genetic effect were included. A pedigree depth of three generations were used. These variance components were estimated using the VCE6 package (Groeneveld *et al.*, 2010) based on REML methodology. Restricted maximum likelihood (REML) has become the main method of variance component estimation in animal breeding. Linear mixed models are used to account for genetic and environmental effects, with the variance and covariance terms of these models usually being estimated by REML.

The Multi-trait Animal model has the form:

$$y = Xb + Za + e$$

Where:

y = vector of observations
b = vector of fixed effects
X = design matric to link observations to appropriate fixed effects
a = vector of random additive genetic animal effects
Z = design matrix to link observations to appropriate random effects
e = random residual vector

The dataset used for variance component estimation included all traits evaluated in this study, the significant environmental effects and contemporary groups. The dataset excluded animals born before 2009 and therefore only included animals born between the years of 2009 and 2022, to ensure that relevant and reliable estimates were produced based on recent generations. The dataset and pedigree file were initially put through PEST software (Groeneveld *et al.*, 2019) for recoding that is needed for interpretation by the VCE6 package. The recoded dataset and pedigree file were then applied in the VCE6 package (Groeneveld *et al.*, 2010) for variance component estimation. Before conducting the multi-trait evaluation, variance components were first estimated for each trait separately, followed by all bi-trait combinations, after which a multi-trait evaluation was performed, where all the traits were included simultaneously. This was to ensure that the multi-trait evaluation produced estimates that were accurate, logical and in-line with the single and bi-trait analyses. The genetic models used for the multi-trait variance component estimation of the weight and wool traits are listed below:

The final genetic model for weaning weight was: [Model 1]

$$y_{ijklmnopqrs} = \mu + CG_{ij} + sex_{ik} + rstat_{il} + bstat_{im} + age_{in} + dam\ age_{io} + HXS_{ip} + PE_{iq} + maternal_{ir} + animal_{is} + e_{ijklmnopqrs}$$

Where:

$y_{ijklmnopqrs}$ = weaning weight of the ith animal
μ = population mean
CG_{ij} = contemporary group of the ith animal i (where CG is reference number x environmental code x management group)
sex_{ik} = sex k of animal i
$rstat_{il}$ = Rearing status l of animal i (reared as a single, twin, triplet or quadruplet lamb)
$bstat_{im}$ = birth status m of animal i
age_{in} = linear regression of age n of animal i on weaning weight
$dam\ age_{io}$ = linear regression o of the age of the dam of animal i on weaning weight
HXS_{ip} = random herd by sire effect p for animal i
PE_{iq} = random permanent environmental effect q for dam of animal i
$Maternal_{ir}$ = random maternal additive genetic effect r of dam for animal i
$animal_{is}$ = random direct additive genetic effect s of animal i
$e_{ijklmnopqrs}$ = random residual effect

The final genetic model for the wool traits was: [Model 2]

$$y_{ijklmno} = \mu + CG_{ij} + rstat_{ik} + age_{il} + dam\ age_{im} + maternal_{in} + animal_{io} + e_{ijklmno}$$

Where:

$y_{ijklmno}$ = wool trait of the ith animal
μ = population mean
CG_{ij} = contemporary group of the ith animal i (where CG is reference number x environmental code x group code)
$rstat_{ik}$ = Rearing status k of animal i (reared as a single, twin, triplet or quadruplet lamb)
age_{il} = linear regression of age l of animal i on wool trait
$Dam\ age_{im}$ = linear regression m of the age of the dam of animal i (excluded for staple length)
$maternal_{in}$ = random maternal additive genetic effect n of dam for animal i
$animal_{io}$ = random direct additive genetic effect o of animal
$e_{ijklmno}$ = random residual effect

Bodyweight at wool test, clean fleece weight, fibre diameter and coefficient of variation of fibre diameter all followed the same model. Staple length, however, differed as the age of the dam was not included in the model as it did not have a significant influence on the trait. Unlike the model used for weaning weight, the models used for the wool traits excluded the random HXS and permanent environmental effects.

3.3.4 Determining estimated breeding values (EBVs)

Conventional breeding values were estimated using the PEST2 statistical software programme (Groeneveld *et al.*, 2019), based on Best Linear Unbiased Prediction (BLUP) methodology. The same genetic models used for variance component estimation were used in the estimation of breeding values. The complete, edited dataset containing all animals over all the years was used, with the pedigree built back over all generations.

The estimated breeding values obtained from the PEST2 evaluation were then used to calculate genetic trends by averaging the breeding values of measured animals, per year of birth, for every trait. For comparison to the national genetic trends, a base year of 2018 was implemented for all traits by determining the average breeding value for the year 2018 of measured animals and then deducting it from all the animals' breeding values for each trait. This ensured that the average of 2018 was set to zero, similar to that of the national trends. Genetic trends in the form of line graphs were constructed in R (RStudio Team, 2020) and compared to the national Merino genetic trends obtained from SA Stud Book.

The top ten sires and top ten young rams for each trait based on their EBVs were identified using R (R Studio team, 2020). To identify the top ten sires, the following criteria was followed: The sire must have had an active status, the sire must have had offspring in the last 4 years, the sire must have had at least 25 progeny that participated in wool testing, the clean fleece weight, staple length, body weight at wool test, coefficient of variation of fibre diameter and weaning weight EBV index must have been between 88 and 160, as well as the fibre diameter EBV index must have been between 0 and 124. In order to identify the top ten young rams, the animal must have had an active status, the animal must have been born in the last 4 years, the animal must have had a body weight measurement, the animal must be older than 269 days for wool testing, the clean fleece weight, staple length, body weight at wool test, coefficient of variation of fibre diameter and weaning weight EBV index must have been between 88 and 160, as well as the fibre diameter EBV index must have been between 0 and 124. Furthermore, rams that qualified for the sire list were excluded from the young ram list. The top ten sires and young rams were then identified and listed for each trait (Addendum B, Table B1 to B7).

3.3.5 Determining genomically enhanced breeding values (GEBVs)

The genomically enhanced breeding values (GEBVs) used in this study were estimated and made available by SA Stud Book. In order for the estimation of GEBVs, SNP data was incorporated using MIX99 (Lidauer *et al.*, 2013), with a Single-Step GBLUP Model. The genetic models and variance components that are used in the National Genomic Evaluation were implemented for prediction of the GEBVs of a highly heritable (fibre diameter) and a lowly heritable (wean maternal) trait. Two runs were completed: The first run including genomic information, and the second run excluding genomic information. Genetic trends were estimated, in which the average GEBVs per trait, per year of birth were calculated for measured animals, and plotted against that of the EBVs using R (RStudio Team, 2020). This allowed for the comparison of the rate of genetic improvement with the inclusion of genomic information *versus* the use of conventional breeding values. Pearson correlations were determined using R statistical software (RStudio Team, 2020), for fibre diameter and wean maternal for all measured animals, active animals and genotyped animals' EBVs and GEBVs.

Top ten lists for young rams and rams with progeny were constructed based on the GEBVs for all active, genotyped animals. The re-ranking of these animals, when top lists were constructed based on their EBVs, were then investigated. This was done to determine the difference that the inclusion of genotypic information will make on genetic progress. For the young rams, the following criteria were implemented: The ram must have had an active status and be genotyped, be born in the last 4 years, had a body weight measurement, be older than 269 days for wool testing, the clean fleece weight, staple length, body weight at wool test, coefficient of variation of fibre diameter and weaning weight GEBV index must have been between 88 and 160, while the fibre diameter GEBV index must have been between 0 and 124. The criteria for the young rams with progeny followed the same criteria, however, these rams must have had more than 20 progeny in the last 2 years.

3.3.6 Comparing the accuracy of EBVs *versus* GEBVs

Genomically enhanced breeding values (GEBVs) and their accuracy values for the South African Merino sheep breed for fibre diameter and weaning weight maternal were provided by SA Stud Book, using MIX99 (Lidauer *et al*., 2013), for the GEBVs and Method 3 m of APAX for accuracies (Lidauer *et al*., 2013). An assessment on the increase in accuracy and the effect on ranking of the animals with the inclusion of genomic information in breeding value prediction was done using R statistical software (RStudio Team, 2020). This was done by plotting the accuracies of the EBVs against the accuracies of the GEBVs for fibre diameter and wean maternal and determining the Pearson correlation coefficients between the GEBVs and EBVs of the two traits.

Chapter 4: Results

4.1 Descriptive statistics

Descriptive statistics on the clean, edited data were obtained using R (R Studio team, 2020) for the South African Merino sheep breed. This dataset excluded animals with missing measurements or measurements of “NA”, “0” or “null”, and excluded animals with missing dams and sires as well as any duplicated animals and measurements. Table 4.1 shows the clean statistics for each trait evaluated in this study.

Table 4.1 Descriptive statistics of the clean data including mean, median, standard deviation, first and third quartiles and minimum and maximum values of weight and wool traits of the SA Merino population

Trait	Min	1st	Med	Mean	3rd	Max	SD
Weaning Weight (kg)	10.00	24.40	28.50	28.89	33.00	62.50	6.50
Body Weight at Wool Test (kg)	15.60	39.00	46.60	47.38	55.00	100.00	11.58
Staple Length (mm)	50.20	92.29	104.80	105.72	118.10	169.80	19.43
Clean Fleece Weight (kg)	2.60	3.36	4.36	5.45	6.12	10.50	1.07
Fibre Diameter (μm)	11.10	16.20	17.10	17.15	18.10	24.50	01.45
Coefficient of Variation of Fibre Diameter (%)	10.50	15.50	16.90	17.18	18.50	33.50	3.30

[1] Min: minimum; 1st: first quartile; Med: median; 3rd: third quartile; Max: maximum; SD: standard deviation

Table 4.1 highlights the importance of the data cleaning and editing process. The descriptive statistics presented shows more accurate and reliable data, that are within their biological ranges

4.2 Skewness and kurtosis

A widely used procedure in assessing the distribution of data points in a graph is the use of skewness and kurtosis analyses (Blanca *et al.*, 2013). Skewness and kurtosis statistics were estimated in R (R Studio team, 2020) for each trait in order to visualise their distributions. The skewness and kurtosis values are shown in Table 4.2 and their distribution in Figure 4.1.

Table 4.2 Skewness and Kurtosis values, their respective standard errors and the distribution description for weight and wool traits of the South African Merino sheep breed.

Trait	Skewness statistic	Kurtosis statistic	Distribution
Weaning Weight (kg)	0.31 ± 0.0098	3.27 ± 0.0196	Approximately symmetrical distribution (mesokurtic), however slightly skewed to the right.
Body Weight at Wool Test (kg)	0.34 ± 0.0098	2.94 ± 0.0196	Approximately symmetrical distribution (mesokurtic), however slightly skewed to the right.
Clean Fleece Weight (kg)	0.55 ± 0.0098	3.57 ± 0.0196	Skewed to the right with a leptokurtic distribution (heavier tails and a sharper peak).
Staple Length (mm)	0.26 ± 0.0098	3.08 ± 0.0196	Right-skewed, indicating that shorter staple lengths are more common.
Fibre Diameter (μm)	0.18 ± 0.0098	3.08 ± 0.0196	Approximately symmetrical distribution (mesokurtic), however slightly skewed to the right.
Coefficient of Variation of Fibre Diameter (%)	0.69 ± 0.0098	3.82 ± 0.0196	Skewed to the right with a leptokurtic distribution (heavier tails and a sharper peak).

