GENETIC ANALYSIS OF BODY WEIGHT AT DIFFERENT AGES IN THE GROOTFONTEIN MERINO STUD

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ABSTRACT

Body weight is considered an important trait for the selection of replacement animals in both wool and mutton sheep. Knowledge of the genetic variance of each trait and covariances among traits is essential for effective genetic evaluation and improvement programs. It is important that estimated breeding values for performance traits should be estimated as accurately as possible. This could be achieved by fitting the most appropriate statistical model, which accounts for all known non-genetic effects, as well as correctly partitioning the genetic variance into its various sources. The aim of this study was to identify the most appropriate models for estimation of breeding values for body weights recorded at different ages in Merino sheep. Various statistical procedures, including uni- and multivariate linear models employing restricted maximum likelihood methods, random regression and repeatability models were evaluated. The dataset used in this study comprises body weight data recorded at different ages in the Grootfontein Merino stud from 1968 to 2012. The total number of males and females for which birth weight was recorded, were 7794 and 8317 respectively. The univariate direct heritability of body weight increased with an increase in age. Direct heritability estimates were 0.20 ± 0.03 for birth weight, 0.16 ± 0.02 for weaning weight, 0.51 ± 0.04 for 15-month body weight and 0.40 ± 0.05 for 3-year adult body weight. Maternal heritability estimates were 0.11 ± 0.02 for birth weight, 0.04 ± 0.01 for weaning weight and 0.08 ± 0.02 for 15-month body weight. The genetic correlation between direct and maternal effects was negative for all weights where it was included and ranged from -0.95 ± 0.14 for 6-month body weight to -0.28 ± 0.09 for birth weight. The repeatability model including direct and maternal genetic effects, without splines, was the most appropriate repeatability model for estimation of genetic parameters for body weight. The accuracy of the estimated breeding values were determined using Spearman rank correlations and number and proportion of common animals in the Top 10% and Top 1% lists. The comparison of estimated breeding values for body weights obtained with univariate, multivariate and repeatability models revealed that the multivariate model was the most efficient method due to the high accuracies obtained with this procedure. These results will be implemented when estimating breeding values for body weights for the animals in the Merino reference population during the development phase of a suitable SNP key to be used in genomic selection for body weight in South African Merino sheep.

DECLARATION

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Traits

BW	Birth weight
W42	Body weight at 42 days of age
WW	Weaning weight
W6	Body weight at 6 months of age
W8	Body weight at 8 months of age
W12	Body weight at 12 months of age
W15	Body weight at 15 months of age
AW2	Adult body weight at two years
AW3	Adult body weight at three years
AW4	Adult body weight at four years
AW5	Adult body weight at five years
AW6	Adult body weight at six years
WWU	Weaning weight univariate
W15U	15-month body weight univariate
AW3U	3-year adult body weight univariate
WWM	Weaning weight multivariate
W15M	15-month body weight multivariate
AW3M	3-year adult body weight multivariate

(Co)variance components and parameters

σ^2_p	Phenotypic variance
σ^2_a	Direct additive variance
σ^2_m	Maternal additive variance
σ^2_{mpe}	Maternal permanent environmental variance
σ_{am}	Genetic covariance between the animal effects
σ^2_{anim}	Animal permanent environmental variance
σ^2_e	Environmental variance
σ_{p1p2}	Phenotypic covariance
σ_{a1a2}	Direct additive covariance
σ_{e1e2}	Environmental covariance
h^2_a	Direct additive heritability
h^2_m	Maternal heritability
c^2_{mpe}	Maternal permanent environmental effect

c^2_{anim}	Animal permanent environmental effect
r_{am}	Genetic correlation between the animal effects
t	Repeatability
r_{p1p2}	Phenotypic correlation
r_{g1g2}	Genetic correlation
r_m	Maternal correlation
r_e	Environmental correlation

Other

AC	Age class
AIC	Akaike's Information Criterion
ASreml	Restricted maximum likelihood program for estimation of covariances and genetic parameters developed by Arthur Gilmour
BIC	Bayesian Information Criterion
BLUP	Best Linear Unbiased Prediction
BWebv	Estimated breeding value for body weight
CFWebv	Estimated breeding value for clean fleece weight
DAFF	Department of Agriculture, Forestry and Fisheries
DAGRIS	Domestic Animal Genetic Resources Information System
DfReml	Derivative-free restricted maximum likelihood program for estimation of covariances and genetic parameters developed by Karin Meyer
DGV	Direct genomic value
EBV	Estimated breeding value
FDebv	Estimated breeding value for fibre diameter
GEBV	Genomic estimated breeding value
INTERGIS	Integrated Registration and Genetic Information System
LogL	Log likelihood
MTDfReml	Multiple-trait derivative-free restricted maximum likelihood programs for estimation of genetic (co)variances
N/Ktex	Newton per kilotex
NSSIS	National Small Stock Improvement Scheme
REP	Repeatability model
REV	Relative economic value expressed in Rand per small stock unit
SLebv	Estimated breeding value for staple length
SNP	Single nucleotide polymorphism
SSU	Small stock unit

TWWebv	Estimated breeding value for total weight of lamb weaned
WOMBAT	Software package for quantitative genetic analyses of continuous data developed by Karin Meyer (replaced DfReml)
ZAR	South African Rand

1. INTRODUCTION

1.1 Introduction

In sheep production, growth is regarded as one of the most important traits (King *et al*., 2010). Snyman & Cloete (2008) mentioned that body weight is considered an important trait for the selection of replacement animals in wool or mutton sheep. The effect of birth weight on pre-weaning growth rate makes it an economically important trait as it increases the economic success in any sheep production enterprise (Al-Shorepy, 2001). Early growth rate is one of the most important traits contributing to the income of a specific enterprise. The earlier the market weight is reached, the more breeding females can be kept on a specific farm. Factors influencing early growth of a lamb are the lamb's own additive genes for growth, as well as the milk production and general maternal ability of its dam (Snyman & Cloete, 2008). It therefore follows that selection should be based on growth rate or body weight, reproduction and maternal traits (milk production and general maternal behaviour). It has been well documented that maternal effects, genetic or environmental in nature, contribute significantly to variance of early growth traits in sheep (Ligda *et al.*, 2000; Al-Shorepy, 2001; Mandal *et al*., 2006, Mokhtari *et al.*, 2013).

Growth traits are affected by a number of non-genetic factors and the genetic potential of animals can easily be obscured by these factors and not recognised. Hence, the performance records of an animal should be corrected for classifiable non-genetic sources of variation (Hartman, 2000). This is important for achieving accurate estimates of genetic parameters and breeding values for identification of genetically superior animals for genetic improvement (Thiruvenkadan *et al*., 2009). The year and season of birth, sex, birth status, age of the dam and year x sire interaction are important sources of non-genetic variation in body weight traits (Hartman, 2000; Neser *et al*., 2001, Mohamed, 2004). Knowledge of the genetic variance of each trait and covariances among traits is essential for effective genetic evaluation and also for improvement programs (Safari et al., 2005). Bosso et al. (2007) also emphasized that the evaluation of genetic trends provide an indication of the direction of the breed as well as the rate of genetic improvement.

During the past decade genomic selection in farm animals has revolutionised animal breeding as we know it. However, before a genomic selection programme could be implemented in any breed or population, it is imperative that accurate and reliable conventional estimated breeding values (EBV) for performance traits are available (Calus, 2010; Van der Westhuizen *et al*., 2013a, 2013b; Van Marle-Köster *et al*., 2013). These EBVs are incorporated with the direct genomic values (DGVs), which are based on single nucleotide polymorphism (SNP) effects, in order to calculate genomic estimated breeding values (GEBVs) for a specific population. It is therefore important that EBVs for performance traits should be estimated as accurately as possible. This can be achieved by fitting the most appropriate model, which accounts for all known non-genetic effects, as well as correctly partitioning the genetic variance into its various sources.

In order to keep abreast with world trends in animal breeding, it was decided that steps should be taken for the future implementation of genomic selection in the South African sheep industry. The first step is the establishment of a reference population for the Merino sheep breed. As the Merino sheep breed is the most numerous wool sheep breed in South Africa, this MSc project serves as a trial for developing suitable methodology and procedures for the other breeds to follow when implementing the genomic selection program. Several industry, as well as experimental Merino resource flocks form part of this reference population. The Grootfontein Merino stud is one of the experimental resource flocks that forms part of the reference population. Data collected on the Grootfontein Merino stud was used for this study.

This study forms part of the bigger project, which will eventually lead to the implementation of genomic selection in the South African Merino sheep breed. It is also the first phase of a project that will involve a genome wide association study to identify possible genetic markers associated with reproduction and body weight in different sheep flocks.

As body weight is one of the economically important production traits, this study will focus on identifying the most appropriate models for estimation of breeding values for body weights recorded at different ages in Merino sheep. Various statistical procedures were evaluated, including uni- and multivariate linear models employing restricted maximum likelihood methods as implemented in the ASReml software (Gilmour *et al.*, 2009), random regression models (Meyer, 2000) and repeatability models (Meyer & Hill, 1997).

1.2 Aim and objectives

The broad aim of this study was to determine the most suitable statistical models and procedures for estimation of (co)variance components, genetic parameters and breeding values for body weight at various ages in Merino sheep.

The objectives were to:

- Estimate (co)variance components, genetic parameters, genetic relationships and breeding values for and among body weights at various ages (from birth to adult weight) using uni- and multivariate linear models employing restricted maximum likelihood procedures
- Estimate (co)variance components, genetic parameters and breeding values for body weights at various ages (from birth to adult weight) using a repeatability model

- Evaluate (co)variance components, genetic parameters, genetic relationships and breeding values for and among body weights at various ages (from birth to adult weight) using random regression procedures
- Determine the most suitable statistical models for estimation of breeding values for body weight to be used in a genomic selection program for South African Merino sheep.

2. LITERATURE REVIEW

2.1 Introduction

The small stock industry is of vital importance to the agricultural and economic sectors of South Africa and contributes 8.2% of the total gross value of animal products (ZAR 35.28 billion) (Schoeman *et al*., 2010). The sheep and wool industry in South Africa is one of the oldest agricultural industries (Makapela, 2008) and is a foreign exchange earner in the country's economy with employment opportunities to thousands of inhabitants and clothing and feeding millions (Erasmus, 1985). Cloete & Olivier (2010) stated that extensive small stock production is the dominant livestock industry in the drier western and north-western parts of the country, where the grazing capacity is well below 12 ha per large stock unit. In 2015 the total number of sheep in South Africa was estimated at 21.201 million (Abstract of Agricultural Statistics, 2015). The largest proportion of these animals is kept in the Eastern Cape (30%), Northern Cape (25%), Free State (19%) and Western Cape (12%) provinces. The animals are kept mainly for wool and mutton production and the industry is therefore represented by organisations from the mutton as well as the wool industries (DAFF, 2013). The income from slaughtered sheep and wool in South Africa is estimated at R3 571 million and R2 074 million respectively (http://www.gcis.gov.za/content/resourcecentre/sa-info/yearbook2013-14).

In 1789 Merino sheep were introduced into South Africa from the Dutch Government when two Spanish Merino rams and four Spanish Merino ewes were donated to Colonel Jacob Gordon (www.merinosa.co.za). The breed spread over many parts of South Africa during the mid-1800s (Hlope, 2011). Currently the Merino is the most prominent sheep breed, in terms of numbers, in South Africa. The estimated number of Merino sheep in South Africa is currently 11.125 million (Abstract of Agricultural Statistics, 2015).

The South African Merino is a composite of Spanish, Saxony, Rambouillet, American and Australian Merinos (Mason, 1996), characterised by a uni-coloured white, fine to medium wool fleece (Hlope, 2011). South African Merino sheep are mainly found where the climate is semi-arid to sub-humid (DAGRIS, 2009). About 75% of a Merino farmer's income is from the carcass (mutton), while these animals can produce 10-15% of its own live mass in clean wool (South African Livestock Breeding, 1998; Schoeman *et al*., 2010).

The selection criteria of Merino sheep mainly focus on growth and wool traits and to a lesser extent on reproduction traits. Genetic progress in research flocks on growth (Olivier, 1989; Neser *et al*., 1995; Olivier *et al*., 1995; Olivier, 2014), number or weight of lamb weaned per lambing opportunity (Olivier, 1998; Cloete *et al*., 2004; Olivier, 2014), clean fleece weight (Olivier *et al*., 1995; Cloete *et al*., 1998;

Olivier, 2014) and fibre diameter (Olivier *et al*., 1995; Cloete *et al*., 2013; Olivier, 2014) have been reported. Due to unfavourable genetic correlations among some of the economically important traits, a balanced approach should be followed in a Merino stud, which should lead to an appreciable increase in live weight, together with a reduction in fibre diameter, while keeping clean fleece weight constant (Olivier *et al*., 1995; Olivier, 2014).