The skewness and kurtosis statistics indicate that most distributions for six traits were approximately symmetrical (mesokurtic), however exhibited slight right skewness. Notably, clean fleece weight (CFW) and the coefficient of variation of fibre diameter (CVFD) showed more pronounced right skewness and leptokurtic distributions, as shown in Figure 4.1. This was characterized by their heavier tails and sharper peaks.

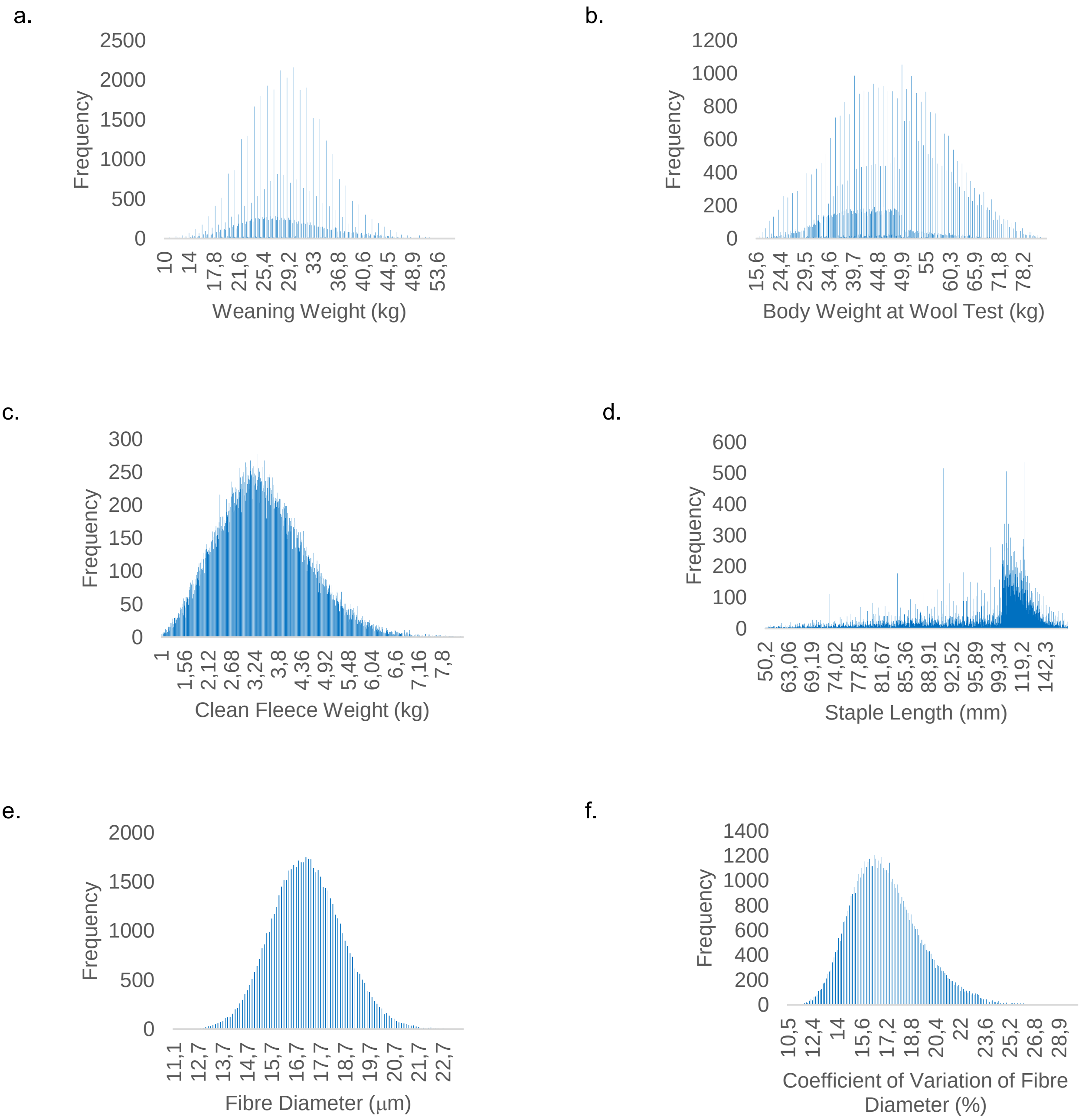


Figure 4.1 The distributions plotted for (a) weaning weight (kg), (b) bodyweight at wool test (kg), (c) clean fleece weight (kg), (d) staple length (mm), (e) fibre diameter (μm), and (f) coefficient of variation of fibre diameter (%) for the South African Merino sheep breed.

The distributions plotted for each trait further show that most traits were normally distributed. Furthermore, staple length (SL) displayed a multi-modal distribution in which multiple peaks were observed, indicative that there were several common values for SL.

4.3 Analysis of Variance tests (ANOVA)

Comparing the analyses of variance (ANOVA) test results for both weight and wool traits, there was little difference between using two or three seasons in the model. However, using three seasons did yield slightly higher R^2 values and a lower mean square error (MSE), and therefore explained slightly more variance. The ANOVA tables for all traits produced in R (R Studio team, 2020), are attached in Addendum A (Table A1 to A6). The ANOVA test for weaning weight (WW) indicated that the dam age and age at weaning tested highly significant as linear and quadratic regressions. The wean contemporary group, which consisted of the flock, environmental code and management group, along with birth status, sex, Herd X Sire effect and rearing status also tested highly significant. The final model for WW [Model 1] produced the lowest MSE and highest R^2 value of 0.5232 and therefore explained the most variance.

The ANOVA test for the wool traits indicated that the age of sheep, dam age, the wool contemporary group, which consisted of the flock, environmental code and group number, along with rearing status tested highly significant. This model produced the lowest MSE and highest R^2 value for the traits body weight at wool test (kg), fibre diameter (μm) and coefficient of variation of fibre diameter (%) and therefore explained the most variance. Staple length (mm), however differed as dam age did not reach significance and therefore was not included in the final model. Table 4.3 shows the fixed and random effects that tested significant for all traits in the ANOVA tests.

Table 4.3 Fixed and random effects that tested significant for each trait as per the ANOVA tests.

Effects	**WW**	**BWW**	**FD**	**CVFD**	**SL**	**CFW**
Weight contemporary group	X					
Wool contemporary group		X	X	X	X	X
Sex	X					
Birth status	X					
Rearing status	X	X	X	X	X	X
Length of test						
Dam age linear regression	X	X	X	X		X
Sheep age linear regression		X	X	X	X	X
Wean age linear regression	X					
Dam age quadratic regression	X					
Wean age quadratic regression	X					
Herd x Sire		X	X	X	X	X
R^2	0.70	0.69	0.45	0.25	0.44	0.55

[2] WW: weaning weight; BWW: body weight at wool test; FD: fibre diameter; CVFD: coefficient of variation of fibre diameter; SL: staple length; CFW: clean fleece weight

Table 4.3 revealed that the significant effects vary across the wool and weight traits. For instance, dam age tested significant across all wool traits, except for staple length. Furthermore, the Herd x Sire effect tested significant for all wool traits, however not for weaning weight. Additionally, the R^2 values suggest that the models explain a substantial proportion of the variance for weaning weight

(0.70) and body weight at wool test (0.69), but less so for the coefficient of variation of fibre diameter (0.25).

4.4 Variance Component Estimation

Table 4.4 shows the results of the multi-trait evaluation including the heritabilities (h^2), the genetic correlations (rg) amongst the traits and respective standard errors (SE) for the South African Merino sheep breed for all traits evaluated in this study.

The direct heritabilities for the traits ranged from 0.25 to 0.63. Notably, weaning weight exhibited the lowest direct heritability (0.25 ± 0.01), whereas the highest heritability was estimated for fibre diameter (0.63 ± 0.00). The maternal heritability estimates for all six traits were significantly lower, spanning from 0.01 to 0.20. In contrast to the pattern observed for the direct heritability estimates, weaning weight had the highest maternal heritability (0.20 ± 0.00), while fibre diameter had the lowest (0.01 ± 0.00). These findings highlight the varying degrees of genetic influence on the traits, emphasizing the importance of considering both direct and maternal heritabilities in breeding programs, especially for weaning weight. Furthermore, all the standard errors (SE) for both the maternal and direct heritability estimates were low, ranging between 0.00 and 0.04, indicating high precision in the estimation of these estimates.

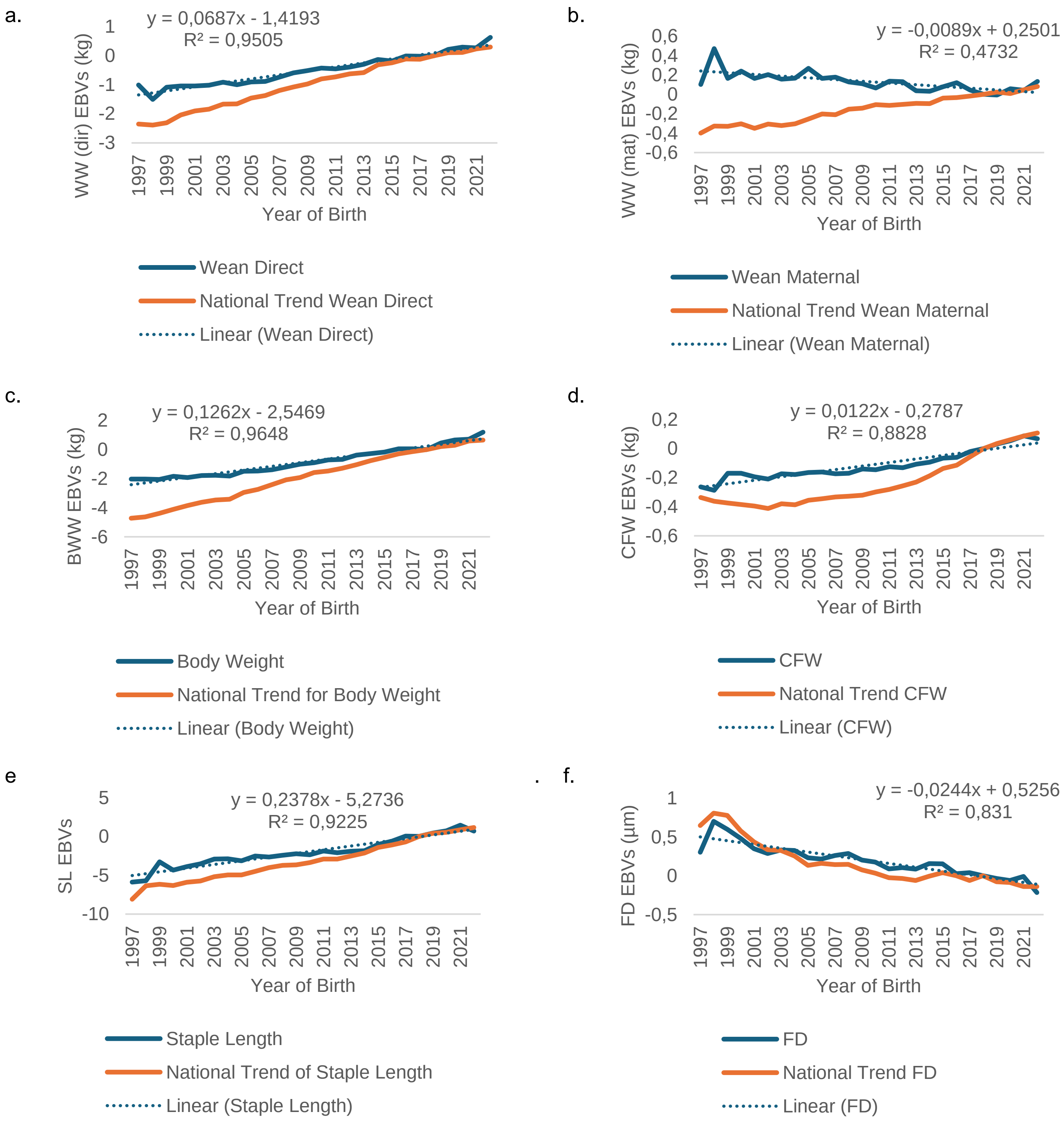
Table 4.4 Multi-trait variance component ratios for direct (dir) and maternal (mat) wool and weight traits and respective standard errors of the SA Merino sheep breed

	WW (dir)	BWW (dir)	CFW (dir)	FD (dir)	SL (dir)	CVFD (dir)	WW (mat)	BWW (mat)	CFW (mat)	FD (mat)	SL (mat)	CVFD (mat)
WW (dir)	0.25 ± 0.01	0.55 ± 0.01	0.07 ± 0.01	0.06 ± 0.00	-0.0 ± 0.00	-0.03 ± 0.00	-0.48 ± 0.01	-0.33 ± 0.02	-0.09 ± 0.02	-0.06 ± 0.03	0.12 ± 0.03	0.18 ± 0.02
BWW (dir)		0.26 ± 0.01	0.00 ± 0.01	0.14 ± 0.00	0.02 ± 0.01	-0.11 ± 0.00	0.07 ± 0.01	-0.04 ± 0.02	0.02 ± 0.02	-0.49 ± 0.04	-0.05 ± 0.03	0.16 ± 0.02
CFW (dir)			0.33 ± 0.01	0.18 ± 0.00	0.24 ± 0.01	0.09 ± 0.00	-0.18 ± 0.01	-0.35 ± 0.02	-0.32 ± 0.02	-0.11 ± 0.03	-0.02 ± 0.03	0.16 ± 0.02
FD (dir)				0.63 ± 0.00	0.20 ± 0.01	-0.07 ± 0.00	0.11 ± 0.01	0.17 ± 0.02	0.13 ± 0.02	-0.12 ± 0.03	0.08 ± 0.03	-0.09 ± 0.10
SL (dir)					0.33 ± 0.00	-0.12 ± 0.00	-0.04 ± 0.01	-0.04 ± 0.02	-0.08 ± 0.02	-0.15 ± 0.03	-0.30 ± 0.04	-0.06 ± 0.01
CVFD (dir)						0.43 ± 0.00	-0.03 ± 0.01	-0.04 ± 0.02	0.04 ± 0.02	0.11 ± 0.03	0.21 ± 0.03	-0.30 ± 0.03
WW (mat)							0.20 ± 0.00	0.91 ± 0.01	0.66 ± 0.02	-0.31 ± 0.03	0.12 ± 0.03	-0.13 ± 0.02
BWW (mat)								0.08 ± 0.00	0.81 ± 0.01	-0.19 ± 0.04	0.17 ± 0.03	-0.18 ± 0.02
CFW (mat)									0.06 ± 0.00	0.10 ± 0.04	0.47 ± 0.03	-0.15 ± 0.02
FD (mat)										0.01 ± 0.00	0.52 ± 0.04	-0.27 ± 0.02
SL (mat)											0.02 ± 0.00	-0.17 ± 0.02
CVFD (mat)												0.02 ± 0.00
Permanent Environmental Effect												
Wean	0.05 ± 0.01											

4.5 Evaluation of conventional breeding values

4.5.1 Estimation of genetic trends

The genetic trends for each trait are shown in Figure 4.2 and were calculated by averaging the breeding values per year of birth for measured animals. The breeding values estimated in this study were then plotted against the national trends, obtained from SA Stud Book, for each trait.



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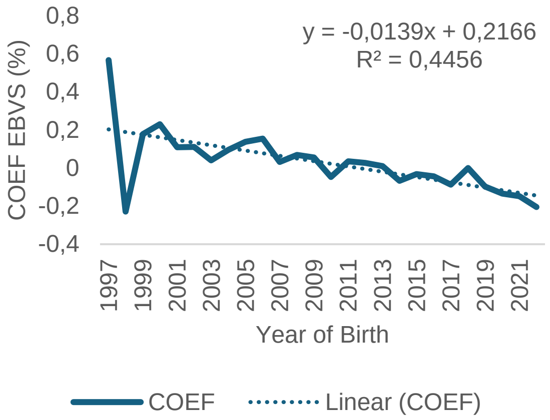

Figure 4.2 The average EBVs plotted against the national trends for (a) direct weaning weight (kg), (b) maternal weaning weight (kg), (c) bodyweight at wool test (kg), (d) clean fleece weight (kg), (e) staple length (mm), (f) fibre diameter (μm), and (g) coefficient of variation of fibre diameter (%) for the South African Merino sheep breed.

Figure 4.2 demonstrates that the traits in this study mostly followed a similar pattern to those of the national estimates. It was expected though, that the trends will differ, as they are based on a different set of variance components and slightly different models compared to that of the National Evaluation.

4.6 Evaluation of genomically enhanced breeding values (GEBVs)

Genomically enhanced breeding values (GEBVs) were estimated for a highly heritable trait (fibre diameter) and a lowly heritable trait (wean maternal) using Single-Step GBLUP methodology and the models and (co)variance structure used in the National Genomic Evaluation done by SA Stud Book. A genomic relationship matrix was implemented in the evaluation for 3 269 genotyped animals. The genetic trends for fibre diameter and wean maternal are shown in Figure 4.3 and were determined by averaging the GEBVs per year of birth for measured animals. The trends based on GEBVs were plotted against those based on EBVs in order to assess the impact of inclusion of genomic information on the trends for these two traits.

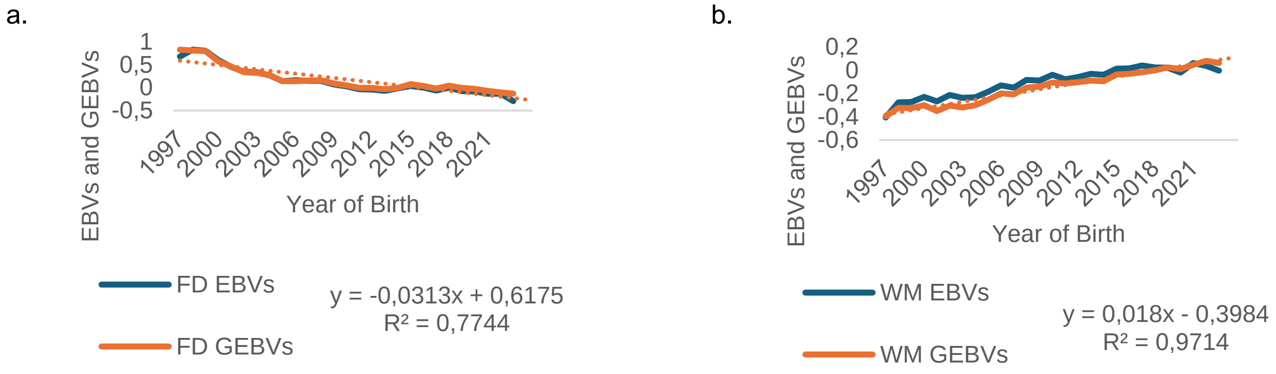

Figure 4.3 Genetic trends for (a) fibre diameter and (b) wean maternal, determined as the average genomic and conventional breeding values per year of birth for measured animals.

Genomic data for the South African Merino Sheep National Evaluation was implemented in October 2021. For fibre diameter, the average EBVs and GEBVs per year followed almost identical trends, however the GEBV trend was slightly higher than that of the EBV trend from 2009. Similarly, the wean maternal trends also followed a comparable pattern over the years, but at a slightly steeper rate for the GEBV trend compared to the EBV trend.

4.7 Pearson Correlations

The GEBVs were plotted against the EBVs and goodness of fit (coefficients of determination) indicated for fibre diameter and wean maternal (Figure 4.4), as well as the Pearson correlation coefficients (Table 4.5) between the GEBVs and EBVs are shown for all animals with measurements, animals with an active status, as well as for all animals that were genotyped.

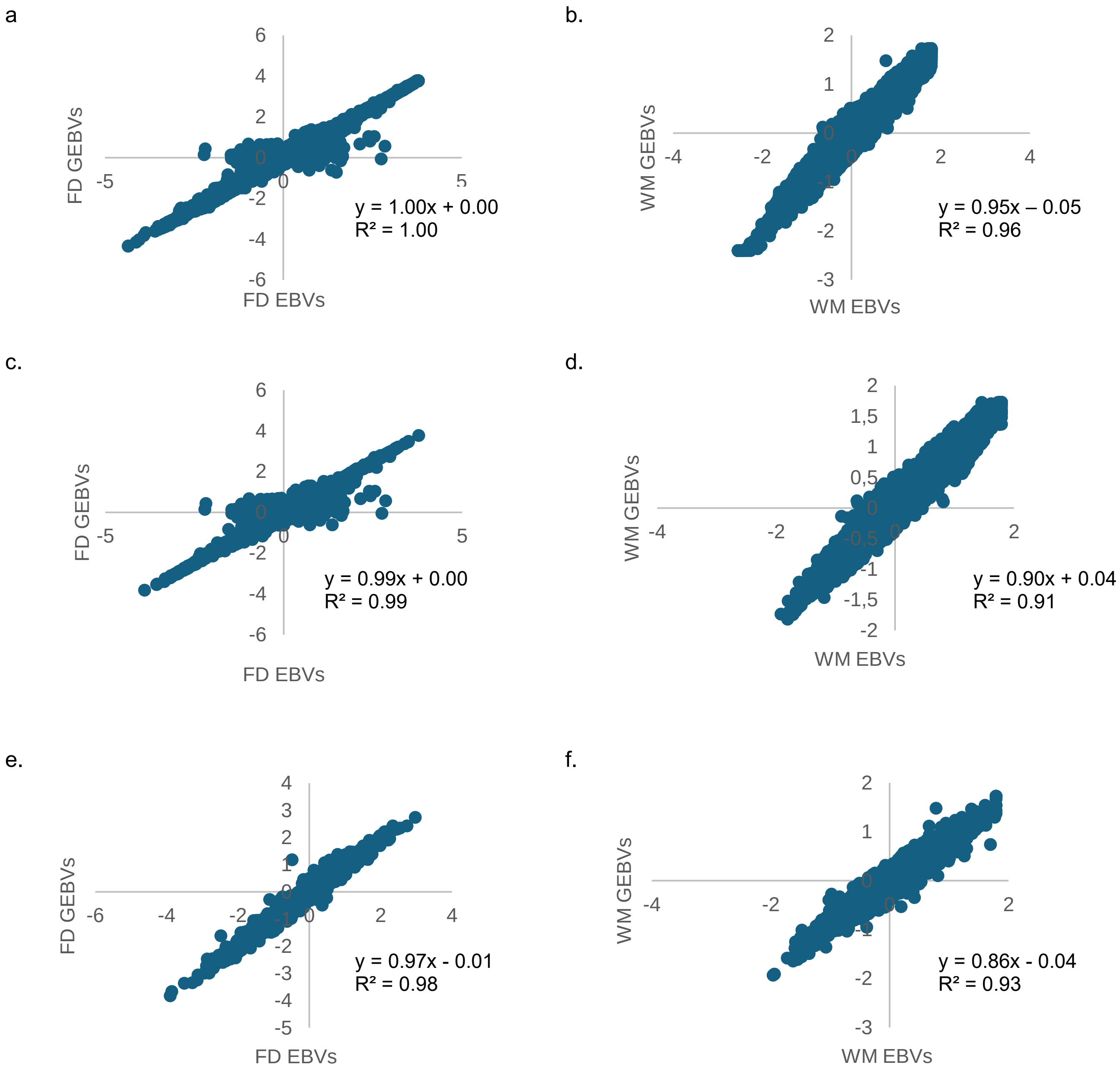

Figure 4.4 Coefficients of determination of GEBVs *versus* EBVs plotted for (a) fibre diameter of measured animals, (b) wean maternal of measured animals, (c) fibre diameter of active animals, (d) wean maternal of active animals, (e) fibre diameter of genotyped animals, and (f) wean maternal of genotyped animals for the South African Merino sheep breed.