2.2 Current selection strategy in the South African Merino stud industry

The National Small Stock Improvement Scheme (NSSIS) of South Africa was initiated in 1965 at the Fleece Testing Centre at Grootfontein, Middelburg, Eastern Cape (Erasmus & Hofmeyr, 1984), where it played a vital role in the improvement of wool in South Africa. Erasmus (1985) stated that through utilisation of available Merino genetic resources, South Africa has become competitive with the wool industry of the rest of the world. Fibre diameter has been decreased and body weight has been increased without decreasing the wool production per sheep. In 1995 the first multi-trait BLUP analysis on body weight, fibre diameter, clean wool production and pleat count on Merino sheep was performed by J.J. Olivier (http://www.arc.agric.za). This was the first multi-trait analysis done on sheep in the world (http://www.arc.agric.za).

Over the years, some modifications took place in the NSSIS as a result of changes in demand, adoption of new production technologies and advanced statistical procedures (Schoeman *et al*., 2010). The NSSIS consists of an integrated pedigree and data recording system, namely the INTERGIS (Schoeman *et al*., 2010). The aim of the NSSIS is to improve traits of economic importance on a genetic level and to ensure that the breed standards are maintained (Olivier, 2002).

The South African breeding policy for the Merino industry has historically been to increase body size, while ensuring that the wool weight remain constant and the fibre diameter is decreased (Olivier *et al*., 1997). Currently reproductive performance is also included (Van Graan *et al*., 2014). A selection index model for Merino sheep was developed that combined the price of wool and meat on a five year rolling average with the estimated breeding values for production and reproduction traits (Herselman & Olivier, 2010; Olivier *et al*., 2014). This formula is update annually during August by the Merino SA Technical Committee. The following equation, which includes reproduction, was used during 2014 and 2015 by the Merino breed of South Africa to calculate the relative economic value (Olivier *et al*., 2014):

$$\text{REV (R/SSU)} = -806.64 - 0.81\text{BWebv} + 85.98\text{CFWebv} + 0.29\text{SLebv} - 97.53\text{FDebv} + 2.0166(20+\text{FDebv})^2 + 9.9\text{TWWebv}$$

where REV (R/SSU) is the relative economic value expressed in Rand (ZAR) per small stock unit, BWebv is the estimated breeding value for body weight, CFWebv is the estimated breeding value for clean fleece weight, SLebv is the estimated breeding value for staple length, FDebv is the estimated breeding value for fibre diameter and TWWebv is the estimated breeding value for total weight of lamb weaned.

2.3 Traits of importance in Merino sheep breeding

In Merino sheep, the main traits of economic importance are reproductive, growth and wool traits. As this study will deal with body weight, the most emphasis in the discussion will be placed on this group of traits. The other economically important traits will also be discussed, albeit in less detail.

2.3.1 Growth and body weight

In sheep production the growth rate and body weight of lambs at different ages determine the profitability of the enterprise (Mohammadi *et al*., 2013). In meat production, growth is regarded as one of the most important traits (King *et al*., 2010). Body weight is positively related to many other traits of economic importance, for example reproduction (Snyman *et al*., 1998; Safari *et al*., 2007b; Olivier & Cloete, 2011; Olivier, 2014), adaptability (Singh *et al*., 2006), wool production (Baneh *et al*., 2013; Olivier, 2014) and survival at birth (Baneh *et al*., 2013).

Body weights at various ages are included as selection criteria in breeding programmes for sheep (Thiruvenkadan, 2009; Mousa *et al*., 2013). Positive genetic responses have been reported where selection was based on body weight in Merino sheep (Olivier, 1989, Olivier *et al*., 1995, Olivier, 2014). Genetic parameters for body weight in Merino sheep will be discussed under paragraph 2.7.

2.3.1.1 Birth weight

The importance of birth weight lies in its relationship with body weight at all ages (Al-Shorepy, 2001; Notter, 2011), and more importantly, survival rate (Borg, 2007). The relationship between birth weight and lamb survival usually has an inverted U-shape (Sawalha *et al*., 2007; Barazandeh *et al*., 2012). From such a relationship it follows that lambs with intermediate birth weights would have a better chance of survival. Lambs with either too low or too heavy birth weights, will have a lower survival rate, as very small lambs will most probably die due to starvation and hypothermia, and very big lambs would cause dystocia (Sawalha *et al*., 2007; Barazandeh *et al*., 2012).

2.3.1.2 Weaning weight

Weaning weight is an important component of total weight of lamb weaned, which in turn determines ewe production efficiency. The weight at weaning is more important than age at weaning (Selaive-

Villarroel *et al*., 2008) and it is affected by several non-genetic factors, such as age of lambs, year and season of birth and weaning, sex, type of birth and age of the dam, as well as genetic factors such as the lamb's direct genetic potential for growth rate and the maternal ability and milk production of the ewe (Babar *et al*., 2004; Iyiola-Tunji *et al*., 2011; Iyiola-Tunji, 2012).

Pre-weaning growth rate, and subsequently weaning weight, is also a determinant of marketing age in lambs that are marketed at an early age. Olivier (2014) stated that by selecting for increased growth rate and lamb weight or an increase in the number of lambs that survived until weaning, meat production could be increased.

Tosh & Kemp (1994) emphasised that growth rate and body weight of lambs must be taken into account in any breeding system. For selection of replacement ewes and rams in wool or mutton sheep, body weight is an important trait to be considered. However, using body weight as the only selection criterion for improved early growth rate could have some detrimental effects. Overall efficiency of pre-weaning growth could be negatively influenced due to a possible negative genetic relationship between additive direct and additive maternal components of traits affected by both direct and maternal effects (Baker, 1980; Robinson, 1996). The maternal component of early growth should therefore also be considered when including early growth traits in the selection program.

2.3.1.3 Post weaning weight

A post weaning weight is routinely recorded in most sheep breeds and is usually related to the marketing weight of the breed. In South African Merino sheep, lambs could be marketed as early as 8 to 9 months of age under favourable conditions. The lambs that have a below average weaning weight or weaning weight index and visual cull faults are culled. These could amount to approximately 25% of the ewe lambs and 50% of the ram lambs (Olivier & Van Graan, 2015). The remaining animals that are not selected as replacement ewes or as castrated males for wool production are slaughtered at 15 to18 months of age. Body weight at 12 to 16 months of age is included in the current selection index used for South African Merino sheep (Olivier *et al.*, 2014).

2.3.1.4 Adult weight

Together with lambing percentage and marketing age, the body weight of the ewe flock to a large extent determines the number of animals that could be kept on a specific farm (Herselman & Olivier, 2010). Increasing adult ewe body weight will increase maintenance requirements. Any increase in body weight should therefore be accompanied by an increase in either lambing percentage or a net increase in income from wool production (Herselman, 2004). This has been illustrated on the Grootfontein Merino stud as well as the Carnarvon Afrino flock and the Cradock Merino stud by Herselman (2004).

2.3.2 Reproduction

Reproductive rate is very important in any sheep enterprise as it is linked to the income and profitability through an increase in meat production and surplus animals for slaughter (Fogarty *et al*., 2006). Olivier (2014) mentioned that by improving reproduction, selection intensity would also be influenced, as more animals will be available for selection. The low heritability values of most reproduction traits have been well reported (Safari *et al*. 2007a; Vatankhah & Talebi, 2008; Zishiri *et al*., 2013) and will have an inhibitory effect on genetic progress. Due to the high economic impact of these traits, they have to be included in breeding programs. A number of selection criteria have been proposed for selection of reproductive efficiency. These include ewe productivity, which is influenced by mothering ability, milk production of the ewe, ovulation rate, twinning rate, embryo survival, age at puberty, fertility, lamb survival and lamb growth (Snowder & Fogarty, 2009).

In any sheep farming enterprise, be it mutton or wool, the two most important contributors to overall economic efficiency are reproductive rate and growth rate. Safari & Fogarty (2003) suggested that the increment on the mutton value also add to the importance of reproduction traits, both in Merino and maternal meat breeds. The profitability of sheep enterprises in South Africa depends on the adult ewe flock's reproduction potential (Olivier, 2014). There is a direct link between reproduction potential, income and profitability of a sheep enterprise through an increase in meat production and surplus animals for slaughter (Wang & Dickerson, 1991; Olivier, 1999; Fogarty *et al*., 2006). Hence, through the improvement of reproduction efficiency, selection intensity will be influenced as a result of more animals being available for selection.

2.3.2.1 Number of lambs born

The number of lambs born per ewe could be expressed as either per ewe joined or per ewe lambed. This trait is influenced by many components including ovulation rate, estrus, fertilization, embryo implantation, pregnancy and parturition (Hafez, 1993). Heritability values ranging from 0.04 to 0.23 are reported in the literature for number of lambs born in Merino sheep (Woolaston *et al*., 1995; Olivier *et al*., 2001; Swan *et al*. 2001; Cloete *et al*., 2004; Olivier, 2014).

Olivier (2014) reported a negative correlation between the number of lambs born and early body weights and concluded that increasing the number of lambs born will result in smaller lambs at birth and pre-weaning age, which could decrease lamb survivability.

2.3.2.2 Number of lambs weaned

The number of lambs weaned per ewe is expressed as the total number of lambs weaned within a year per ewe lambing (Van Wyk *et al*., 2003). This trait is affected by lactation, mothering ability and various environmental conditions, which influence the survival of the lamb. The number of lambs weaned or weaning percentage has a huge impact on the income on the farm. Heritability estimates reported in the literature for number of lambs weaned in Merino sheep ranged from 0.02 to 0.17 (Swan *et al.*, 2001; Olivier *et al.*, 2001; Cloete *et al.*, 2004; Olivier, 2014)

2.3.2.3 Total weight of lamb weaned

The composite trait litter weight weaned or total weight of lamb weaned can be used for selection as biological index for improving reproductive traits in sheep. Olivier *et al.* (2001) explained that the total weight of lamb weaned as a composite trait is influenced by several components and also emphasised that selection could be done on each of these components in order to improve the reproduction potential. Snowder (2007) mentioned that the phenotypic variation of a composite trait is influenced by the level of variability among its component traits and their interactions. Snyman *et al.* (1997) stated that the phenotypic variation is large within total weight of lamb weaned regardless of the reproductive rate of the flock. Duguma *et al.* (2002b) indicated that the variation may have a genetic basis and could be exploited to genetically increase lifetime reproductive efficiency in any flock.

Heritability of litter weight weaned is low and ranges from 0.04 to 0.26, as reported in the literature for South African Merinos (Snyman *et al.*, 1997; Olivier *et al.*, 2001; Cloete *et al.* 2002; Cloete *et al.*, 2004; Olivier, 2014). However, when coupled with intense selection it can result in favourable selection responses and when selection is performed over a long period for this trait, it can result in a balanced biological system within the environment and production system selected upon. The fact that this is a very complex composite trait and is only expressed later in the life of a ewe complicates the selection progress (Olivier, 2014).

2.3.2.4 Lamb survival rate

Lamb survival is an important economic trait that influences overall productivity (Amer *et al.*, 1999; Lopez-Villalobos & Garrick, 1999; Conington *et al.*, 2004; Herselman & Van Heerden, 2013). The rate of lamb survival plays a significant part in the production of sheep. However, environmental factors make it difficult to improve lamb survival through genetic selection (Lopez-Villalobos & Garrick, 1999; Dwyer, 2007; Maxa *et al.*, 2009). Heritability for lamb survival is low, ranging from 0.00 to 0.17 when fitting threshold models (Safari *et al.*, 2005; Welsh *et al.*, 2006; Cloete *et al.*, 2009; Olivier, 2014), and from 0.03 to 0.16 (Ceyhan *et al.*, 2009; Matos *et al.*, 2000; Plush *et al.*, 2011; Zishiri *et al.*, 2013) fitting linear models.

It has therefore been suggested that genetic improvement is doubtful. Hence, management aspects have a better chance to yield success (Olivier, 2014). Olivier (2014) also stated that factors such as the variability in the trait, selection intensity or relationships with other traits included in the selection objective, could have an impact on genetic progress.

2.3.3 Wool production

Wool production can account for up to 40% of total gross income in Merino sheep. Fleece weight is the most indicative of value, but fibre diameter, staple length and clean yield are also major variables influencing wool price (Erasmus & Delport, 1987; Rao, 1997; Herselman & Olivier, 2010). The quantity of wool produced by the sheep is dependent on the breed, genetic makeup, nutrition, and shearing interval (Sahoo & Soren, 2011). Visser (1985) stated that purposeful breeding, selection and feeding practices can increase the clean fleece production.

2.3.3.1 Wool weight

Sidwell *et al*. (1956) and Olivier & Olivier (2007) mentioned density of the fleece, surface area on which it grows, length and fineness of the fibre as the main determinants of the weight of clean wool to be produced by a sheep and also stated that wool sheep productiveness is measured accurately by clean wool.

In a study conducted by Blackwell & Henderson (1955) on four different breeds (Corriedale, Hampshire, Shropshire and Dorset), it was concluded that the age differences between ewes and differences associated with years were the major sources of environmental variation in fleece weight. Rams produces more wool compared to ewes of the same breed, mainly due to the larger body size of rams (Sahoo & Soren, 2011). The average clean fleece weight produced by the Grootfontein Merino stud rams at 16 months of age was 3.3 kg, while the ewes produced 2.8 kg clean fleece weight (Snyman, 2014).