These plots indicate that although the coefficients of determination were very high, there were animals that deviated substantially from their EBVs when genomic information is included. Furthermore, the impact of inclusion of genomic information was higher for wean maternal compared to fibre diameter, with the greatest impact for the animals that were genotyped themselves, as can be expected.

Table 4.5 Pearson correlation coefficients for all measured, active and genotyped animals for FD and WM traits

Trait	Selection of Animals	Pearson Correlation Coefficient
Fibre Diameter	Measured animals	1.00
	Active animals	0.99
	Genotyped animals	0.99
Wean Maternal	Measured animals	0.98
	Active animals	0.95
	Genotyped animals	0.96

Table 4.5 highlights that while the Pearson correlation coefficients for both fibre diameter and wean maternal traits were high, there are still notable changes in the ranking of animals when genomic information is included in the estimation of the breeding values. This change in ranking is more pronounced for WM compared to FD, particularly in genotyped animals, as can be expected. This suggests that the inclusion of genomic data has a significant impact on the accuracy of EBVs, especially for maternal traits.

4.8 Evaluation of accuracies for EBVs and GEBVs

The accuracies for the GEBVs for fibre diameter and wean maternal were compared to the accuracies from the conventional breeding values. This was done by plotting the accuracies for the GEBVs against the accuracies for the conventional breeding values of the genotyped animals in R (R Studio team, 2020) (Figure 4.5).

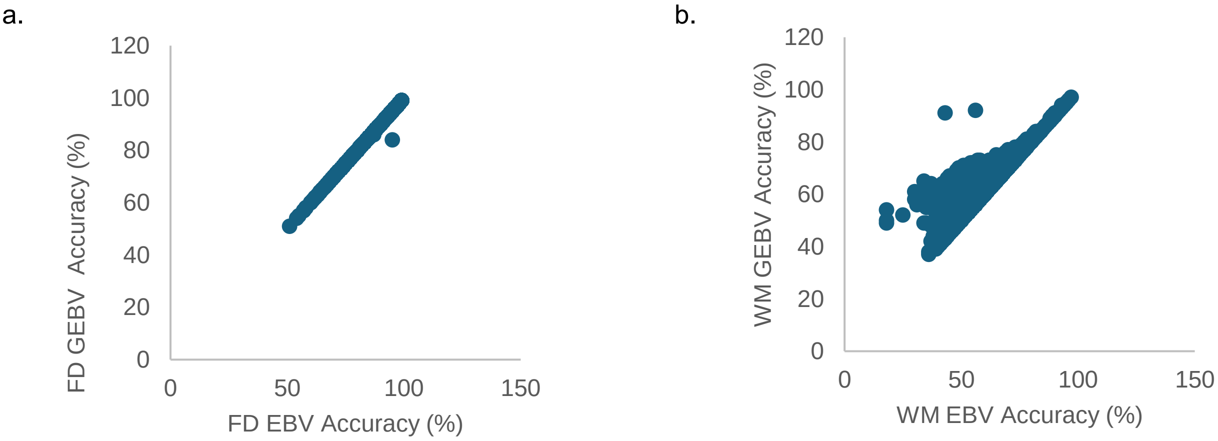

Figure 4.5 GEBV accuracies plotted against EBV accuracies of genotyped animals for (a) fibre diameter and (b) wean maternal for the South African Merino sheep breed

Figure 4.5 illustrates the relationship between the accuracies of the GEBVs *versus* that of the EBVs for FD and WM traits in the South African Merino sheep based on the animals that were genotyped. For FD, the accuracies for both the EBVs and GEBVs ranged from 51% to 99% for the genotyped animals, with no increase in accuracy observed when incorporating genomic information. One animal had a decrease in accuracy with the inclusion of genomic information which is probably due to a parent conflict, resulting in the animal being linked to a different parental line with less relatives being measured for the trait. In contrast, for WM, the accuracies for the EBVs ranged from 18% to 97% for the genotyped animals, while the accuracies for the GEBVs ranged from 37% to 97% for the genotyped animals. Furthermore, for WM, more marked increases in the accuracies can be observed when genomic information is included, ranging from a minimum increase of 1% to a maximum increase of 48% with an average increase of 5.05% over all genotyped animals.

4.9 Ranking of top ten young rams and rams with progeny based on EBVs *versus* GEBVs

The top ten rankings of all active sires and young rams were determined based on the estimated breeding values for each trait and are displayed in Addendum B (Table B1 to B7). The top ten young rams, as well as the top ten young rams with progeny based on their GEBVs and EBVs, respectively, for fibre diameter and wean maternal were identified in order to determine the effects on the animals' rankings. Table 4.6 and Table 4.7 show the top ten rankings for young rams for the traits FD and WM, and how those rankings differ between the use of EBVs and GEBVs. Table 4.6 presents a comparison of the EBVs and GEBVs for the top ten young rams for fibre diameter.

Table 4.6 Comparison of the rankings for the top ten young rams for fibre diameter based on EBVs *versus* GEBVs.

EBV Rank	Ram Number	EBVs	Change in Ranking	Ram Number	GEBVs
1	90259169	-3.82	1	90259169	-3.82
2	85670354	-2.99	2	85670354	-2.99
3	83421057	-2.78	3	83421057	-2.78
4	92115443	-2.33	4	92115443	-2.33
5	93951093	-2.02	5	93951093	-2.02
6	82937632	-2.02	6	82937632	-2.02
7	89927677	-1.93	7	89927677	-1.93
8	81263568	-1.87	10	86407376	-1.89
9	93550747	-1.70	8	81263568	-1.87
10	86407376	-1.65	9	93550747	-1.75

The rankings for both EBVs and GEBVs for FD were highly consistent, with the same rams occupying the top seven positions in both lists. However, slight variations were observed in the lower ranks, particularly for rams ranked eighth to tenth, where the order and values differed. The consistency observed between the EBVs and the GEBVs for FD is due to the high heritability of the trait, which indicates that measurements are an accurate indication of the animal’s genetic potential for FD. The inclusion of genomic information therefore has a smaller benefit for animals that were measured and especially for those that also have measured relatives.

Table 4.7 compares the EBVs and GEBVs for the top ten young rams for wean maternal. The rankings show little consistency between the EBVs and GEBVs. Only the first and ninth rankings remained in the same positions, while all others ranking positions changed. Wean maternal is a lowly heritable trait, with information for estimation of rams’ genetic potential only available from their female relatives. A much greater benefit is therefore obtained on the accuracy of estimation when genomic information is included for this trait and rankings can be obtained with much greater accuracy.

Table 4.7 Comparison of the rankings for the top ten young rams for wean maternal based on EBVs *versus* GEBVs.

EBV Rank	Ram Number	EBVs	Change in Ranking	Ram Number	GEBVs
1	87785382	1.38	1	87785382	1.46
2	93525012	1.10	3	91579110	1.15
3	91579110	1.10	6	93179125	1.15
4	88995105	1.06	5	93951093	0.93
5	93951093	1.01	7	86196938	0.91
6	93179125	1.01	4	88995105	0.89
7	86196938	0.97	2	93525012	0.85
8	92486687	0.86	10	85140903	0.80
9	83145847	0.86	9	83145847	0.78
10	85140903	0.84	8	92486687	0.78

The top ten rankings for young rams with progeny for FD and WM were identified. Table 4.8 and Table 4.9 show how the rankings for FD and WM differ between the use of EBVs *versus* GEBVs.

Table 4.8 Comparison of the rankings for the top ten young rams with progeny for fibre diameter based on EBVs *versus* GEBVs.

EBV Rank	Ram Number	EBVs	Change in Ranking	Ram Number	GEBVs
1	90259169	-3.82	1	90259169	-3.82
2	85670354	-2.99	2	85670354	-2.99
3	83421057	-2.78	3	83421057	-2.78
4	92115443	-2.33	4	92115443	-2.33
5	93951093	-2.02	6	92055862	-2.09
6	92055862	-2.12	5	93951093	-2.02
7	82937632	-2.01	7	82937632	-2.02
8	89927677	-1.91	8	89927677	-3.82
9	81263568	-1.85	10	86407376	-2.99
10	86407376	-1.65	9	81263568	-2.78

Table 4.8 shows consistency between the rankings for fibre diameter of the young rams with progeny when using EBVs *versus* GEBVs. The top positions in both the EBV and GEBV rankings remained the same, while changes in the ranking were only observed for the last three positions. This indicates that for highly heritable traits such as fibre diameter, minor changes in rankings are observed when incorporating genomic information, especially if rams have measured progeny already.

Table 4.9 Comparison of the rankings for the top ten young rams with progeny for wean maternal based on EBVs *versus* GEBVs.

EBV Rank	Ram Number	EBVs	Change in Ranking	Ram Number	GEBVs
1	87785382	1.38	1	87785382	1.46
2	93525012	1.11	3	91579110	1.15
3	91579110	1.10	4	93951093	0.93
4	93951093	1.01	6	86196938	0.91
5	88995105	1.06	5	88995105	0.89
6	86196938	0.97	2	93525012	0.85
7	92486687	0.86	9	85140903	0.80
8	83145847	0.86	8	83145847	0.78
9	85140903	0.84	7	92486687	0.78
10	93185775	0.76	10	93185775	0.76

Table 4.9 compares the rankings of the top ten young rams with progeny for wean maternal based on the EBVs and GEBVs. The rankings between the EBVs and GEBVs for WM were inconsistent, with only the first, fifth and tenth positions remaining the same. The variation observed between the rankings of the EBVs and GEBVs suggests that the inclusion of genomic information in the estimation of EBVs results in more accurate rankings, especially for the lowly heritable traits.

Chapter 5: Discussion

5.1 Introduction

Sheep production is a crucial contributor to food security, employment, income generation and the provision of affordable manure. Additionally, sheep farming is well-suited to thrive in harsh climatic conditions, which is particularly significant in South Africa. Consequently, sheep farming plays a vital role in sustaining the livelihoods of numerous communities across South Africa (Nyam *et al*., 2020). Due to the economic importance of sheep production systems, genetic progress in both growth and wool traits of interest for the South African Merino sheep breed are essential. The primary objective of this study was to estimate variance components in order to estimate breeding values for the South African Merino sheep breed. It is important to frequently re-estimate genetic parameters as the gene frequencies within a population are continuously changing as a result of selection, mutations and migrations that might have occurred (Mayo, 2008). The accurate estimation of genetic parameters, such as heritabilities and genetic and phenotypic correlations, are crucial for the accurate prediction of breeding values (EBVs) (Hofer, 1998). The more performance and pedigree data that are analysed for animals and their relatives within a breed, the higher the accuracy of the EBVs (Bijma, 2012).

Additionally, this study estimated the genomically enhanced breeding values (GEBVs) for traits with varying heritability, including fibre diameter (a highly heritable trait) and wean maternal (a lowly heritable trait). This approach allowed for an estimation of the increase in accuracy percentages, as well as an assessment on the effect of ranking of animals when conventional breeding values were used *versus* when incorporating genomic data. This study has resulted in updated genetic parameters and re-estimated breeding values that are based on more representative population parameters of the SA Merino population, thereby facilitating a faster rate of genetic improvement.

5.2 Multi-trait Variance Component Estimation

Variance components for six key traits, including WW, BWW, CFW, FD, CVFD and SL, were estimated for the South African Merino sheep breed. These estimations were conducted using Multi-trait Animal Models based on the Restricted Maximum Likelihood (REML) methodology. The final models incorporated significant environmental effects as fixed or continuous variables, as well as random permanent environmental and sire x herd effects, depending on the trait. In this study, a moderate, direct heritability of 0.25 with a standard error (SE) of ± 0.01 for WW was estimated. This heritability and SE estimate for WW were consistent with those reported in other studies such as, Mortimer & Atkins (1995) and Vaez Torshizi *et al*. (1996) who reported heritability estimates of 0.27 ± 0.03 and 0.27 ± 0.04, respectively. Both Mortimer & Atkins (1995) and Vaez Torshizi *et al*. (1996) also used Multi-trait Animal Models, with Vaez Torshizi *et al*. (1996) conducting the study on the Australian Merino sheep breed, while Mortimer & Atkins (1995) conducting the study on the South African Merino sheep breed. Safari *et al.* (2005), however, reported slightly lower estimates than that of this study of 0.23 ± 0.02, on a population of Australian Merino sheep from various research flocks, 0.18 ± 0.02, on a different subset of the Merino population, focusing on fine wool bloodlines and 0.18 ± 0.04, on a subset of the Merino population, focusing on medium and broad wool bloodlines. The comparison of estimates with that of Safari *et al*. (2005), indicates that slightly more genetic variation was identified for WW in this study. A reason for the lower estimates reported in Safari *et al*. (2005) can be due to the use of a Random Regression Model, not a Multi-trait Animal Model, as used in this study. Furthermore, a lower SE (± 0.01) value was obtained in this study, which suggests a more precise and accurate estimate. The heritability estimate for WW in this study indicate that moderate genetic progress can be achieved by selecting in this population, which is particularly important as WW directly impacts the growth and overall productivity of the flock, making it a crucial trait for enhancing the economic viability and efficiency of sheep breeding programs (Wang *et al*., 2024).

In this study, a low to moderate, maternal heritability and SE value of 0.20 ± 0.00 for WW was estimated. This maternal heritability and SE estimate for WW was within the range of those reported in previous studies, which also used a Multi-trait Animal Model, such as, Mortimer & Atkins (1995), Vaez Torshizi *et al*. (1996) and Annalla & Serradilla (1998), who reported heritability estimates of 0.11 ± 0.01 on a SA Merino population, 0.38 ± 0.07 on an Australian Merino population and 0.16 ± 0.03 on a Spanish Merino population, respectively. Furthermore, a low SE (± 0.00) value was obtained in this study, which suggests a more precise and accurate estimate. The maternal heritability estimate for WW in this study indicate that moderate genetic progress can be achieved by selecting in this population, which is especially important as maternal WW significantly influences lamb growth and overall health. Furthermore, higher maternal WW leads to heavier weaning weights, reduced lamb mortality and an overall increase in the productivity of the flock. The genetic correlation and SE between direct WW and maternal WW was -0.48 ± 0.01, which indicates a moderate, negative relationship. This unfavourable genetic correlation suggests that the selection for increased direct weaning weight, will result in a decreased maternal weaning weight and *vice versa,* which should be kept in mind when defining a breeding plan for the flock and breed.

The direct heritability and SE estimates for bodyweight at wool test in this study were 0.26 ± 0.01. These estimates were slightly lower than those reported in other studies. For instance, Brown *et al*. (2002a) and Clarke *et al*. (2003), who both used multi-trait animal models on the Australian Merino sheep breed, reported heritability estimates of 0.33 ± 0.15 and 0.35 ± 0.02, respectively. Additionally, Safari *et al*. (2003) and Safari *et al*. (2005) reported estimates of 0.41 ± 0.02 and 0.31 ± 0.03, also on the Australian Merino sheep breed, respectively. The estimates reported by Safari *et al*. (2003), and Safari *et al*. (2005), were higher compared to this study which could be a result of using the Random Regression Model, rather than the multi-trait animal model that was used in this study. Although the heritability estimate for BWW in this study was somewhat lower than those found in other studies, it remained relatively close to these previous estimates. Notably, the SE (± 0.01) calculated in this study was smaller than those reported in other studies, indicating a high level of reliability of estimation. The genetic correlations between the traits were also estimated in the Multi-trait evaluation. The direct correlation between WW and BWW was 0.55 ± 0.01. This correlation estimate indicates a strong, positive relationship between these two traits, therefore selection for WW of sheep will also result in an increase in the BWW, and *vice versa*. The genetic correlation obtained between WW and BWW in this study was similar, but slightly higher than the estimate of 0.47 obtained by Safari *et al.* (2005). This correlation is regarded as favourable, as WW and BWW are both economically important traits and improvements in both these traits can lead to improved growth rates, increased productivity, a better market value and therefore an overall increase in the profitability of the sheep enterprise (Wang *et al*., 2024).

The direct heritability estimate for clean fleece weight in this study was 0.33 with a SE of ± 0.01. This estimate was higher than the 0.28 ± 0.05 reported by Cloete *et al*. (2005), who also used the Multi-trait Animal Model on a SA Merino population with a smaller SE, indicating greater precision in the estimation of the heritability. However, the estimates reported by Safari *et al*. (2005) were slightly higher, at 0.36 ± 0.02 on a population of Australian Merino sheep from various research flocks and 0.51 ± 0.07, for a different subset of the Merino population, focusing on fine wool bloodlines. Despite these higher heritabilities, the SE's reported by Safari *et al*. (2005) were larger, at ± 0.02 and ± 0.07, respectively, compared to the SE of ± 0.01 in this study. Additional estimates for CFW reported by Naidoo & Cloete (2006), as well as Matebesi *et al*. (2009a), were 0.44 ± 0.07 and 0.40 ± 0.05, respectively, of which both studies utilized the Multi-trait Animal Model on the SA Merino population. Both of these studies had slightly higher heritabilities and SE's compared to this study. While the heritability estimate for CFW in this study was generally lower than those reported in other studies, it is still in the range reported in the literature. The genetic correlation between body weight and clean fleece weight was 0.00021 ± 0.01, indicative of a negligible relationship between these two traits. This suggests that changes in BWW had almost no direct impact on CFW, and *vice versa*. Furthermore, since the traits are nearly independent, selecting for one trait is unlikely to affect the other. The standard error (± 0.01) was small, indicating that the estimate was accurate. However, this genetic correlation was much lower than those reported in other studies which also used multi-trait animal models to analyse the South African Merino population. Cloete *et al*. (1998) and Cloete *et al.* (2006) found estimates of 0.37 ± 0.03 and 0.26 ± 0.11, respectively. Oliver *et al.* (2006) found lower estimates of 0.06 ± 0.06 on the SA Merino population, however this estimate was still higher than the correlation estimate obtained in this study. The low genetic correlation between BWW and CFW observed in this study could be due to the selection and structure of the data and the data editing process that was followed.

In this study, fibre diameter had the highest heritability of 0.63 ± 0.00 out of all six traits. The heritability for FD estimated was similar to that of other studies, for example Safari *et al.* (2005) reported direct heritability estimates and SE's of 0.59 ± 0.02 for a population of Australian Merino sheep from various research flocks and 0.57 ± 0.05, for a different subset of the Merino population, focusing on fine wool bloodlines. Matebesi *et al*. (2009a) as well as Brown *et al*. (2010) reported heritability estimates of 0.68 ± 0.05 on the SA Merino sheep breed and 0.62 ± 0.03 on the Australian Merino sheep breed, respectively, further showing similar estimates to this study. Given that FD is the most economically significant wool trait, the high heritability of 0.63 is particularly advantageous. FD is a critical trait in the wool industry due to its significant impact on both wool quality and market value. A high heritability of 0.63 for FD indicates that a large proportion of the variation in this trait is attributable to genetic factors, making it highly responsive to selective breeding. This is economically important because finer wool, which is indicated by a lower FD, generally commands higher prices in the market. Therefore, the ability to effectively select and breed for desirable FD traits can lead to substantial improvements in wool quality and profitability. This high heritability indicates that substantial genetic gains can be achieved through selective breeding, thereby enhancing wool quality and resultingly, profitability (Holman & Malau-Aduli, 2012).

FD however, had a genetic correlation of 0.18 ± 0.00 with CFW, indicating that there is a slight tendency for sheep with a heavier CFW to also have coarser fibres. This represents an unfavourable correlation, as a finer FD is preferred as it results in softer, higher-quality wool. Therefore, a positive correlation, even if weak, suggests that increasing the fleece weight might lead to coarser fibres, reducing the wool's overall market value. The genetic correlation obtained in this study was lower, but still within the range to those estimated in other studies, for example the estimate of 0.28 obtained in Safari *et al*. (2005) on the Australian Merino population was slightly higher compared with this study, while the estimates obtained in Cloete *et al*. (2005) and Cloete *et al*. (2006), on the SA Merino populations, were higher at 0.36 ± 0.04 and 0.35, respectively.

The direct heritability and SE estimate for coefficient of variation of fibre diameter in this study was 0.43 ± 0.01. Other studies, such as those by Hill (2001), Wuliji *et al*. (2001), and Matebesi *et al*. (2009a), reported higher heritability estimates of 0.60 ± 0.08, 0.60 ± 0.06, and 0.61 ± 0.04, respectively. Hill (2001) and Matebesi *et al.* (2009a) both analysed the South African Merino sheep breed using a multi-trait animal model, whereas Wuliji *et al*. (2001) analysed New Zealand Merino sheep. It is important to genetically improve CVFD as the improvement of this trait can lead to more uniform fibres, thereby improving overall wool quality and increasing economic returns (Liu *et al*., 2020). Therefore, the relatively high heritability value of 0.43 and a low SE estimate of ± 0.01, suggest that significant genetic progress for CVFD can occur through selection. The genetic correlation between FD and the CVFD was -0.07 ± 0.00, which indicates a weak, unfavourable relationship between these two traits. The negative correlation suggests that as FD increases, the variability in FD tends to decrease, and *vice versa.* This genetic correlation is similar to those obtained in other studies, as shown by the estimates of -0.12 ± 0.07 (Cloete *et al*., 2006), -0.11 (Naidoo & Cloete, 2006) and -0.08 ± 0.05 (Matebesi *et al.,* 2009a), obtained also on the SA Merino population The genetic correlation between FD and CVFD is unfavourable, meaning that selection for a decrease in FD will result in an increase in CVFD. While reducing variation and achieving a more uniform fleece is generally desirable, this outcome is undesirable if it coincides with an increase in FD. Therefore, even though a lower CVFD indicates a more consistent fleece, the associated increase in FD negates this benefit by compromising wool quality and economic value. This should be kept in mind when constructing selection strategies and breeding plans.