2.3.3.2 Fibre diameter

Fibre diameter is the trait measuring the fineness of a fibre and it is measured in micrometres (µm).The importance of fibre diameter on the income from wool production has led to emphasis being placed on the selection for reduced fibre diameter (Olivier, 2014). Olivier *et al*. (2012) reported that reduced fibre diameter is a selection criterion in many Merino sheep flocks and selection for fibre diameter is exercised at performance testing age but little attention is given to wool fibre diameter of adult ewes. The average fibre diameter of the Grootfontein Merino stud rams and ewes were 18.2 and 18.3 µm respectively at 16 months of age (Snyman, 2014).

2.3.3.3 Staple length

The measure of staple length is the average length of the unstretched staple in millimetres (Atkins, 1997). Valera *et al*. (2009) mentioned the wool quality and value as been increasingly determined by the length of the staple. The average staple length for the Grootfontein Merino stud rams at 16 months of age was 108.5 mm, while the ewes produced fleeces with 106.1 mm staple lengths (Snyman, 2014).

2.3.3.4 Staple strength

Staple strength is the average force required to break staples of a specific thickness, expressed in Newton per kilotex (N/Ktex). The critical minimum strength for non-tender wool is in the range of 30-35 N/Ktex, but it depends on the fibre diameter (Atkins, 1997). The importance of staple strength as a determinant of the value of Merino wool has increased, especially in fine wool (Rose & Pepper, 2000). Olivier & Olivier (2007) concluded that staple strength is influenced by the amount of nutrients available to the wool follicles. Staple strength of the Grootfontein Merino stud rams and ewes were 34.9 and 33.6 N/Ktex respectively at 16 months of age (Snyman, 2014).

2.3.3.5 Heritability of wool traits

Heritability estimates for wool traits in woolled sheep are presented in Table 2.1. These estimates were high for all the wool traits, which indicate that genetic progress with conventional selection methods could be achieved (Olivier *et al*., 1995; Cloete *et al*., 1998; Cloete *et al*., 2013; Olivier, 2014).

Table 2.1 The average variance ratio estimates for wool traits in woolled sheep (Safari et al., 2005)

Trait	h^2_a ± s.e.	h^2_m ± s.e.	c^2_{mpe} ± s.e.
Greasy fleece weight	0.37	0.08	0.15
Clean fleece weight	0.36	0.06	0.21
Fibre diameter	0.59		
Coefficient of variation of fibre diameter	0.52		
Standard deviation of fibre diameter	0.52		
Staple length	0.46		
Staple strength	0.34		
Clean yield	0.56		

h^2_a – direct heritability; h^2_m – maternal heritability; c^2_{mpe} – maternal permanent environmental effect

2.4 Sources of variance

For genetic improvement, the influence of genetic and non-genetic factors is of vital importance. Snyman *et al*. (1995b) suggested that an important part of any breeding plan is knowledge of genetic and environmental components of variance and their ratios. These components should be known, as it is important to know the magnitude of the contribution of non-genetic influences on a trait under selection, in order to choose the correct selection method. It is also important to correct for these effects in an effort to obtain accurate values on which to base selection. Therefore, information on the extent to which genetic and environmental factors influence performance traits is a pre-requisite in designing breeding plans (Qureshi *et al*., 2010).

2.4.1 Non-genetic factors

The environmental conditions and animal management play an important role in the genetic improvement of any breed. It is important to determine the possible contribution of non-genetic sources of variation to economically important traits (Hartman, 2000). Best linear unbiased prediction (BLUP) of breeding values has become an important tool in selection programs. For the most accurate prediction of true breeding values, the identification and reduction of (correction for) important non-genetic sources of variation is essential.

There are numerous examples of the influence of environmental or non-genetic factors on various production traits in different breeds in literature. Schoeman (1998) reported that both internal and external environmental effects influence fur traits in Karakul sheep. Various studies reported influences of different non-genetic effects on the various wool traits (Blackwell & Henderson, 1955; Snyman *et al*., 1995a; Sahoo & Soren, 2011; Olivier *et al*. 2012).

Neser *et al*. (2001) stated age of dam, herd, birth year, sex, birth type and season as a few of the non-genetic factors affecting growth. In the study by Hartman (2000) on S.A. Mutton Merinos, year, sex, birth status, season, age of dam and year x sire interaction were highly significant for growth traits. Age of the dam had a significant effect on weight of lamb weaned per ewe per year, while year, lambing season, pre-mating weight of ewe and year x sire interaction significantly influenced the number of lambs born per ewe lambing. Other studies also reported environmental influences on reproductive traits and survival rate (Belay & Haile, 2011).

The most common non-genetic effects in sheep production and their influence on growth and body weight will be discussed in more detail.

2.4.1.1 Year and season of birth

Belay & Haile (2009) reported the effect of year as significant on the weight of lambs at 60, 70 and 120 days, where lambs born in 1996 where superior to lambs born in 1997 by 6.12% at 60 days of age and by 8.91% for weight at 120 days of age. However, it is also mentioned that management, disease, herdsman's skills and environmental factors might have influenced the outcomes, as these are in most cases confounded with the year effect.

In a study conducted by Thiruvenkadan *et al*. (2008) on factors affecting birth weight of Mecheri sheep it was reported that birth weight of lambs was significantly influenced by the season of birth, where the lambs born during September to February had higher birth weights than those born during March to August. The difference was due to the fact that the gestation periods of the ewes were during either unfavourable (less feed) or favourable environmental conditions (more feed), which contributed to the higher or lower weights at birth. Season has an effect on the birth weight through availability of feed and occurrence of diseases. Hence, lambing during wet seasons may result in impaired growth performance due to a high parasite load (Belay & Haile, 2009).

2.4.1.2 Sex of the lamb

The sex of the lamb had a significant effect on birth weight of lambs (Thiruvenkadan *et al*., 2008). Male and female average birth weights show that males weigh heavier at birth than females. Kuchtik & Dobes (2006) reported that sex of the lamb had a significant effect on all daily gains, except from birth to 70 days of age in Improved Wallachian and East Friesian breeds. Akhtar *et al*. (2001) also concluded that at weaning male lambs are heavier than females.

In a study conducted by Belay & Haile (2009) it was reported that males were always superior on body weight at all ages (60, 120, 300 and 360 days weight) compared to females. Snyman *et al*. (1995a) in a study on Afrino sheep concluded that male lambs are always heavier than the females throughout their lives. It was also mentioned that the weight ratio difference between males and females tend to increase with age, where a difference of 0.27 kg at birth increased to 2.30 kg at weaning and 11.87 kg at 18 months of age (Snyman *et al*., 1995a). Van Wyk et a1. (1993) reported the same trend in Dormer sheep where a 0.26 kg difference at birth increased to 2.80 kg at weaning.

2.4.1.3 Birth status

The litter size in which a lamb is born and reared influences the growth rate. Van Wyk *et al*. (1993) reported that single born Dormer lambs performed much better than twins for birth weight, weaning weight, growth rate and Kleiber ratio by 0.68 kg, 5.41 kg, 47 g/day and 0.972 respectively. In a study conducted by Hanrahan (1999) on sheep, the evaluation of the effects of rearing type on growth and carcass traits proved that lambs that were born and reared as singles were approximately 6 kg heavier at weaning than lambs that were born and reared as twins and their carcasses were more than 1 kg heavier at the same level of fatness.

Boujenane *et al.* (1991), Van Wyk *et al.* (1993) and Snyman *et al.* (1995a) concluded in their studies that the proportionate difference between weight of multiple born lambs and single born lambs decreased as the lambs grew older.

2.4.1.4 Age of dam

The age of the dam has a big influence on all the early growth traits of her lambs. Van Wyk *et al.* (1993) concluded that older dams gave birth to lambs that are heavier than lambs of younger dams. Van Wyk *et al.* (1993) also reported a positive correlation between the age of dam and the birth weight of lambs where there was an increase in birth weight of lambs with an increase in age of dam up to seven years. This study also showed that there is consistency in different breeds and flocks on the effect of age of dam on birth weight.

Qwabe (2011) stated that growth rate of lambs is significantly influenced by the age of dam at recording, resulting in lambs of older dams being heavier than those of younger dams. Snyman *et al.* (1995a) mentioned stress of pregnancy and lactation in young ewes as one of the factors that contributes to difference due to age of dam at recording.

2.4.1.5 Age of animal at recording

Due to the length of a normal breeding season (usually 4 to 6 weeks), the age difference between the oldest and youngest lambs vary a lot in the same lambing season. This difference in age has a marked effect on especially traits recorded early in life, such as weaning weight (Van Wyk *et al.*, 1993; Snyman *et al.*, 1995a). Therefore it is essential to correct for this difference in age, especially for early body weights.

2.4.1.6 Maternal Permanent environmental effect

Variations between females in maternal performance arise from either genetic or environmental causes (Saatci *et al.*, 1999). It has been well established that maternal effects, genetic or environmental in nature, contribute significantly to variance in early growth traits in sheep (Wilson *et al.*, 2005). Neser *et al.* (2000) stated that the dam uterine environment and multiple births had permanent maternal environmental effects on birth weights of Dorper sheep, and milk production of the dam was the main determinant of permanent maternal environmental effects on 42-day weight.

2.4.2 Genetic factors

Knowledge of the genetic variance of each trait and covariances among traits is essential for effective genetic evaluation and also for improvement programs (Safari *et al.*, 2005). The genetic variance can be divided into various sources, of which the direct additive genetic variance and maternal additive genetic variance are the most important in selection programs.

2.4.2.1 Direct additive genetic effect

The genotypic value appearing in the basic model for quantitative traits ($P = \mu + G + E + I_{ge}$) represents the overall effect of genes of an individual on its own performance for a trait. In this instance, gene combination effects (dominance and epistasis) are included. Because the gene combinations don't withstand segregation and independent assortment during meiosis, the transmission of a specific allelic combination from parent to offspring is not possible (Bourdon, 1997). The direct additive gene effects represents only that part of an animal's genotypic value that is due to independent gene effects that can be transmitted to the progeny. This is the breeding value. These effects are heritable and as they could be selected for, they form the central component of genetic improvement (Birwe, 2006). Mrode (2005) stated that these effects are subjected to a number of effects such as the Bulmer effect (reduction in the additive variance), which comes after several generations of selection and tends to enhance genetic relatedness.

2.4.2.2 Maternal additive genetic effect

Maternal effects entail the mother's influence on her offspring other than through the genes she transmits to it and arising from the ability of the mother to produce milk required for lamb growth and her maternal behavior (Bradford, 1972; Albuquerque *et al.*, 1998). Through the genes responsible for maternal traits, the dam contributes to the offspring's phenotypic value (Ligda *et al.*, 2000). An animal's own genetic potential and maternal environment determines both the birth weight of the animal and its early growth rate until weaning. The dam's milk production and mothering ability are vital for birth weight and growth rate; also uterine environment and extra-chromosomal inheritance may contribute (Meyer, 1992). Studies on different sheep breeds (Snyman *et al.*, 1995b; Abbasi & Ghafouri-Kesbi, 2011; Shokrollahi & Zandieh, 2012) concluded that maternal effects decline while direct genetic variance components for body weight increase with age.

2.5 Models of analysis

It is important for any breeding program that the genetic and environmental components of variance for the traits under selection are known, so that accurate genetic parameters could be estimated for incorporation in genetic evaluation and selection schemes (Maxa *et al.*, 2007). The correct model of analysis should thus be used to estimate these parameters.

By including direct additive and maternal additive genetic effects, with or without a covariance between them, and maternal permanent environmental effects in different combinations, various possible models could be obtained (Meyer, 1989; Gilmour *et al*., 2009). The differentiation between the maternal genetic and environmental effects requires repeated records on individual dams and the presence of these dams and their dams and grand-dams in the data set (Robinson, 1996; Maniatis & Pollott, 2003). Therefore, several well-linked generations of records and many relationships between relatives related to the dam are required in the data to accomplish accurate partitioning of variance (Gerstmayer, 1991; Hagger & Schneeberger, 1995). The data structure of field datasets often do not conform to these requirements and accurate partitioning of maternal effects in such cases is not always possible.

Numerous studies have been performed to investigate the importance of applying the most appropriate animal model for the estimation of (co)variance components and genetic parameters for traits, such as early body weight, that are influenced by maternal effects in sheep (Vaez Torshizi *et al*., 1996; Lewis & Beatson, 1999; Ligda *et al*., 2000; Maniatis & Pollott, 2003; Mandal *et al*., 2006; Ghafouri-Kesbi & Eskandarinasab, 2008; Jafaroghli *et al*., 2010; Abbasi *et al*., 2012). The main conclusions of these studies were that ignoring maternal effects may result in the over estimation of direct heritabilities. Furthermore, overestimation of maternal heritability can occur if the maternal permanent environmental effect is left out in cases where it has a significant effect (Ligda *et al*., 2000). In such instances, all the maternal variance is partitioned to the maternal genetic variance component.