The direct heritability and SE for staple length was estimated as 0.33 ± 0.00. This estimate was comparable to those reported by Cloete *et al*. (2006), which found heritability estimates of 0.39 ± 0.08, derived from a population of South African Merino sheep divergently selected for multiple rearing ability, and 0.37 ± 0.03, on the SA Merino sheep from a broader genetic base. Although slightly lower, the estimates in this study were within a similar range, indicating consistency across different studies. Safari *et al.* (2005) reported higher heritability estimates for SL, of 0.46 ± 0.04 on a population of Australian Merino sheep from various research flocks and 0.48 ± 0.03, for a different subset of the Merino population, focusing on fine wool bloodlines. While these estimates were higher than those obtained in this study, the values had higher SE estimates, suggesting lower reliability compared to the current study's estimates. The relatively high heritability for SL indicates that fast genetic gain can be expected in selection programs for this trait, which is particularly beneficial as increasing the SL is more commercially desired as it increases wool quality by forming strong and more even yarns, and therefore results in a greater economic value (Holman & Malau-Aduli, 2012).

The genetic correlation between SL and FD in this study, was 0.20 ± 0.01, which indicates a moderate, positive relationship between these two traits. It indicates that selection for a decrease in FD will result in a decrease in SL and *vice versa*, implying that there is a small but noticeable tendency for sheep with coarser fibres to also have longer staple lengths. The positive correlation between FD and SL is considered unfavourable, as a longer SL is desirable, but finer FD is also preferred. This makes it challenging to achieve genetic progress for both traits simultaneously. Naidoo & Cloete (2006), Olivier & Cloete (2007), as well as Matebesi *et al*. (2009a), reported correlation estimates between these traits on the SA Merino population of 0.24, 0.16, and 0.15 ± 0.05, respectively. The genetic correlation between CFW and SL was 0.24 ± 0.01, also indicating a moderate, positive relationship. Selection for CFW will therefore also increase SL and *vice versa*. This means there is a noticeable tendency for sheep with heavier fleeces to also have longer staple lengths. This is consistent with the estimate of 0.23 reported by Olivier & Cloete (2007) on the SA Merino population. By selecting for a heavier CFW, breeders can also achieve longer staple lengths, which are both desirable traits in wool production and therefore this correlation is considered favourable. Heavier fleeces and longer staple lengths can enhance the overall market value of the wool, making this correlation beneficial from an economic standpoint (Holman & Malau-Aduli, 2012).

Furthermore, SL and CVFD had a correlation estimate of -0.12 ± 0.00. This negative, favourable correlation estimate between SL and CVFD are similar to those of other studies. Notter *et al*. (2007) and Matebesi *et al*. (2009a) reported estimates of -0.06 and -0.11 ± 0.06 respectively on the SA Merino population, while Naidoo & Cloete (2006) reported a higher estimate of -0.38, also on the SA Merino population. The negative correlation between SL and CVFD is generally considered favourable as breeders can reduce the variability of the wool fibres, and increase the SL, further improving wool quality and increasing profitability.

5.3 Conventional Breeding Values

5.3.1 Genetic trends based on averaged EBVs per year of birth, per trait

Based on the same multi-trait animal models used to estimate variance components, breeding values for the South African Merino sheep breed were estimated for growth and wool traits of economic importance. EBVs were estimated using 2018 as the base year and genetic trends for each trait were determined by averaging the breeding values per year of birth for measured animals. These trends were then compared to those obtained from the National Genetic Evaluation, which uses the same base year of 2018. Genetic groups were included in the National Evaluation to ensure that animals with unknown parent information were incorporated at appropriate genetic levels in the genetic evaluation, while this was ignored in this study. The inclusion of CVFD in this study's evaluation furthermore influenced the genetic correlations amongst the traits, which also had an influence on the genetic trends. Nevertheless, the data analysed for the South African Merino sheep breed in this study was consistent with the broader patterns observed in the national evaluation. The traits WW, FD and SL followed almost identical genetic trends to those of the national trends, indicating very similar EBV averages per year of birth, while maternal WW, BWW, and CFW showed more variation in the earlier years, and only aligned and followed a similar trend to those of the national estimates, in the later years. No comparison against the national trends for CVFD could be conducted as CVFD is not included in the National Genetic Evaluation for the SA Merino breed. In summary, while maternal WW, BWW, and CFW initially showed slight deviations, these traits ultimately aligned with those of the national trends, demonstrating consistency and reliability of the observed data over time.

The genetic trends for WW and BWW followed a similar, upward trajectory. Direct weaning weight increased genetically from an average of -1.01kg for animals born in 1997 to 0.26kg for animals born in 2021. This is an increase of 2.35 standard deviation units. The general increase in the average EBVs over time showed that breeding strategies have been successful in the genetic improvement for direct weaning weight. Maternal weaning weight, however, decreased genetically from an average of 0.10kg for animals born in 1997 to 0.04kg for animals born in 2021. This is a decrease of 0.61 standard deviation units. The observed decreasing trend of EBVs per year of birth for WM indicates a decline in the genetic potential for this trait over time. This is further evidenced by the negative, unfavourable genetic correlation between direct and maternal WW discussed previously, as direct WW increases, the maternal WW tends to decrease.

Bodyweight at wool test followed a similar pattern to that of direct WW, in which a steady increase in the average breeding value per year of birth was observed. The genetic potential of the animals increased on average from -2.03kg for animals born in 1997 to 0.71kg for animals born in 2021. This is an increase of 2.79 standard deviation units. The national trend for BWW show an increased rate of genetic gain over the years compared to this study's genetic trend. The increases in the average EBV per year of birth observed for WW and BWW shows continuous genetic progress for these traits, which are largely beneficial, as higher weights generally indicate better growth performance in young animals. This may lead to heavier animals that are better prepared for the subsequent stages of development (Fraser & Saville, 2000). Increased weaning weights also result in an increase in overall profitability as animals that are weaned heavier, are sold for higher prices in the market. Furthermore, animals with higher weaning weights require less time and resources to reach market weight, resulting in reduced input costs (Madikadike & Tyasi, 2024).

Clean fleece weight and staple length also followed a similar, upward trajectory. CFW increased genetically from an average of -0.26kg for animals born in 1997 to 0.08kg for animals born in 2021. This is an increase of 3.54 standard deviation units. The average EBVs from the national trends were -0.34kg in 1997 and increased to 0.08kg in 2021. This showed that the average EBVs per year of birth from the national trends followed a similar trend to the trend obtained in this study, both reaching 0.08kg in 2021. For SL, the genetic merit of the animals increased from -5.88mm in 1997 to 1.46mm for animals born in 2021, showing an increase of 3.87 standard deviation units. The national trend for staple length increased from -8.09mm for animals born in 1997 to 0.86mm for animals born in 2021, indicating a steeper slope and therefore a faster rate of genetic improvement compared to the trend of this study. The increases in the genetic trends observed for both CFW and SL indicate that genetic improvement has been made with regards to these wool traits. CFW is an economically important trait as higher prices are offered for wools with a heavier fleece yield and therefore is directly related to the commercial value of wool (Holman & Malau-Aduli, 2012). A longer staple length is further beneficial as it is more commercially desired due to its tendency to spin more easily, as well as its ability to perform better during wool processing and therefore has a greater economic value (Holman & Malau-Aduli, 2012).

Fibre diameter, as well as coefficient of variation of fibre diameter both followed a downward trajectory, with the average EBVs over the birth years decreasing. The genetic potential of animals for FD decreased on average from 0.30µm for animals born in 1997 to -0.01µm for animals born in 2021. This is a decline of 1.52 standard deviation units. The average EBV per year of birth from the national trends for FD decreased from 0.65µm to -0.14µm between 1997 and 2021, which is a steeper slope compared to the trend obtained from this study, indicating a faster rate of genetic improvement. A decrease in the average breeding value per year of birth for CVFD was also observed. The genetic potential of the animals decreased on average from 0.57% for animals born in 1997 to -0.15% for animals born in 2021. This is a decline of 4.49 standard deviation units. As CVFD is not included in the National Genetic Evaluation, no comparison to the national trend could be made. The steady decline in the average EBVs for both traits over the years indicate that genetic gain has been achieved. A lower EBV for both traits are beneficial as a fine, soft and more uniform wool is considered more desirable as it can be processed into high value textiles and thus has a higher economic value (Khan, 2012).

5.3.2 Top ten rankings based on EBVs

The ranking of animals, particularly sires and young rams, based on their EBVs, allows breeders to identify and select top performing animals, leading to overall genetic improvement in traits of economic importance. By identifying these top ten lists for each trait, breeders have the ability to choose the best sire or ram for breeding and can prioritize rams and sires with high rankings to improve specific traits of interest. It is important to regularly update and review these rankings per trait in order to monitor the genetic progress achieved over time. Therefore, the ranking of animals based on EBVs and identifying the top ten lists for each trait is essential in animal breeding, as these lists aid breeders in making informed breeding decisions, help increase the rate of genetic improvement and ultimately lead to a more productive and profitable production system.

The top ten rankings of all active sires and young rams were determined based on the estimated breeding values for each trait and are displayed in Addendum B (Table B1 to B7). Subsequently, the sires and rams that consistently appeared in the top ten rankings across all traits were identified. For the top ten sire list, sire 74296302 was notable for appearing in the top ten rankings for five traits: Direct and maternal WW, BWW, CFW and SL. This sire, however, did not rank in the top ten for FD and CVFD. Additionally, two sires, identified by registration numbers 79245015 and 72363427, ranked in the top ten for four traits. Sire 79245015 ranked for direct WW, BWW, CFW and CVFD in the top ten, while sire 72363427 ranked for direct and maternal WW, CFW and SL in the top ten. For the list of top ten young rams, three rams, identified by registration numbers 94416716, 93091981 and 93090686, each appeared in the top ten rankings for three traits. Ram 94416716 ranked for WW, BWW and FD in the top ten; ram 93091981 ranked for BWW, CFW and CVFD in the top ten; and ram 93090686 ranked for maternal WW, BWW and SL in the top ten.

Animals that ranked highly across multiple traits demonstrated an overall genetic superiority and were indicative that they possess a well-rounded genetic profile, making them valuable for improving multiple aspects of the herd or flock simultaneously. Selecting animals that excel in several traits helps to maintain a balanced breeding program as it ensures that improvement in one trait does not come at the expense of another, promoting overall flock productivity (Smith *et al*., 2023). Using sires and rams that are top-ranked in multiple traits can also accelerate genetic progress as these animals contribute superior genes for several traits, leading to faster and more comprehensive genetic improvement in the population. In summary, identifying sires and rams that appear in multiple top-ranking lists based on their EBVs for various traits is crucial for achieving comprehensive genetic improvement, economic efficiency, and long-term sustainability in animal breeding programs.

Construction of selection indices, where various traits are combined into a single selection value, weighed according to the traits' economic importance, is therefore an invaluable tool for selection for balanced genetic improvement in the next generation (Smith *et al*., 2023).