2.6 Statistical procedures

For a trait such as body weight, various statistical procedures could be used for the estimation of (co)variance components between weights recorded at different ages (Speidel *et al*., 2010).

2.6.1 Uni- or multivariate linear models

Various software programs based on restricted maximum likelihood procedures are available for the estimation of (co)variance components and genetic parameters in animal breeding for uni- or multivariate linear models, for example ASReml (Gilmour *et al*., 2009), DfReml (Meyer, 1989), MTDfReml (Boldman *et al*., 1995) and WOMBAT (Meyer, 2006).

Restricted maximum likelihood methods have been used extensively to estimate (co)variance components for body weight in sheep (Vaez Torshizi *et al*., 1996; Ligda *et al*., 2000; Maniatis & Pollott, 2003; Miraei-Ashtiani *et al*., 2007) because they can partition the phenotypic variance of a quantitative trait into additive genetic variance, environmental variance and other effects such as maternal, common environmental, or permanent environmental effects (Meyer, 1989). Currently, estimated breeding values for the production traits of Merino sheep in South Africa are being estimated with a multivariate linear model (Olivier & Gilmour, 2015).

In a study by Rose at al. (2013) multivariate analysis was advantageous when compared to random regression as it fitted the data better according to the Akaike's Information Criterion (AIC) and Schwartz Bayesian Information Criterion (BIC). Multivariate animal models, incorporating the genetic and residual covariances between the traits, treat the various body weights as separate but genetically correlated traits (Mrode, 2005). The limitation of multi-trait analysis is its inability to estimate (co)variances between or at every time point, as compared to the random regression model (Olivier, 2014). More parameters are needed to describe the same data set when compared to the random regression model (Huisman *et al.*, 2002) and that create computational disadvantages as more memory and time is needed for the analysis (Nobre *et al.*, 2002; Mrode, 2005).

2.6.2 Random regression procedures

Repeated measures of body weight in growing animals are used to describe their growth from birth to maturity; this is called longitudinal data (Lewis & Brotherstone, 2002). The Gompertz growth curve is used to describe growth with only a few parameters (most importantly mature size and a rate parameter). However, using such a function to differentiate between genetic merits of individual animals to grow is problematic, as the estimates of these parameters are highly correlated and differences in the shape of the growth curve among animals could occur (Lewis & Brotherstone, 2002).

An alternative is random regression methodology. The random regression model (RR) allows environmental effects specific to the time of recording to be accounted for and can also accommodate genetic differences in the shape of each animal's growth curve (Meyer, 2004; Schaeffer, 2004; Speidel *et al.*, 2010).

Schaeffer *et al.* (1994), fitting random regression models to dairy cattle data, were able to account for the change in correlation structure of repeated records on individuals over time. The random regression model has an advantage over multivariate models due to its possibility to estimate variances for any age or between any pair of ages in the data set (Ghafouri-Kesbi & Eskandarinasab, 2008; Olivier, 2014). The estimates of breeding values are more accurate with a random regression model for any age within the interval of the records considered as compared to conventional multi-trait models (Tier & Meyer, 2004), due to utilising a larger amount of data from each animal.

Kirkpatrick *et al.* (1990) argued that the random regression model (co)variance estimates were smoother and less biased compared to the values estimated with multivariate models. The random regression model has a computational advantage (Huisman *et al*., 2002) as it requires fewer parameters to describe the same data set as compared to multivariate models and the memory and time needed is less for analysis compared to some multivariate analyses (Nobre *et al*., 2002). This ability of the random regression model to properly account for the changing correlation structure has been shown to result in an increase in prediction accuracy of 5.9% when compared to the multivariate model (Meyer, 2004). Accuracy in estimated parameter values is different where the frequency of live weight recording varies between the animals (Lewis & Brotherstone, 2002).

Genetic parameters obtained with random regression models are comparable with those estimated with general linear models (Fischer *et al*., 2004; Ghafouri-Kesbi & Eskandarinasab, 2008; Kariuki *et al*., 2010). The inclusion of all available data without pre-adjustment to particular ages, no records taken outside certain age ranges, and reduction in the number of parameters to be estimated by fitting parsimonious models makes random regression advantageous over multiple trait models (Kirkpatrick *et al*., 1990, Meyer & Hill 1997).

Implementing a random regression model would not only remove the current limits on the number of records per animal that can be utilised and eliminate the need for age correction, but also provide estimates of genetic merit for any age within the recording period. Additionally, selection on the shape of the growth curve to suit specific objectives would be possible. Lewis & Brotherstone (2002) stated that random regression models make use of a fixed regression in the description of the average shape of a lactation or growth curve, and a random regression for each animal to account for deviations from the fixed regression. The repeated records that are collected on animals are allowed to be incorporated into the evaluation of genetics directly.

2.6.3 Repeatability model

Arguably the simplest method of analysis of repeated measure data is the repeatability model. In this model, each observation is treated as a repeated record of the same trait on the same individual. This model has been implemented in the past for traits such as milk yield in successive lactations in dairy cattle (Jamrozik *et al*., 1997; Interbull, 2000). Olivier (2014) stated that analysis of data with a repeatability model assumes equal variances for repeated records and that the genetic correlation among expressions of the same trait at different ages are unity or not significantly different from one. Jennrick & Schluchter (1986), using the repeatability model assumed that the observations from the same individual measured at different ages have a constant variance and a common correlation with each other. However, such an assumption does not hold where individual variance changes according to the amount of time that has passed between measurements (Meyer & Hill, 1997). This problem could be overcome by defining different variances for observations recorded at different ages.

In cases where the repeated observations follow growth or lactation curves, correlations among observations taken close together in time are higher when compared to those taken further apart from each other. Highly complex models that account for the differing correlation structure among successive observations are vital in these situations (Speidel, 2010).

2.7 Genetic parameters for body weight

Heritability, repeatability and genetic correlations are the most important genetic parameters in animal breeding (Hussain *et al*., 2013). An overview of published values for these parameters obtained with different procedures for body weight in Merino sheep will be presented.

2.7.1 Univariate and multivariate linear models

Heritability is a measure of the strength of the correlation between performance (phenotypic values) and breeding value for a trait in a population (Bourdon, 1997). It can also be defined as that proportion of the phenotypic variance that is due to additive genetic effects and that can thus be transferred to the progeny. Variance ratios for growth traits estimated with restricted maximum likelihood animal models are presented in Table 2.2. Direct heritabilities were generally moderate to high in magnitude and ranged from 0.13 to 0.61 with standard errors ranging from 0.01 to 0.15. The range for maternal heritabilities is low to moderate ranging from 0.02 to 0.21.

Maternal heritability for body weight tends to decline with increasing age from birth to 15-month weight (Table 2.2). There are significant maternal permanent environmental effects reported for growth traits, which tended to be higher for birth weight and weaning weight than weights recorded at a later stage in life.

Table 2.2 Summary of literature values of direct and maternal heritability, maternal permanent environmental effects and correlation between direct and maternal genetic effects in Merino sheep

Age (months)	h^2_a ± s.e.	h^2_m ± s.e.	c^2_{mpe} ± s.e.	r_{am} ± s.e.	Reference
Birth weight					
	0.18 ± 0.01	0.19 ± 0.01	0.07 ± 0.01	-0.15 ± 0.01	Safari *et al*., 2007b
	0.21 ± 0.04	0.21 ± 0.04	0.14 ± 0.02	-0.46 ± 0.09	Olivier, 2014
	0.23 ± 0.02	0.14 ± 0.02	0.12 ± 0.01	-0.40	Mortimer & Atkins, 1995
	0.32 ± 0.08	-	-	-	Lewer *et al*., 1994
	0.35 ± 0.08	-	-	-	Wuliji *et al*., 2001
Pre-weaning and weaning weight					
3	0.37 ± 0.08	-	-	-	Lewer *et al*., 1994
4-5	0.27 ± 0.03	0.11 ± 0.01	0.07 ± 0.01	-0.20	Mortimer & Atkins, 1995
3	0.13 ± 0.05	0.04 ± 0.03	0.06 ± 0.02	0.07	Annalla & Serradilla, 1998
3	0.34 ± 0.08	0.16 ± 0.04	-	-	Wuliji *et al*., 2001
4	0.09 ± 0.02	0.10 ± 0.02	0.12 ± 0.02	-	Olivier, 2014
6 Month body weight / post weaning					
	0.18 ± 0.04	0.10 ± 0.04	-	0.86 ± 0.30	Snyman *et al*., 1996
5	0.28 ± 0.08	0.04 ± 0.04	-	-	Ingham *et al*., 2003
6	0.26 ± 0.03	0.12 ± 0.02	-	-	Olivier, 2014
6	0.44 ± 0.09	0.08 ± 0.04	-	-	Wuliji *et al*., 2001
12 - 16 Month body weight					
12	0.33 ± 0.15	-	-	-	Brown *et al*., 2002
12	0.35 ± 0.02	-	-	-	Clarke *et al*., 2003
12	0.47 ± 0.03	0.04 ± 0.01	-	-	Olivier, 2014
13	0.25 ± 0.10	-	-	-	Woolaston *et al*., 1995
14	0.13 ± 0.01	-	-	-	Nagy *et al*., 1999
15	0.13 ± 0.01	0.02 ± 0.01	0.04 ± 0.02	0.42 ± 0.01	Van Wyk *et al*., 2008
15	0.36 ± 0.02	0.05 ± 0.01	-		Brown *et al*., 2005
15	0.37 ± 0.10	-	-	-	Rose & Pepper, 1999
15	0.38 ± 0.01	0.03 ± 0.01	-	0.25 ± 0.08	Safari *et al*., 2007a
15	0.38 ± 0.05	-	-	-	Cloete *et al*., 2006
15	0.38 ± 0.05	0.05 ± 0.02	-	-0.28 ± 0.12	Matebesi *et al*., 2009
15	0.39 ± 0.04	0.04 ± 0.03	0.00 ± 0.03	0.42	Mortimer & Atkins, 1995
15	0.49 ± 0.02	-	-	-	Clarke *et al*., 2003
15	0.49 ± 0.03	0.05 ± 0.01	-	-	Olivier, 2014

Age (months)	h^2_a ± s.e.	h^2_m ± s.e.	c^2_{mpe} ± s.e.	r_{am} ± s.e.	Reference
15	0.61 ± 0.06		-		Brown *et al*., 2010
16	0.29 ± 0.05	0.02 ± 0.09	0.00 ± 0.06	1.00	Vaez Torshizi *et al*., 1996
16	0.32 ± 0.05	-	-	-	Greeff & Karlsson, 1999
16	0.33 ± 0.09	-	-	-	Brash *et al*., 1997
16	0.49 ± 0.12	0.06 ± 0.05	-	-	Wuliji *et al*., 2001
16	0.52 ± 0.05	-	-	-	Duguma *et al*., 2002a
			Adult weight		
Adult	0.31 ± 0.03	-	-	-	Safari *et al*., 2005
Adult	0.31 ± 0.03	-	-	-	Fogarty , 1995
Adult	0.41 ± 0.02	-	-	-	Safari *et al*., 2005
Adult	0.57 ± 0.05	-	-	-	Fogarty , 1995

h^2_a – direct heritability; h^2_m – maternal heritability; r_{am} – covariance between animal effects; c^2_{mpe} – maternal permanent environmental effects

The sign and magnitude of the direct-maternal correlation varies between different studies performed on different breeds and conditions. Direct-maternal genetic correlation estimates of early body weight and growth traits in woolled sheep reported in literature are summarised in Table 2.3. The estimates ranged from -0.74 to 0.19 for birth weight and from -0.81 to 0.47 for weaning weight.

Table 2.3 Summary of direct-maternal genetic correlation estimates (± s.e.) of early body weight in woolled sheep, reported in literature

Trait [a]	r_{Gam}	Breed	Reference
BW	-0.18 to -0.74	Ranbouillet, Targhee	Burfening & Kress, 1993
WW120	-0.41 to -0.81	Columbia	
BW	-0.35	Polled Dorset	Tosh & Kemp, 1994
WW50	-0.42		
WW100	-0.31		
BW	-0.40	Merino	Mortimer & Atkins, 1995
WW120	-0.20		
BW	0.11	Swedish Fine wool	Näsholm & Danell, 1996
WW120	0.47		
BW	-0.43	Australian Merino	Vaez Torshizi *et al*., 1996
WW100	-0.59		

Trait [a]	$\mathbf{r_{Gam}}$	**Breed**	**Reference**
WW84	-0.13 ± 0.38	New Zealand Coopworth flocks	Lewis & Beatson, 1999
	-0.26 ± 0.15		
	-0.26 ± 0.22		
	0.30 ± 0.36		
	-0.54 ± 0.10		
	-0.68 ± 0.10		
	-0.78 ± 0.05		
WW84	0.06 to 0.10	Welsh Mountain	Saatci *et al*., 1999
BW	0.09 ± 0.05	Targhee	Hanford *et al*., 2003
WW120	-0.04 ± 0.06		
BW	0.08 to 0.12	Targhee	Van Vleck *et al*., 2003
WW120	-0.01 to -0.04		
BW	0.03 ± 0.04	Rambouillet	Hanford *et al*., 2005
WW	0.33 ± 0.07		
BW	0.19 ± 0.11	Polypay	Hanford *et al*., 2006
WW	0.06 ± 0.16		

[a] BW = Birth weight; WWx = Weaning weight recorded at x days of age

Genetic correlations between the traits must also be taken into consideration when the breeding plan is drawn up, as unfavourable correlations could lead to unwanted selection responses in correlated traits (Olivier & Greyling, 2011). Genetic correlations between the various growth traits are presented in Table 2.4. The genetic correlations are higher for weights at adjacent age classes and increased with age from birth to adult weight.

Table 2.4 Genetic correlations (r_g) among body weight at different ages in Merino sheep

Traits	r_g	Reference
Birth weight with:		
PWW	0.54	Olivier, 2014
WW	0.37	Olivier, 2014
WW	0.47	Safari *et al*., 2005
WW	0.79	Ozcan *et al*., 2005
BW6	0.51	Olivier, 2014
BW6	0.93	Safari *et al*., 2005
BW12	0.61	Olivier, 2014
BW12	0.65	Ozcan *et al*., 2005
BW15	0.53	Olivier, 2014
Adult	0.22	Safari *et al*., 2005
Weaning weight with:		
BW6	0.85	Safari *et al*., 2005
BW6	0.91	Olivier, 2014
BW15	0.81	Olivier, 2014
Adult	0.75	Safari *et al*., 2005
Post-Weaning weight with:		
BW15	0.87	Olivier, 2014
Adult	0.93	Safari *et al*., 2005

PWW – pre-weaning (42 days of age); WW – weaning; BW6 – 6 months of age; BW12 – 12 months of age; BW15 – 15 months of age

2.7.2 Random regression models

As opposed to restricted likelihood procedures, genetic parameters and (co)variance components for body weight in sheep estimated with random regression models are relatively scarce (Lewis & Brotherstone, 2002; Fischer *et al*., 2004; Molina *et al*., 2007; Ghafouri-Kesbi & Eskandarinasab, 2008; Kariuki *et al*., 2010; Wolc *et al*., 2011). Fischer *et al*. (2004), Abegaz *et al*. (2010) and Kariuki *et al*. (2010) respectively analysed body weights of Poll Dorset (50 to 500 days of age), Horro sheep (birth to 396 days of age) and Dorper sheep (20 to 380 days of age) with random regression procedures. Safari & Fogarty (2003) also mentioned that genetic parameters obtained with random regression models for body weight in sheep are limited. Recently, random regression models have become a more common method to use for the analyses of growth traits (Schaeffer & Jamrozik, 2008).

Wolc *et al*. (2011) published variance components for five consecutive measurements of body weight in Polish sheep, estimated with random regression and multi-trait animal models. Direct heritability tended to increase with age, whereas maternal effects decreased for body weights recorded at older ages. Olivier (2014) reported an increase in direct heritability for body weight with age obtained with random regression models in Merino sheep, ranging from 0.14 for 4 months of age to 0.84 for 94 months of age. The latter value is in accordance with estimates obtained with single- or multi-trait analyses (Safari & Fogarty, 2003). Snyman *et al*. (1995b), fitting univariate animal models employing restricted maximum likelihood procedures, also reported similar trends in variance components for body weight at various ages in Afrino sheep.

Heritability values of the various growth traits estimated with random regression models are presented in Table 2.5. Direct heritability in Table 2.5 tended to increase from birth towards adult weight, as supported by literature values summarised by Safari & Fogarty (2003) for linear models.

Table 2.5 Summary of literature values on direct (h^2_a) and maternal (h^2_m) heritability estimated with random regression models on different breeds

Age (days/months)	**h^2_a**	**h^2_m**	**Breed**	**Reference**
Birth weight				
	0.14	-	Horro	Abegaz *et al*., 2010
	0.18	0.16	Dorper	Kariuki *et al*., 2010
Weaning weight				
	0.28	0.19	Dorper	Kariuki *et al*., 2010
100 days	0.20	-	Poll Dorset	Fischer *et al*., 2004
Post weaning				
200 days	0.23	-	Poll Dorset	Fischer *et al*., 2004
6 months	0.21	0.21	Dorper	Kariuki *et al*., 2010
9 months	0.14	0.18	Dorper	Kariuki *et al*., 2010
Yearling weight				
	0.29	-	Dorper	Kariuki *et al*., 2010
350 days	0.25	-	Poll Dorset	Fischer *et al*., 2004
390 days	0.36	-	Horro	Abegaz *et al*., 2010

2.7.3 Repeatability models

The following genetic parameters for body weight (data included body weights from weaning to 94 months of age) were reported by Olivier (2014) for fine wool Merino sheep, namely direct heritability of 0.17 ± 0.03, maternal heritability of 0.02 ± 0.02, animal permanent environmental effect of 0.10 ± 0.02, maternal permanent environmental effect of 0.01 ± 0.01 and a repeatability of 0.26 ± 0.02. The repeatability estimated for body weight done on several studies ranged between 0.46 to 0.75 as reported in the literature (Morley, 1951; Katada & Takeda, 1959; Young *et al*., 1960; Beattie, 1961; Turner & Young, 1969; Mortimer, 1987; Said *et al*., 1999; Hatcher & Atkins, 2000; Cloete *et al*., 2004; Hatcher *et al*., 2005; Wolc *et al*., 2011; Boujenane *et al*., 2013).

Table 2.6 Summary of literature values of repeatability (t) of body weight in different breeds obtained using a repeatability model

Trait	T	Breed	Reference
Body weight	0.25	D'man	Boujenane *et al*., 2013
Growth rate of progeny	0.26	Awassi	Said *et al*., 1999
Ewe body weight	0.46	Awassi	Said *et al*., 1999
Ewe body weight	0.62	D'man	Boujenane *et al*., 2013
Body weight	0.64	Corriedale	Katada & Takeda., 1959
Body weight	0.64	Polish	Wolc *et al*., 2011
Body weight	0.64	Merino	Hatcher *et al*., 2005
Body weight	0.67	Merino	Young *et al*., 1960
Body weight	0.70	Merino	Hatcher & Atkins, 2000

2.8 Estimation of breeding values

Very limited studies comparing breeding values for body weight in sheep obtained with different procedures have been done to date. Molina *et al*. (2007) reported changes in ranking of the animals based on the conventional breeding value estimation compared to breeding values estimated with the random regression procedure for growth in Spanish Merino sheep. The latter procedure provides more information and would thus yield more accurate breeding values in the case of longitudinal data such as growth traits.

Lewis & Brotherstone (2002) found that when comparing breeding values for 56- and 150-day body weight predicted by random regression and by the Gompertz approach, the ranking of the animals was similar and the same animals would be selected. What remains unclear, however, is which technique yields the more accurate breeding values.

Krejčová *et al*. (2007) compared breeding values for daily gain of bulls estimated with multi-trait models to those estimated with random regression models of 3rd and 4th polynomial degree. High estimated rank correlations between the models as well as high numbers of common animals in different top-lists of animals were reported. They concluded that random regression models become a necessity when all available repeated records per animal are to be considered instead of only those few nearest to a specific recording age.

2.9 Genomic selection

Genomic technology has an ever-increasing influence on the world of animal breeding and genetics and genomic selection has been widely applied successfully in some overseas countries in the beef (Garrick, 2010; MacNeil, 2016) and dairy cattle industries (Verbyla *et al*., 2009; Fritz *et al*., 2010; Harris & Johnson, 2010; Su *et al*., 2010; Su *et al*., 2011). It has also recently been implemented in the Australian (Daetwyler *et al*., 2012; Rowe *et al*., 2013; Swan et al., 2014), New Zealand (Dodds et al., 2014) and French (Baloche et al., 2014; Larroque et al., 2014) sheep industries.

With genomic selection, the genetic merit of the genotyped animals has been based on the relationship derived from whole-genome dense markers (VanRaden, 2008), where the effects of a very large number of markers across the genome are used to obtain genomic estimated breeding values (Meuwissen *et al*., 2001). These increase the prediction accuracy when compared to conventional estimated breeding values.

In South Africa genomic selection is currently being considered as a possible selection strategy in many livestock species. Genomic selection could greatly benefit the South African sheep industry; especially as far as hard-to-measure and lowly heritable traits, like reproduction, disease resistance and meat quality, are concerned. The establishment of reference populations is a key phase in this process. The South African Merino sheep breed has been identified as one of the possible small stock species in which genomic selection could make a significant contribution. It is also the most numerous sheep breed in the country, and as such should contribute largely to across-breed genomic evaluations. Before genomic selection can be successfully implemented, it is crucial to estimate accurate breed-specific genetic parameters. These will also be used in the estimation of breeding values, which is of utmost importance in the calculation of prediction equations.

2.10 Closing remarks

The implementation of genomic selection in the South African Merino sheep breed is dependent on the most accurate model being used when breeding values are estimated for animals in the reference population, as it will have an influence on the accuracy of the prediction equation associating the EBVs with the direct genomic value. The aim of this study is to determine the most suitable statistical models and procedures for the estimation of breeding values for body weight to be used in a genomic selection program for South African Merino sheep.

3. MATERIALS AND METHODS

3.1 Introduction

The aim of the study was to determine the most suitable statistical model and procedures for estimation of (co)variance components and genetic parameters for body weight at various ages in Merino sheep. This was performed using data obtained from the Grootfontein Merino stud and analysing it with ASReml software (Gilmour *et al*., 2009) by fitting uni- and multivariate restricted maximum likelihood, random regression and repeatability models.

3.2 Description of the Grootfontein Merino stud

3.2.1 History of the Grootfontein Merino stud

The Grootfontein Merino stud was founded in 1955. The base ewe flock consisted of 227 ewes bought from local breeders, 63 ewes donated by local breeders and 105 ewes from the three selection lines present at Grootfontein at that time. In the same year four rams were imported from Australia for use in the newly founded Grootfontein Merino stud (Stud no. 888) (Olivier, 1989). In 1962 two rams and in 1964 an additional 11 ewes were bought from local breeders. Rams and ewes from the Cradock fine wool Merino stud and ewes from the Grootfontein fine wool Merino flock were incorporated into the stud in 2002 to establish genetic linkages between the studs and to increase the number of ewes in the Grootfontein stud. Since 2002, rams from the Cradock fine wool Merino stud have been used in the stud on a regular basis, while since 2009, one or two industry rams were also used annually in the stud.

3.2.2 Selection strategy followed in the stud

The main selection objectives from 1956 to 1983 were to obtain sheep with good conformation and wool traits. Animals with conformation and wool faults, as well as animals with low 120-day weights were culled. Selection was based on overall excellence, with body size, wool quality (crimp definition and softness) and quantity being the most important criteria (Olivier *et al*., 1995). Apparently, some attention was given to measured performance of growth and wool traits, but no records are available to quantify this. From 1985 onwards, animals with definite conformation and wool faults were still culled, but final selection was done on animal model-based best linear unbiased predictions (BLUP) of breeding values. The main selection objectives were to increase body weight, maintain clean fleece weight and decrease mean fibre diameter and pleat score. Due to the role of the Grootfontein Merino stud in the stud industry, the maintenance or improvement of visually assessed traits was also regarded as important. Olivier (1989, 1998) and Olivier *et al*. (1995) described the selection procedures followed in the stud in more detail.

In 2002 the Grootfontein Merino stud was divided into a control and fine wool line. The control line was selected within the line for reduced fibre diameter, while rams from the Cradock fine wool Merino stud were used as breeding sires in the fine wool line. The aim of this was to compare the effect of selection for reduced fibre diameter through either within flock selection or through the use of genetically fine wool rams. The effect of these methods on other wool characteristics of Merino sheep was also investigated. The main selection objectives were to increase body weight, maintain clean fleece weight, decrease mean fibre diameter and to increase staple length. In 2007 the Grootfontein Merino stud was included in the "selection for increased profitability" project and the selection objectives were changed. Breeding sires and dams were rather selected on the basis of profitability, according to the formula developed by Herselman (2004). The selection objectives in body weight, clean fleece weight, fibre diameter and relative economic value during the various periods mentioned above, have been achieved.

Since 2009 the stud has been part of the project: "Maintenance of two Merino flocks as resource flocks for research and reference flocks for a biological bank for Merino sheep in South Africa" and no selection for any specific trait was carried out.

3.3 Experimental location

The Grootfontein Merino stud was kept at Grootfontein Agricultural Development Institute near Middelburg (31° 28'S, 25° 1'E) in the Eastern Cape Province. The average annual rainfall is approximately 350 mm of which 246 mm on average occurs in summer, 60 mm in autumn and 19 mm in winter. The rainfall is highest during the period October to March, with peak levels during February and March (Worldweatheronline, 2014; Weatherbase, 2015). Frost occurs from April to September. Mucina & Rutherford (2006) described the veld type as Eastern Upper Karoo (Veld type Nku4). The stud was run under natural veld conditions and received strategic supplementary feeding.