5.4 GEBV *versus* EBV evaluation

5.4.1 Genetic trends based on GEBVs *versus* EBVs

The EBVs and GEBVs were estimated for a highly heritable trait, fibre diameter and a lowly heritable trait, wean maternal. The genetic trends were constructed based on the average EBVs and GEBVs per year of birth of measured animals, for both FD and WM. The genetic trends for the GEBVs were then compared to the genetic trends of the EBVs in order to highlight the impact of incorporating genomic information and the effect it has on the accuracy of estimation and ranking of animals. A downward trend in both EBVs and GEBVs for FD was observed from 1997 to 2023, indicating an overall reduction in FD. The genetic merit of the animals averaged 0.68µm for animals born in 1997 and decreased to -0.29µm for animals born in 2023 when based on EBVs, while the average GEBV in 1997 was 0.83µm and decreased to -0.13µm in 2023. This consistent downward trend reflects the effectiveness of breeding programs and successful genetic selection over time, as finer wool is more economically desirable and commands a premium price, thereby increasing revenue for wool producers (Holman & Malau-Aduli, 2012). The comparison of trends for FD between the GEBVs and EBVs revealed that there was a close alignment between the two estimates, indicating that there was not a major benefit observed for the prediction of the genetic merit of measured animals for this trait when genomic information is included. Both EBVs and GEBVs were effective in accurately selecting for a finer FD. The high heritability of the trait indicates that genetic factors strongly influence FD, making traditional EBVs, based only on measurements, nearly as effective as GEBVs in predicting genetic potential of the animals. Another reason for the minimal difference observed between the trends based on EBVs and GEBVs for FD is that genomic information for the South African Merino sheep breed was only incorporated in October 2021, therefore selection programs based on GEBVs are still at an early stage so that the impact on the genetic trend is not yet visible.

For wean maternal, an upward trend in both the EBVs and GEBVs were observed between 1997 and 2023. This indicated an improvement in WM over time for the SA Merino sheep breed. The genetic merit of animals born in 1997 was on average -0.41kg for WM and it increased to an average of -0.002kg for animals born in 2023, while the average GEBV for WM was -0.40kg for animals born in 1997 and increased to 0.06kg for animals born in 2023. The trends based on the average EBVs and GEBVs per year of birth for WM show that the inclusion of genomic information caused a steeper slope in the trend, therefore the response to selection is slightly under-estimated when ignoring genomic information. Despite the low heritability of this trait, the consistent upward trend reflects the effectiveness of breeding programs for the SA Merino sheep breed. It is important to select for a heavier maternal weaning weight, as better genetic potential for this trait indicates better maternal ability, i.e. improvement in milk production and nurturing behaviour, which can lead to healthier and more robust offspring (Esmaeili-Fard *et al*., 2021). This study therefore confirms that the advantage of inclusion of genomic information in the estimation of genetic potential of animals is more pronounced in traits with lower heritability (Pérez-Enciso & Steibel, 2021).

5.4.2 Accuracy comparison of EBVs *versus* GEBVs

Accuracy of prediction of GEBVs as compared to that of conventional breeding values were done for the traits fibre diameter and wean maternal. There was no increase in accuracy observed when incorporating genomic information for FD. Due to the high heritability of FD, the range of the accuracies were narrow, as well as minimal difference was observed between the ranges and the means of the accuracies for the EBVs and GEBVs. The high heritability of FD indicates that genetic factors strongly influence this trait, therefore the measurement of the animal within its contemporary group is a reliable indication of the animals genetic potential for the trait and consequently, the accuracy percentages for the EBVs and GEBVs were closely aligned, as illustrated by the tight clustering of points in Figure 4.5 (a). This minimal difference in accuracy between EBVs and GEBVs is due to the already high predictive power of conventional EBVs for FD, making the additional genomic information less impactful.

For wean maternal the ranges of the accuracies differed more pronounced between the use of EBVs and GEBVs. The accuracies for the EBVs ranged between 18% and 97%, while the accuracies for the GEBVs ranged between 37% and 97%. This shows that a higher accuracy range for GEBVs compared to EBVs were observed. However, the ranges for WM were much wider compared to FD, indicative of WM’s low heritability. Furthermore, a higher average accuracy for the GEBVs (65.02%) was observed for WM, with the average accuracy for the EBVs was lower at 59.97%. A marked increase in the accuracies was observed when genomic information was included, ranging from a minimum increase of 1% to a maximum increase of 48% and an average increase of 5.05% over all genotyped animals. Wean maternal, which had the lowest heritability value, indicative of heavy influence by the environment, resulted in lower and more variable accuracies from the conventional estimation of EBVs. By incorporating genomic data, GEBVs can more precisely capture the genetic component of this trait, leading to more reliable estimates of an animal’s genetic potential. Therefore, a much larger increase in accuracy was observed between the EBVs and GEBVs for WM than for FD.

The variation in accuracies amongst traits generally arises due to the differences in heritabilities of the traits. The heritability significantly impacts the accuracy of conventional and genomic predictions and should be factored into breeding value estimations (Calus, 2010). In this study, MW, which exhibited the lowest heritability, experienced the largest increase in accuracy when incorporating genomic information. Conversely, FD, which displayed the highest heritability value, experienced only a minor increase in accuracy between the use of EBVs and GEBVs. This highlights the importance of using genomic information to improve the accuracy of breeding value estimations, especially for traits with lower heritability. The increase in accuracies when incorporating genomic information using ssGBLUP methodology arises from the distinct relationship matrices (Calus, 2010; Forni *et al*., 2011; Meuwissen *et al*., 2016) that are being implemented. Specifically, the ssGBLUP method employs the inverse of the H-matrix, which is based on genomic relationships amongst the genotyped animals, whereas the conventional BLUP method uses the inverse of the A-matrix, which is based on pedigree relationships only (Calus, 2010; Forni *et al*., 2011; Meuwissen *et al*., 2016). The ssGBLUP method yields breeding values with higher accuracy compared to the conventional BLUP methodology, as the genomic relationship matrix provides a more precise representation of the genomic information shared among siblings (Meuwissen *et al*., 2016).

5.4.3 Top ten rankings based on EBVs *versus* GEBVs

For fibre diameter and wean maternal, the top ten young rams and top ten rams with progeny for all animals that had genotypic information were identified based on their EBVs and GEBVs to determine whether the inclusion of genomic information influenced the ranking of the animals. It was found that the rankings of the young rams and rams with progeny for FD remained relatively consistent, while the rankings for the young rams and rams with progeny for WM both changed markedly and therefore did not result in the same outcome. For FD, the rankings of the young rams and rams with progeny between the GEBVs and EBVs remained relatively consistent, with the exception of the last three animals. The top seven young rams and rams with progeny maintained their positions, with only the last three positions differing. The consistency in rankings suggests that both EBVs and GEBVs are reliable for selecting top-performing rams, ensuring stable genetic progress. The minor discrepancies in the last three positions highlight the potential for GEBVs to provide additional refinement in breeding decisions, particularly for animals with less progeny data. Therefore, the rankings of the young rams and rams with progeny based on EBVs were almost identical to the rankings based on the GEBVs, suggesting that the incorporation of genomic information did not significantly affect the rankings of the rams.

In contrast, the rankings for young rams and rams with progeny for wean maternal based on EBVs and GEBVs were inconsistent. For the ranking of the young rams, the first and ninth positions were the only consistent rankings based on the EBVs and GEBVs, while the rankings for all other rams varied significantly. A similar pattern was observed when comparing the rankings of rams with progeny based on their EBVs and GEBVs. Only the first, fifth, and tenth positions remained the same, while all other positions in the ranking varied. This inconsistency between the EBVs and GEBVs highlights the potential impact of incorporating genomic data into breeding value estimations, particularly for traits with lower heritability. The significant variation in rankings suggests that GEBVs may provide additional insights and refinement over conventional EBVs, potentially leading to more accurate selection decisions. Therefore, the rankings of the young rams and rams with progeny based on EBVs differed significantly to the rankings based on the GEBVs, suggesting that the incorporation of genomic information for a lowly heritable trait, such as WM, did significantly influence the rankings of the rams. This will result in more accurate selection of top animals and therefore genetic progress in the breed.

The rankings for fibre diameter, for both young rams and rams with progeny, remained relatively consistent due to the high heritability of this trait. A high heritability value indicates that FD is strongly influenced by genetics, and therefore results in EBVs, based on the measurements of the animals and theoretical relationships and GEBVs, where theoretical relationships are replaced with genomic relationships for the genotyped animals, both being able to capture the genetic potential of the animals more accurately. In contrast, wean maternal has a relatively low heritability, which indicates that a larger proportion of the variation is due to environmental factors (Oldenbroek & Van der Waaij, 2014). Due to greater differences between the EBVs and GEBVs, the rankings for WM were less consistent and changed more drastically, leading to more precise identification of top animals in selection programs and therefore selection progress when including genomic information in the estimation of breeding values for WM.

Other reasons for the consistent rankings observed for fibre diameter and the inconsistent rankings observed for wean maternal, are the ease of measurability of these traits, as well as the ability of GEBVs to capture genetic variation that is not accounted for in conventional EBVs (Zhang *et al.*, 2013). Due to instruments such as the Optical Fibre Diameter Analysis (OFDA), FD is relatively easy to measure accurately, leading to high-quality data and estimates (Holman & Malau-Aduli, 2012). This results in both EBVs and GEBVs reliably capturing the genetic potential of the animals, resulting in consistent rankings. In contrast, wean maternal is more challenging to measure accurately and can only be measured on the ewes. Wean maternal is largely influenced by various environmental factors such as nutrition, management practices, and the health status of the dam (Oldenbroek & Van der Waaij, 2014). Due to these complexities, the data collected for WM may be less precise, leading to lower accuracies in the estimation of EBVs. Moreover, GEBVs have the advantage of capturing more genetic variation than conventional EBVs (Goddard, 2012). This is particularly important for traits with complex inheritance patterns and low heritabilities such as WM (Zhang *et al.*, 2013). Therefore, the inclusion of genomic data can reveal genetic influences that are not apparent through pedigree and performance data alone, leading to differences in rankings between EBVs and GEBVs (Goddard, 2012). These results highlighted the significance of incorporating genomic information into breeding value estimations to achieve the most accurate rankings of animals.

Chapter 6: Conclusion and Recommendations

6.1 Conclusion

The systematic recording of animal performance and the use of pedigree data are essential for identifying optimal breeding strategies and serves as a powerful tool for driving genetic progress and enhancing livestock development (Mosconi, 2011). Data collected through performance recording enables precise genetic evaluations, thereby facilitating sustained genetic progress. Stud breeders and animal scientists rely on updated genetic parameters, such as heritability, repeatability and genetic correlations, as well as estimated breeding values (EBVs) for accurate genetic selection and improvement to occur. The purpose of this study was to estimate the genetic parameters of the South African Merino sheep breed, capturing the latest generation's information, in order for accurate breeding values to be estimated based on these representative variance components. Multi-trait Animal Models were constructed by identifying the effects that had a significant influence on the traits through the application of analyses of variance (ANOVA). These Multi-trait Animal Models were implemented to estimate variance components, using PEST (Groeneveld *et al.,* 2019) and VCE (Groeneveld *et al.,* 2010). Direct and maternal heritabilities along with genetic correlation estimates, permanent environmental and sire x herd and residual variances were therefore obtained for six traits: Weaning weight (WW), body weight at wool test (BWW), clean fleece weight CFW), fibre diameter (FD), coefficient of variation of fibre diameter (CVFD) and staple length (SL).