3.4 Available data set

The dataset comprises body weight data recorded at different ages in the Grootfontein Merino stud from 1968 to 2012. From 1968 to 1972 the data was collected during two annual lambing seasons (March/April; Autumn = Season 1 and September/October; Spring = Season 2). During this period, a total of 487 male and 468 female lambs were born in Season 1, and 701 males and 704 females in Season 2, respectively. From 1973 to 2012 there was only one lambing season, namely September/October (Season 2), during which 6845 males and 7148 female lambs were born. The total number of males and females for which birth weight was recorded, were 7794 and 8317 respectively. All lambs were run as one group with their dams until weaning. After weaning, ram and ewes lambs were run separately, as a single group each, up until selection age. The traits included were birth weight (BW), body weight at 42-days of age (W42), weaning weight (WW), body weight at 6 months (W6), 8 months (W8), 12 months (W12) and 15 months (W15) of age and adult weights recorded on the ewe flock from 2 to 7 years of age.

3.5 Statistical analysis

3.5.1 Fixed effects

The fixed effects tested for significance were year-season of birth, sex, birth status, rearing status, age of the dam and their respective two way interactions. Age of the animal at recording was included as a covariate. The PROC GLM procedure of the SAS statistical package was used to determine which of these fixed effects had a significant influence on the different body weights (SAS, 2009).

The following model was applied for all body weights:

$Y_{ijklmn} = \mu + ys_i + s_j + bs_k + rs_l + ad_m + (yss)_{ij} + b_1AL + e_{ijkl}$

Where

Y_{ijklmn} = trait of the n'th animal of the m'th age of dam of the l'th rearing status of the k'th birth status of the j'th sex of the i'th year-season of birth,

μ = overall mean,

ys_i = fixed effect of the i'th year-season of birth (1969 – 2012; depending on weight),

s_j = fixed effect of the j'th sex (ram, ewe),

bs_k = fixed effect of the k'th birth status (1, 2, 3; only for birth weight),

rs_l = fixed effect of the l'th rearing status (11, 21, 22, 31, 32, 33; for all except birth weight),

ad_m = fixed effect of the m'th age of dam (2 to 6 years),

$(yss)_{ij}$ = effect of the interaction between the i'th year-season of birth and the j'th sex,

b_1 = linear regression coefficient of the appropriate deviation from the mean of age of the lamb at recording (AL; except for birth weight),

e_{ijklmn} = random error with zero mean and variance $I\sigma^2_e$.

3.5.2 Uni- and multivariate linear models

Uni- and multivariate linear animal models were fitted with the ASReml program (Gilmour *et al.*, 2009). Direct additive and maternal additive genetic effects, with or without a covariance between them, and maternal permanent environmental effects were tested for all traits in six different combinations. The six models were:

$y = Xb + Z_1a + e$ (1)

$y = Xb + Z_1a + Z_2mpe + e$ (2)

$y = Xb + Z_1a + Z_2m + e$; with $cov(a,m) = 0$ (3)

$y = Xb + Z_1a + Z_2m + e$; with $cov(a,m) = A\sigma_{am}$ (4)

$y = Xb + Z_1a + Z_2m + Z_3mpe + e$; with $cov(a,m) = 0$ (5)

$y = Xb + Z_1a + Z_2m + Z_3mpe + e$; with $cov(a,m) = A\sigma_{am}$ (6)

where y was a vector of observed traits of animals; b, a, m and mpe were vectors of fixed effects, direct additive genetic effects, maternal additive genetic effects and maternal permanent environmental effects respectively; X, Z_1, Z_2 and Z_3 were incidence matrices respectively relating fixed effects, direct additive genetic effects, maternal additive genetic effects and maternal permanent environmental effects to y; e was the vector of residuals; A was a numerator relationship matrix, and σ_{am} was the covariance between direct additive genetic and maternal additive genetic effects. It was assumed that $V(a) = A\sigma^2_a$; $V(m) = A\sigma^2_m$; $V(mpe) = I\sigma^2_{mpe}$; $V(e) = I\sigma^2_e$, where I was an identity matrix, σ^2_a, σ^2_m, σ^2_{mpe} and σ^2_e were the direct additive genetic variance, maternal additive genetic variance, maternal permanent environmental variance and environmental variance respectively. All components, with the phenotypic variance (σ^2_p), being the sum of σ^2_a, σ^2_m, σ_{am}, σ^2_{mpe}, and σ^2_e, were derived at convergence.

Depending on the model, variance ratios were computed as direct heritability ($h^2_a = \sigma_a^2/\sigma_p^2$), maternal heritability ($h^2_m = \sigma_m^2/\sigma_p^2$) and the direct-maternal covariance as proportion of phenotypic variance ($c_{am} = \sigma_{am}/\sigma_p^2$), with a corresponding estimate of the direct-maternal correlation [$r_{am} = c_{am} / \surd(\sigma_a^2 \text{ x } \sigma_m^2)$]. Similarly, the maternal environmental variance ratio was estimated by the permanent maternal environmental variance as a proportion of σ_p^2 ($c^2_{mpe} = \sigma_{mpe}^2/\sigma_p^2$).

Different methods were used to determine the most suitable model for analysis. The likelihood ratio statistic [LogL; $\log\sigma = L(b_2) - L(b_1)$, where $L(b)$ is the log likelihood function evaluated at the maximum likelihood estimator (b)], was one method used (Morrell, 1998). The statistic $-2(\log L_2 - \log L_1)$ has a χ^2 distribution with degrees of freedom equal to the difference between the number of parameters for the two models being compared. An effect was considered to have a significant influence when its inclusion caused a significant increase in log likelihood, compared to the model in which it is ignored. For the purpose of this study, a significance level of $P < 0.05$ was applied throughout. Meyer (2004) stated that this test favours the model with the most parameters.

Akaike information criterion (AIC; Akaike, 1974), is AIC = -2 log L + 2k, where L is the likelihood and k is the number of parameters. The model with the smallest AIC is preferred. Schwarz Bayesian information criterion (BIC, Schwarz, 1978; Huisman *et al*., 2002), is BIC = -2 log L + k log *n*, where L is the likelihood, k is the number of parameters and *n* is the number of observations (sample size). The model with the lower value of BIC is preferred.

Subsequently, bivariate analyses were performed to estimate (co)variance components and correlations among the relevant traits, fitting the most suitable model for each trait, as determined under single-trait analyses.

A multivariate analysis, including weaning weight, 12-month body weight, 15-month body weight and adult ewe body weight at three years of age, was also done. The most suitable model for each trait, as determined under single-trait analyses, was fitted for each weight.

3.5.3 Repeatability model

The estimation of the genetic parameters with the repeatability models was done with the ASReml program (Gilmour *et al.*, 2009). Fixed effects for year-season of birth, sex, rearing status and age of the dam were included in the models. Direct additive and maternal additive genetic effects, with or without a covariance between them, animal permanent environmental effects and maternal permanent environmental effects were tested for all body weights in different combinations to yield six possible models. The six models were:

$$\mathbf{y} = X\mathbf{b} + Z_1\mathbf{a} + W_1\mathbf{anim} + \mathbf{e} \qquad (1)$$

$$\mathbf{y} = X\mathbf{b} + Z_1\mathbf{a} + W_1\mathbf{anim} + W_2\mathbf{mpe} + \mathbf{e} \qquad (2)$$

$$\mathbf{y} = X\mathbf{b} + Z_1\mathbf{a} + Z_2\mathbf{m} + W_1\mathbf{anim} + \mathbf{e;}\ \text{with cov(a,m)} = 0 \qquad (3)$$

$$\mathbf{y} = X\mathbf{b} + Z_1\mathbf{a} + Z_2\mathbf{m} + W_1\mathbf{anim} + \mathbf{e;}\ \text{with cov(a,m)} = A\sigma_{am} \qquad (4)$$

$$\mathbf{y} = X\mathbf{b} + Z_1\mathbf{a} + Z_2\mathbf{m} + W_1\mathbf{anim} + W_2\mathbf{mpe} + \mathbf{e;}\ \text{with cov(a,m)} = 0 \qquad (5)$$

$$\mathbf{y} = X\mathbf{b} + Z_1\mathbf{a} + Z_2\mathbf{m} + W_1\mathbf{anim} + W_2\mathbf{mpe} + \mathbf{e;}\ \text{with cov(a,m)} = A\sigma_{am} \qquad (6)$$

where **y** was a vector of observed traits of animals; **b**, **a**, **m, anim** and **mpe** were vectors of fixed effects, direct additive genetic effects, maternal additive genetic effects, animal permanent environmental effects and maternal permanent environmental effects respectively; X, Z_1, Z_2, W_1 and W_2 were incidence matrices respectively relating fixed effects, direct additive genetic effects, maternal additive genetic effects, animal permanent environmental effects and maternal permanent environmental effects to **y**; **e** was the vector of residuals; A was a numerator relationship matrix, and σ_{am} was the covariance between direct additive genetic and maternal additive genetic effects. It was assumed that $V(a) = A\sigma^2_a$; $V(m) = A\sigma^2_m$; $V(anim) = I\sigma^2_{anim}$; $V(mpe) = I\sigma^2_{mpe}$; $V(e) = I\sigma^2_e$, where I was an identity matrix, σ^2_a, σ^2_m, σ^2_{anim}, σ^2_{mpe} and σ^2_e were the direct additive genetic variance, maternal additive genetic variance, animal permanent environmental variance, maternal permanent environmental variance and environmental variance respectively. All components, with the phenotypic variance (σ^2_p), were derived at convergence.

Two sets of these models were run. In the first, splines were fitted to separate ages 1, 2, 4, 6, 8, 12, 15, 20, 32, 44, 56 and 68 months, thus fitting age as a fixed effect. The second set of six models was run without the splines. The same statistics, namely, LogL, AIC and BIC were used to determine the most suitable model for analyses.

3.5.4 Random regression model

The estimation of the genetic parameters with random regression models were also done with the ASReml program (Gilmour *et al*., 2009). Fixed effects for year-season of birth, sex, rearing status and age of the dam were included in the models. The models fitted included direct genetic, maternal genetic and animal and maternal permanent environmental effects as random effects in various combinations, in addition to residual effects.

The matrix representation of the models is:

$$\mathbf{y} = X\mathbf{b} + Z_1\mathbf{a} + Z_2\mathbf{m} + W_1\mathbf{anim} + W_2\mathbf{mpe} + \mathbf{e};$$

where y was the vector of observed body weights of animals, **b** was the vector of fixed effects, **a** was the vector of random coefficients for additive direct effects, **m** was the vector of random coefficients for additive maternal effects, **anim** was the vector of random coefficients for animal permanent environmental effects, **mpe** was the vector of random coefficients for maternal permanent environmental effects, **e** was the vector of residual effects and X, Z_1, Z_2, W_1 and W_2 were the corresponding incidence matrices.

The above-mentioned models were fitted with splines separating ages 1, 2, 4, 8, 12, 15, 20, 32, 44, 56 and 68 months, splines separating ages 1, 4, 15 and 68 months or no splines. The random effects were modelled using cubic spline functions. Polynomials up to the second degree were fitted for the direct genetic and maternal genetic random effects. Residual variances were modelled considering one (assuming homogeneity of variances across all ages) or two age classes divided as follows: 1 to 12 and 15 to 68 months of age.

3.5.5 Comparison of estimated breeding values

The breeding values obtained for weaning weight, weight at 15 months and 3-year body weight estimated using the most suitable univariate models, multivariate model and repeatability model, were compared. Estimated breeding values and accuracies of body weights of individual animals were obtained as back solutions with the ASReml program (Gilmour *et al*., 2009). Accuracy of EBVs were calculated as √{1 - [(predicted error variance reported with each BLUP value)^2 / additive genetic variance of the specific trait]}.

Three datasets were created. The first comprised EBVs for all animals in the pedigree file, the second comprised EBVs for animals with a 15-month body weight record, and the third comprised EBVs for all sires used that were born in the flock.

The Spearman rank correlation under the PROC CORR-procedure of SAS (SAS, 2009) was used to estimate the correlations between the ranks of these estimated breeding values for all three data sets.

Furthermore, lists were compiled of the Top 10% and Top 1% of the animals having the highest EBVs for weaning weight, weight at 15 months and 3-year body weight, estimated with the different procedures. These lists were compiled for all animals in the pedigree file, for all animals having a record for 15-month body weight and for all sires born with the flock. The number and percentage of animals common to the different top lists were evaluated among the procedures.

4. RESULTS

4.1 Description of the data set

Information on the pedigree structure of the animals included in the study is summarised in Table 4.1. Different types of parents were recorded in pedigree data namely sires, sires of sire, dams of sire, dams, sires of dam and dams of dam).

Table 4.1 Pedigree information

Type of Parent	Number
Sires	359
Sires of Sire	153
Dams of Sire	250
Dams	3814
Sires of Dam	325
Dams of Dam	1981

The number of records, mean and coefficient of variation (CV) of the different body weights for the ewes and rams are presented in Tables 4.2 and 4.3 respectively. The total number of ewe records available for analysis ranged from 231 for 7-year body weight to 8317 for birth weight respectively (Table 4.2). The reason for the fewer records available for 6-, 8- and 12-month body weights was that body weights at these specific ages were not regularly recorded each year over the study period. The fewer records for the 6-year-old and 7-year-old ewes were due to the fact that most of the ewes have been culled from the flock by that age. The results of 7-year body weight will not be presented and discussed, as non-reliable parameters were estimated due to the few data records available.

The mean body weights recorded for ewes ranged from 4.3 kg for birth weight to 56.6 kg for adult body weight at 5 years of age. The coefficient of variation (CV) for the body weights ranged from 12.6% for adult body weight at 3 years of age to 24.5% at 42-day body weight.

Table 4.2 Number of records, mean and coefficient of variation for the ewe body weights

Trait	Number of records	Mean	Coefficient of variation (%)
Birth weight	8317	4.3	21.1
42-Day body weight	4077	16.5	24.5
Weaning weight	7602	26.1	21.4
6-Month body weight	641	32.5	20.0
8-Month body weight	848	36.5	15.6
12-Month body weight	1679	40.5	14.6
15-Month body weight	6441	42.4	16.2
2-Year body weight	2590	52.0	13.1
3-Year body weight	2313	55.4	12.6
4-Year body weight	1817	56.6	12.7
5-Year body weight	1437	56.6	13.4
6-Year body weight	703	56.0	12.7
7-Year body weight	231	52.7	14.4

The total number of ram records available for analysis ranged from 538 for 6-month body weight to 7794 for birth weight respectively (Table 4.3). The mean ranged from 4.5 kg for birth weight to 61.5 kg for 15-month body weight. The CV for body weights of the rams ranged from 16.8% for body weight at 8 months of age to 25.1% for 42-day body weight.

Table 4.3 Number of records, mean and coefficient of variation for the ram body weights

Trait	Number of records	Mean	Coefficient of variation (%)
Birth weight	7794	4.5	20.3
42-Day body weight	3782	17.5	25.1
Weaning weight	7070	27.8	21.4
6-Month body weight	538	35.5	20.1
8-Month body weight	727	44.4	16.8
12-Month body weight	1515	53.7	23.7
15-Month body weight	4404	61.5	23.6

4.2 Non-genetic effects

The results of the non-genetic effects tested for significance for each trait, are summarised in Table 4.4. Only effects and interactions that had a significant influence on at least one trait and that were included in the models fitted are shown here.

Table 4.4 Significance level of the different non-genetic effects, tested for the respective traits

Trait	**Year/season of birth**	**Sex**	**Birth status**	**Rearing status**	**Age of dam**	**Year/season of birth * Sex**	**Age of animal**
BW	*	*	*	-	ns	ns	-
W42	*	*	*	-	ns	ns	*
WW	*	*	-	*	*	*	*
W6	*	*	-	*	*	ns	*
W8	*	*	-	*	*	*	*
W12	*	*	-	*	ns	-	*
W15	*	*	-	*	*	*	*
AW2	*	-	-	ns	ns	ns	ns
AW3	*	-	-	ns	ns	ns	ns
AW4	*	-	-	ns	ns	ns	ns
AW5	*	-	-	ns	ns	ns	ns
AW6	*	-	-	ns	ns	ns	ns

*$P < 0.001$; ns = not significant, - = not included;

BW = birth weight; W42 = body weight at 42 days of age; WW = Weaning weight; W6 = body weight at 6 months of age; W8 = body weight at 8 months of age; W12 = body weight at 12 months of age; W15 = body weight at 15 months of age; AW2 = adult body weight at two years; AW3 = adult body weight at three years; AW4 = adult body weight at four years; AW5 = adult body weight at five years; AW6 = adult body weight at six years

The effects included were year/season of birth, sex (male/female), birth status (single/multiple), rearing status, age of dam in years (2 to 6) and the two-factor interaction between year/season of birth and sex. Age of the animal for a specific trait was fitted as a linear regression.

It is evident from Table 4.4 that year/season of birth had a significant (P <0.001) effect on all the traits studied. Sex and birth status also had a significant (P <0.001) effect on all the traits for which these effects were included. Rearing status had a significant (P <0.001) effect on body weight from weaning until 15 months of age, while age of dam also affected these weights, with the exception of 12-month body weight. The two-factor interaction between year/season of birth and sex only affected weaning weight, 8- and 15-month body weights. Age of the animal at recording had a significant influence on body weight from 42-days of age until 15 months of age.

4.3 Univariate linear animal models employing restricted maximum likelihood procedures

Log likelihood (logL) values for the various univariate models are summarised for the different body weights in Tables 4.5 and 4.6. In Tables 4.5 and 4.6, models with the highest LogL values were the most suitable models. The Akaike's Information Criterion (AIC) and the Bayesian Information Criterion (BIC) are presented in Tables 4.7 and 4.8. For all parameters in Tables 4.7 and 4.8, the lowest value indicated the most suitable model.

From the Log L, AIC and BIC information criteria given in Tables 4.5 to 4.8, it follows that the most suitable model for birth weight (BW), 42-day body weight (W42), 6-month body weight (W6) and 8-month body weight (W8) was Model 6. This model included all the random effects, as well as the covariance between additive and maternal genetic effects. Model 5, including all the random effects, but excluding the covariance between the additive and maternal genetic effects was the most suitable for weaning weight (WW). The most suitable model for 12-month body weight (W12) included only the additive genetic and maternal permanent environmental effects (Model 2). Model 4, including additive and maternal genetic effects, as well as the covariance between these effects, was the most suitable model for 15-month body weight (W15).

Table 4.5 The log-likelihood values (LogL) for the different models evaluated for each trait

Trait	M1	M2	M3	M4	M5	M6
BW	-3420.74	-3032.40	-3052.39	-3047.43	-3007.38	-3003.76
W42	-13302.40	-13158.13	-13182.52	-13156.60	-13155.81	-13132.92
WW	-28497.52	-28023.94	-28039.23	-28038.51	-28011.87	-28010.77
W6	-2418.44	-2414.77	-2418.06	-2415.87	-2414.77	-2411.14
W8	-3361.47	-3349.11	-3358.14	-3352.74	-3349.11	-3342.32
W12	-6754.46	-6751.07	-6753.39	-6752.74	-6751.07	-6751.30
W15	-23579.84	-23576.08	-23570.76	-23554.39	-23570.76	-23553.74
AW2	-5460.18	-5324.93	-5326.57	-5326.47	-5324.93	-5325.71
AW3	-4966.55	-4877.01	-4877.01	-4877.67	-4877.01	-4877.54
AW4	-4041.97	-3957.77	-3957.50	-3957.21	-3957.50	-3957.21
AW5	-3106.58	-3039.96	-3039.96	-3039.95	-3039.96	-3039.95
AW6	-1427.01	-1401.91	-1401.75	-1400.33	-1401.75	-1400.33

BW = birth weight; W42 = body weight at 42 days of age; WW = Weaning weight; W6 = body weight at 6 months of age; W8 = body weight at 8 months of age; W12 = body weight at 12 months of age; W15 = body weight at 15 months of age; AW2 = adult body weight at two years; AW3 = adult body weight at three years; AW4 = adult body weight at four years; AW5 = adult body weight at five years; AW6 = adult body weight at six years

For all the adult body weights, either maternal genetic or maternal permanent environmental effects were included in addition to the additive genetic effect. The most suitable model for adult body weight at 2 years of age (AW2) was Model 2. Model 3 was the best model for 4-year adult body weight (AW4). The most suitable model for 6-year adult body weight (AW6) was Model 4, also including a covariance between additive and maternal genetic effects (Tables 4.6, 4.7 and 4.8). For 3-year (AW3) and 5-year (AW5) adult body weights there was no difference between Model 2 and Model 3, either in information criteria of genetic parameters (Tables 4.6, 4.7 and 4.8). With both models, the maternal component had a 0.000 variance. Model 3 was chosen for further analyses and discussion of variances and genetic parameters.

Table 4.6 LogL values as a deviation from the most suitable model (Most suitable model highlighted)

Trait	**M1**	**M2**	**M3**	**M4**	**M5**	**M6**
BW	833.96	57.28	97.26	87.34	7.24	0
W42	338.96	50.42	99.2	47.36	45.78	0
WW	973.50	26.34	56.92	55.48	2.20	0
W6	14.60	7.26	13.84	9.46	7.26	0
W8	38.30	13.58	31.64	20.84	13.58	0
W12	6.78	0	4.64	3.34	0	0.46
W15	52.20	44.68	34.04	1.30	34.04	0
AW2	270.50	0	3.28	3.08	0	1.56
AW3	179.08	0	0	1.32	0	1.06
AW4	169.52	1.12	0.58	0	0.58	0
AW5	133.26	0.02	0.02	0	0.02	0
AW6	53.36	3.16	2.84	0	2.84	0

BW = birth weight; W42 = body weight at 42 days of age; WW = Weaning weight; W6 = body weight at 6 months of age; W8 = body weight at 8 months of age; W12 = body weight at 12 months of age; W15 = body weight at 15 months of age; AW2 = adult body weight at two years; AW3 = adult body weight at three years; AW4 = adult body weight at four years; AW5 = adult body weight at five years; AW6 = adult body weight at six years

Table 4.7 Akaike's Information Criterion (AIC) for the different models evaluated for each trait (Most suitable model highlighted)

Trait	M1	M2	M3	M4	M7	M8
BW	6845.48	6070.80	6110.78	6102.86	6022.76	6017.52
W42	26608.80	26322.26	26371.04	26321.20	26319.62	26275.84
WW	56999.04	56053.88	56084.46	56085.02	56031.74	56031.54
W6	4840.88	4835.54	4842.12	4839.74	4837.54	4832.28
W8	6726.94	6704.22	6722.28	6713.48	6706.22	6694.64
W12	13512.92	13508.14	13512.78	13513.48	13510.14	13512.60
W15	47163.68	47158.16	47147.52	47116.78	47149.52	47117.48
AW2	10924.36	10655.86	10659.14	10660.94	10657.86	10661.42
AW3	9937.10	9760.02	9760.02	9763.34	9762.02	9765.08
AW4	8087.94	7921.54	7921.00	7922.42	7923.00	7924.42
AW5	6217.16	6085.92	6085.92	6087.90	6087.92	6089.90
AW6	2858.02	2809.82	2809.50	2808.66	2811.50	2810.66

BW = birth weight; W42 = body weight at 42 days of age; WW = Weaning weight; W6 = body weight at 6 months of age; W8 = body weight at 8 months of age; W12 = body weight at 12 months of age; W15 = body weight at 15 months of age; AW2 = adult body weight at two years; AW3 = adult body weight at three years; AW4 = adult body weight at four years; AW5 = adult body weight at five years; AW6 = adult body weight at six years

Table 4.8 Bayesian Information Criterion (BIC) for the different models evaluated for each trait (Most suitable model highlighted)

Trait	M1	M2	M3	M4	M5	M6
BW	6849.89	6077.42	6117.40	6111.69	6031.59	6028.56
W42	26612.59	26327.95	26376.73	26328.78	26327.20	26285.32
WW	57003.37	56060.38	56090.96	56093.69	56040.41	56042.37
W6	4843.02	4838.75	4845.33	4844.03	4841.83	4837.64
W8	6729.33	6707.81	6725.87	6718.27	6711.01	6700.63
W12	13515.93	13512.65	13517.29	13519.50	13516.16	13520.12
W15	47167.75	47164.27	47153.63	47124.92	47157.66	47127.66
AW2	10927.19	10660.10	10663.38	10666.60	10663.52	10668.49
AW3	9939.83	9764.12	9764.12	9768.80	9767.48	9771.91
AW4	8090.48	7925.34	7924.80	7927.49	7928.07	7930.76
AW5	6219.48	6089.40	6089.40	6092.54	6092.56	6095.70
AW6	2859.71	2812.36	2812.04	2812.05	2814.89	2814.89

BW = birth weight; W42 = body weight at 42 days of age; WW = Weaning weight; W6 = body weight at 6 months of age; W8 = body weight at 8 months of age; W12 = body weight at 12 months of age; W15 = body weight at 15 months of age; AW2 = adult body weight at two years; AW3 = adult body weight at three years; AW4 = adult body weight at four years; AW5 = adult body weight at five years; AW6 = adult body weight at six years

Table 4.9 summarises the (co)variance ratios for the different body weights obtained using the most suitable model for each trait. Phenotypic and direct additive variance increased with age until W15, after which it tended to level off. Environmental variance on the other hand kept increasing with an increase in age. No definite trend in maternal genetic variance, maternal permanent environmental variance or the genetic covariance between the animal effects could be discerned with an increase in age.