The heritabilities for all traits examined in this study were generally consistent with those reported in previous studies. The heritability estimates for the traits WW, BWW and FD were slightly higher than those found in earlier studies. This suggests a strong genetic influence on these traits, indicating that selective breeding is effective in enhancing these traits in the SA Merino breed populations. The heritability estimates for CFW, CVFD and SL showed more variability, with some estimates being higher and others lower compared to previous studies. Despite this variability, the overall estimates remained similar to those reported in previous literature, reinforcing the reliability of the estimates. Overall, the results emphasize the importance of regularly re-estimating the genetic parameters of a population to enhance the accuracy and effectiveness of breeding programs. This will enable breeders to make more informed decisions, ultimately leading to improved livestock performance, profitability and sustainability.

Based on the same multi-trait animal models used to estimate the variance components, breeding values for the same economically important traits were predicted. Genetic trends based on these EBVs were compared to those obtained from the National Genetic Evaluation trends, using the same base year of 2018. The national trends for these traits exhibited a faster rate of genetic progress, as indicated by the steeper slopes in their respective graphs. For CFW, the average EBVs per year of birth calculated in this study closely mirrored that of the national trends, where both sets of EBVs demonstrated a similar rate of genetic progress, ultimately converging at the same average EBV value by 2021. The average EBVs for FD and CVFD per year of birth followed a downward trajectory over the years. A comparison for CVFD could not be made with the national trends due to the trait not being included in the National Genetic Evaluation. The differences in the trends as estimated in this study and those obtained from the National Evaluation highlight the importance of regularly updating population genetic parameters and EBVs to enhance the genetic selection and progress of economically important traits.

Furthermore, this study evaluated the impact on the ranking of animals and accuracy values when incorporating genomic information to select for a highly heritable trait, FD, and a lowly heritable trait, wean maternal (WM). The results indicated that the highly heritable trait, FD, showed no significant change in ranking or accuracy when genomic information was included. Conversely, for the lowly heritable trait, WM, incorporating genomic information resulted in substantial changes in the rankings of animals and improved accuracy, with an observed average increase of 5.05% when genomic information was incorporated. These results highlight the importance of integrating genomic data into breeding programs, particularly for traits with low heritability, to enhance genetic progress and accuracy.

6.2 Recommendations

It is recommended to estimate genomically enhanced breeding values (GEBVs) for all traits included in this study, rather than limiting the comparison to just fibre diameter (a trait of high heritability) and wean maternal (a trait of low heritability). Although the analysis between a highly heritable and a lowly heritable trait revealed differences that including genomic information can make, by analysing other traits of economic importance, such as weaning weight (WW), bodyweight at wool test (BWW), clean fleece weight (CFW), coefficient of variation of fibre diameter (CVFD) and staple length (SL), a more comprehensive comparison can be made between the use of Estimated Breeding Values (EBVs) and GEBVs. This broader analysis will highlight the differences in the rate of genetic gain and accuracy between EBVs and GEBVs across all traits, leading to more informed selection decisions and potentially increasing the overall rate of genetic gain.

Furthermore, it would be informative to include an evaluation of fertility traits of the South African Merino sheep breed, alongside the wool and weight traits assessed in this study. Reproductive performance plays a crucial role in the profitability of sheep enterprises making the estimation of variance components, EBVs and GEBVs for fertility traits particularly valuable. Given that fertility traits typically exhibit low heritability, the incorporation of genomic information could lead to significantly greater genetic gains. By broadening the scope of the analysis to include fertility traits, a more comprehensive understanding of the genetic potential can be achieved. This approach will not only enhance the accuracy of selection decisions, but also ensure that improvements are made across a wider array of economically important traits. Ultimately, this holistic evaluation will contribute to the sustainability and profitability of sheep production by optimizing genetic progress in both reproductive and production traits, thereby supporting the long-term success of sheep enterprises.

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Addendum A

Table A1: Analysis of variance (ANOVA) and significance levels for direct weaning weight (kg)

	Sum Sq	DF	F-Value	Pr(>F)	Level of Significance
Weaning age (days)	1.7792e+08	1	883.588	<2.2e-16	***
Dam age (months)	1.5038+08	1	746.819	<2.2e-16	***
Weaning age quadratic	6.3133e+07	1	313.529	<2.2e-16	***
Dam age quadratic	1.1550e+08	1	573.606	<2.2e-16	***
Wean contemporary group	6.889373e+20	62458	215.68	<2.2e-16	***
Sex	8.2827e+08	1	4113.320	<2.2e-16	***
Birth status	1.2753e+08	4	158.331	<2.2e-16	***
Rearing status	18841.74	4	148.278	<2.2e-16	***
Herd x Sire	9.6883e+09	1245	38.646	<2.2e-16	***
Residuals	1.2324e+10	61201			

[1] Sum Sq: sum of squares; DF: degrees of freedom; F-Value: F statistic; Pr(>F): P-value for F-statistic

Table A2: ANOVA and significance levels for body weight at wool test (kg)

	Sum Sq	DF	F-Value	Pr(>F)	Level of Significance
Dam age (months)	6325	1	274.85	<2.2e-16	***
Sheep age (days)	43918	1	1908.57	<2.2e-16	***
Wool contemporary group	6875747	666	448.65	<2.2e-16	***
Rearing status	34877	3	505.23	<2.2e-16	***
Residuals	1421781	61787			

[2] Sum Sq: sum of squares; DF: degrees of freedom; F-Value: F statistic; Pr(>F): P-value for F-statistic

Table A3: ANOVA and significance levels for clean fleece weight (kg)

	Sum Sq	DF	F-Value	Pr(>F)	Level of Significance
Dam age (months)	99	1	332.93	<2.2e-16	***
Sheep age (days)	261	1	874.71	<2.2e-16	***
Wool contemporary group	52730	666	265.33	<2.2e-16	***
Rearing status	422	3	471.34	<2.2e-16	***
Residuals	18438	61787			

[3] Sum Sq: sum of squares; DF: degrees of freedom; F-Value: F statistic; Pr(>F): P-value for F-statistic

Table A4: ANOVA and significance levels for staple length (mm)

	Sum Sq	DF	F-Value	Pr(>F)	Level of Significance
Sheep age (days)	23655	1	150.844	<2.2e-16	***
Wool contemporary group	13848569	666	132.600	<2.2e-16	***
Rearing status	7476	3	15.891	2.522e-10	***
Residuals	9689310	61788			

[4] Sum Sq: sum of squares; DF: degrees of freedom; F-Value: F statistic; Pr(>F): P-value for F-statistic

Table A5: ANOVA and significance levels for fibre diameter (µm)

	Sum Sq	DF	F-Value	Pr(>F)	Level of Significance
Dam age (months)	36	1	35.550	<2.5e-09	***
Sheep age	290	1	288.007	<2.2e-16	***
Wool contemporary group	62311	666	92.868	<2.2e-16	***
Rearing status	445	3	147,299	<2.2e-16	***
Residuals	62247	61787			

[5] Sum Sq: sum of squares; DF: degrees of freedom; F-Value: F statistic; Pr(>F): P-value for F-statistic

Table A6: ANOVA and significance levels for coefficient of variation of fibre diameter (%)

	Sum Sq	DF	F-Value	Pr(>F)	Level of Significance
Dam age (months)	309	1	85.1860	<2.2e-16	***
Sheep age (days)	487	1	134.3799	<2.2e-16	***
Wool contemporary group	100823	666	41.7962	<2.2e-16	***
Rearing status	60	3	5.5353	0.0008526	***
Residuals	223792	61787			

[6] Sum Sq: sum of squares; DF: degrees of freedom; F-Value: F statistic; Pr(>F): P-value for F-statistic

Addendum B

Table B1 The top ten sires and top ten young rams identified based on the average breeding values for direct weaning weight (kg)

Sire number	Breeding Value	Ram number	Breeding Value
85670719	3.77	96294624	3.49
74296302	3.76	96293386	3.07
78885266	3.33	96294376	2.90
79928982	3.23	91981159	2.90
82937632	3.07	96295498	2.88
79245015	2.98	94416716	2.81
80253347	2.95	94416997	2.68
72363427	2.90	91981274	2.59
80405368	2.85	90526468	2.53
85899136	2.82	91982264	2.51

Table B2 The top ten sires and top ten young rams identified based on the average breeding values for maternal weaning weight (kg)

Sire number	Breeding Value	Ram number	Breeding Value
75928424	2.39	96293964	1.96
74296302	2.31	94502408	1.87
86158623	1.87	92804152	1.46
79929766	1.69	91986877	1.45
80252885	1.63	91482000	1.32
80705239	1.61	92805654	1.31
73314767	1.56	93185775	1.28
74294513	1.53	93090686	1.20
72363427	1.52	92805969	1.14
79007266	1.49	92046531	1.12

Table B3 The top ten sires and top ten young rams identified based on the average breeding values for body weight at wool test (kg)

Sire number	Breeding Value	Ram number	Breeding Value
82937632	7.99	96293386	7.99
85670719	7.23	93090686	6.68
78885266	6.46	96293964	6.16
74296302	6.21	93185775	6.07
78976925	6.03	94416997	6.03
80405368	5.82	93092260	5.88
73314767	5.72	94416716	5.67
85899136	5.69	96294327	5.56
79245015	5.52	96294269	5.48
78097227	5.33	93091981	5.44

Table B4 The top ten sires and top ten young rams identified based on the average breeding values for clean fleece weight (kg)

Sire number	Breeding Value	Ram number	Breeding Value
74294513	0.72	89362602	0.72
78097227	0.67	91483842	0.71
80252885	0.65	85672178	0.65
78885266	0.64	91982264	0.61
80593593	0.64	93091908	0.59
79245015	0.61	94503273	0.59
74296302	0.60	93186419	0.58
80705239	0.59	89361042	0.57
74867425	0.59	93091981	0.57
72363427	0.56	94503687	0.56

Table B5 The top ten sires and top ten young rams identified based on the average breeding values for staple length (mm)

Sire number	Breeding Value	Ram number	Breeding Value
80705239	16.47	91986927	15.51
80593593	15.51	94504354	14.11
79929766	15.21	93091908	13.67
78087616	13.98	93090686	13.14
78097227	13.67	94502556	12.91
80252885	12.94	84270966	12.74
79928982	12.91	94503273	11.94
90377383	12.37	90379173	11.76
74296302	12.36	96294061	11.67
72363427	12.22	94500964	11.24

Table B6 The top ten sires and top ten young rams identified based on the average breeding values for fibre diameter (μm)

Sire number	Breeding Value	Ram number	Breeding Value
74867425	-0.69	92891704	0.26
86196938	-0.56	84270966	0.30
90377383	-0.46	92046531	0.30
75928424	-0.45	92891779	0.34
79788758	-0.41	92806637	0.34
85898740	-0.33	93090256	0.38
80706450	-0.21	94416716	0.39
83616888	-0.19	92805654	0.60
76884220	-0.11	94417896	0.64
78992963	0.27	94507308	0.68

Table B7 The top ten sires and top ten young rams identified based on the average breeding values for coefficient of variation of fibre diameter (%)

Sire number	Breeding Value	Ram number	Breeding Value
90377383	-0.42	92804624	0.76
79007266	-0.32	93091981	0.78
82297268	-0.29	91648089	0.81
80593593	-0.25	92046929	0.89
79245015	-0.08	94504172	0.90
78087616	-0.01	89362602	0.94
78692910	-0.01	91483842	1.01
80774276	0.49	92806348	1.02
80706450	1.08	92806637	1.08
80406481	1.18	96071758	2.01