Table 4.9 (Co)variance components for the various body weights estimated with the most suitable model for each weight

Trait	**Model**	σ^2_p	σ^2_a	σ^2_m	σ^2_{mpe}	σ_{am}	σ^2_e
BW	M6	0.570	0.117	0.065	0.071	-0.025	0.343
W42	M6	12.003	5.084	1.748	1.272	-2.407	6.306
WW	M5	19.262	3.088	0.943	1.661		13.570
W6	M6	26.335	14.280	7.565	3.829	-9.860	10.521
W8	M6	28.980	12.571	5.131	5.982	-7.436	12.732
W12	M2	29.608	10.837		1.375		17.396
W15	M4	34.264	17.558	2.693		-3.540	17.553
AW2	M2	28.466	12.357		1.476		14.633
AW3	M3	31.525	12.467	0.000			19.059
AW4	M3	34.315	10.569	0.736			23.010
AW5	M3	34.223	11.397	0.000			22.826
AW6	M4	32.752	13.408	4.958		-5.307	19.693

σ^2_p = Phenotypic variance; σ^2_a = direct additive variance; σ^2_m = maternal additive variance; σ^2_{mpe} = maternal permanent environmental variance; σ_{am} = genetic covariance between the animal effects; σ^2_e = environmental variance; BW = birth weight; W42 = body weight at 42 days of age; WW = Weaning weight; W6 = body weight at 6 months of age; W8 = body weight at 8 months of age; W12 = body weight at 12 months of age; W15 = body weight at 15 months of age; AW2 = adult body weight at two years; AW3 = adult body weight at three years; AW4 = adult body weight at four years; AW5 = adult body weight at five years; AW6 = adult body weight at six years

Table 4.10 presents the genetic parameters for the different body weights obtained using the most suitable model for each trait. Direct heritability estimates were medium to high, ranging from 0.16 (WW) to 0.54 (W6). Direct heritability tended to increase with increasing age up until 15 months of age, after which it reached a plateau. Maternal heritability values were correspondingly lower, with the highest value of 0.28 reported for W6. The c^2_{mpe} estimates were rather high and ranged from 0.05 for W12 and AW2 to 0.21 for W8. The genetic correlation between direct and maternal effects was negative for all weights where it was included. Direct-maternal genetic correlation estimates of early body weight in this study ranged from -0.95 ± 0.14 to -0.28 ± 0.09. The relatively high standard errors of the parameters estimated for 6- and 8-month body weight could most probably be ascribed to the fewer records available for these traits, namely less than 1200 for W6 and less than 1600 for W8.

Table 4.10 Direct additive heritability (h^2_a), maternal heritability (h^2_m), maternal permanent environmental effect (c^2_{mpe}) and the genetic correlation between the animal effects (r_{am}) for the various body weights (± s.e.)

Trait	**Model**	h^2_a	h^2_m	c^2_{mpe}	r_{am}
BW	M6	0.20 ± 0.03	0.11 ± 0.02	0.12 ± 0.01	-0.28 ± 0.09
W42	M6	0.42 ± 0.06	0.15 ± 0.03	0.10 ± 0.02	-0.81 ± 0.05
WW	M5	0.16 ± 0.02	0.04 ± 0.01	0.09 ± 0.01	
W6	M6	0.54 ± 0.15	0.28 ± 0.17	0.15 ±0.05	-0.95 ± 0.14
W8	M6	0.43 ± 0.11	0.18 ± 0.08	0.21 ± 0.04	-0.93 ± 0.10
W12	M2	0.37 ± 0.05		0.05 ± 0.02	
W15	M4	0.51 ± 0.04	0.08 ± 0.02		-0.51 ± 0.06
AW2	M2	0.43 ± 0.05		0.05 ± 0.03	
AW3	M3	0.40 ± 0.05	0.00 ± 0.00		
AW4	M3	0.31 ± 0.06	0.02 ± 0.03		
AW5	M3	0.33 ± 0.06	0.00 ± 0.00		
AW6	M4	0.41 ± 0.17	0.15 ± 0.12		-0.65 ± 0.23

BW = birth weight; W42 = body weight at 42 days of age; WW = Weaning weight; W6 = body weight at 6 months of age; W8 = body weight at 8 months of age; W12 = body weight at 12 months of age; W15 = body weight at 15 months of age; AW2 = adult body weight at two years; AW3 = adult body weight at three years; AW4 = adult body weight at four years; AW5 = adult body weight at five years; AW6 = adult body weight at six years

4.4 Bivariate and multivariate linear animal models employing restricted maximum likelihood procedures

Table 4.11 summarises the genetic and phenotypic correlations among body weight at different ages obtained with bivariate analyses. The genetic correlations (r_g) of BW with the other younger body weights ranged from 0.11 ± 0.19 (W6) to 0.51 ± 0.09 (W42). BW had a medium genetic correlation with all the adult body weights. Genetic correlations of W42 with the other younger body weights ranged from medium to high. All models where W42 was included together with an adult weight did not converge. High r_g were estimated among body weights from weaning until 15 months of age, while very high r_g (0.92 to 0.99) were obtained among the adult ewe body weights. Phenotypic correlations were moderate to high, and followed the same trend as the genetic correlations, where adjacent weights had higher correlations between them.

Table 4.11 Genetic (above diagonal) and phenotypic (below diagonal) correlations among body weight at different ages

Trait	BW	W42	WW	W6	W8	W12	W15	AW2	AW3	AW4	AW5
BW		0.51 ± 0.09	0.44 ± 0.07	0.11± 0.19	0.48 ± 0.16	0.40 ± 0.09	0.31 ± 0.06	0.57 ± 0.10	0.57 ± 0.11	0.52 ± 0.13	0.38 ± 0.16
W42	0.32 ± 0.01		0.72 ± 0.06	0.23 ± 0.18	0.55 ± 0.13	0.53 ± 0.10	0.50 ± 0.06	-	-	-	-
WW	0.30 ± 0.01	0.51 ± 0.01		0.98 ± 0.05	0.98 ± 0.03	0.88 ± 0.05	0.72 ± 0.04	0.63 ± 0.09	0.71± 0.09	0.51 ± 0.13	0.66 ± 0.12
W6	0.14 ± 0.03	0.46 ± 0.02	0.67 ± 0.02		0.99 ± 0.03	0.96 ± 0.11	0.76 ± 0.07	0.57 ± 0.11	0.59 ± 0.12	0.49 ± 0.14	0.36 ± 0.16
W8	0.21 ± 0.02	0.51 ± 0.02	0.69 ± 0.01	0.77 ± 0.01		0.98 ± 0.02	0.94 ± 0.03	0.61 ± 0.11	0.78± 0.09	0.52 ± 0.14	0.63 ± 0.13
W12	0.16 ± 0.02	0.39 ± 0.02	0.57 ± 0.01	0.61 ± 0.04	0.82 ± 0.01		0.69 ± 0.04	0.73 ± 0.09	0.72± 0.12	0.60 ± 0.13	0.61 ± 0.14
W15	0.19 ± 0.01	0.33 ± 0.01	0.49 ± 0.01	0.65 ± 0.02	0.75 ± 0.01	0.66 ± 0.01		0.75 ± 0.04	0.78± 0.05	0.76 ± 0.06	0.71 ± 0.06
AW2	0.53 ± 0.05	-	0.54 ± 0.04	0.54 ± 0.04	0.53 ± 0.04	0.53 ± 0.03	0.68 ± 0.01		0.98 ± 0.02	0.99 ± 0.03	0.95 ± 0.05
AW3	0.44 ± 0.06	-	0.59 ± 0.04	0.45 ± 0.05	0.58 ± 0.04	0.42 ± 0.03	0.63 ± 0.01	0.62 ± 0.01		0.99 ± 0.03	0.93 ± 0.05
AW4	0.44 ± 0.06	-	0.33 ± 0.06	0.41 ± 0.06	0.34 ± 0.06	0.39 ± 0.04	0.66 ± 0.01	0.57 ± 0.02	0.62 ± 0.02		0.92 ± 0.06
AW5	0.45 ± 0.07	-	0.51 ± 0.05	0.43 ± 0.07	0.50 ± 0.05	0.30 ± 0.05	0.57 ± 0.02	0.53 ± 0.02	0.57 ± 0.02	0.58 ± 0.02	

BW = birth weight; W42 = body weight at 42 days of age; WW = Weaning weight; W6 = body weight at 6 months of age; W8 = body weight at 8 months of age; W12 = body weight at 12 months of age; W15 = body weight at 15 months of age; AW2 = adult body weight at two years; AW3 = adult body weight at three years; AW4 = adult body weight at four years; AW5 = adult body weight at five years; - not fitted

Table 4.12 summarises maternal and environmental correlations among the body weights obtained with bivariate analyses. When including maternal effects in the respective models for the various adult weights, the models did not converge. Therefore these models were rerun excluding all maternal effects. Maternal correlations (r_m) between BW and the other younger weights ranged from 0.12 ± 0.16 (W6) to 0.88 ± 0.08 (W8), while r_m between W42 and these body weights ranged from 0.31 ± 0.05 (W6) to 0.75 ± 0.07 (WW). A high r_m was also obtained between WW and W15. The environmental correlations from BW up to W15 tended to decrease with an increase in age. Environmental correlations among the adult weights ranged from 0.27 ± 0.05 to 0.43 ±0.03.

Table 4.12 Maternal (above diagonal) and environmental (below diagonal) correlations among body weight at different ages

Trait	**BW**	**W42**	**WW**	**W6**	**W8**	**W12**	**W15**	**AW2**	**AW3**	**AW4**
BW		0.55 ± 0.09	0.62 ± 0.08	0.12± 0.16	0.88 ± 0.08	-	0.39 ± 0.08	-	-	-
W42	0.28 ± 0.02		0.75 ± 0.07	0.34 ± 0.05	0.62 ± 0.07	-	0.31 ± 0.10	-	-	-
WW	0.25 ± 0.01	0.59 ± 0.01		-	-	-	0.61 ± 0.06	-	-	-
W6	0.18 ± 0.05	0.56 ± 0.03	0.68 ± 0.02		-	-	-	-	-	-
W8	0.12 ± 0.04	0.58 ± 0.03	0.55 ± 0.02	0.62 ± 0.04		-	-	-	-	-
W12	0.08 ± 0.04	0.39 ± 0.02	0.55 ± 0.02	0.46 ± 0.09	0.71 ± 0.02		-	-	-	-
W15	0.11 ± 0.02	0.30 ± 0.02	0.44 ± 0.02	0.57 ± 0.04	0.60 ± 0.03	0.63 ± 0.02		-	-	-
AW2	0.50 ± 0.10	-	0.47 ± 0.07	0.45 ± 0.04	0.52 ± 0.07	0.51 ± 0.04	0.66 ± 0.02		-	-
AW3	0.34 ± 0.11	-	0.50 ± 0.07	0.35 ± 0.11	0.49 ± 0.07	0.37 ± 0.05	0.59 ± 0.02	0.34 ± 0.04		-
AW4	0.40 ± 0.12	-	0.22 ± 0.10	0.37 ± 0.12	0.26 ± 0.09	0.34 ± 0.05	0.64 ± 0.02	0.30 ± 0.04	0.43 ± 0.03	
AW5	0.51 ± 0.13	-	0.42 ± 0.09	0.49 ± 0.13	0.45 ± 0.09	0.22 ± 0.07	0.53 ± 0.03	0.27 ± 0.05	0.38 ± 0.04	0.42 ± 0.04

BW = birth weight; W42 = body weight at 42 days of age; WW = Weaning weight; W6 = body weight at 6 months of age; W8 = body weight at 8 months of age; W12 = body weight at 12 months of age; W15 = body weight at 15 months of age; AW2 = adult body weight at two years; AW3 = adult body weight at three years; AW4 = adult body weight at four years; AW5 = adult body weight at five years; - not fitted

The (co)variance components, correlations and heritabilities obtained with multivariate analyses of WW, W12, W15 and AW3 are summarised in Table 4.13. Direct heritability increased from 0.17 ± 0.02 for WW to 0.29 ± 0.04 for AW3. Phenotypic correlations among the traits ranged from low (0.36 ± 0.02 between WW and AW3) to high (0.73 ± 0.01 between W12 and W15). Genetic correlations were generally high and ranged from 0.73 ± 0.07 between W12 and AW3 to 0.85 ± 0.05 between WW and W12.

Table 4.13 Covariance components, correlations and heritabilities among WW, W12, W15 and AW3 obtained with multivariate analyses

Trait	Parameter	WW	W12	W15	AW3
WW	σ_{p1p2}	22.387	16.932	14.950	12.030
W12	σ_{p1p2}		58.723	46.328	33.808
W15	σ_{p1p2}			67.799	39.852
AW3	σ_{p1p2}				51.143
WW	σ_{a1a2}	3.851	5.980	6.477	5.757
W12	σ_{a1a2}		12.792	9.828	10.032
W15	σ_{a1a2}			15.967	11.644
AW3	σ_{a1a2}				14.852
WW	σ^2_{m}	0.411			
W15	σ^2_{m}			0.419	
WW	σ^2_{mpe}	1.861			
W12	σ^2_{mpe}		0.000		
WW	σ_{e1e2}	16.234	10.952	8.473	6.273
W12	σ_{e1e2}		45.931	36.500	23.775
W15	σ_{e1e2}			51.413	28.208
AW3	σ_{e1e2}				36.291
WW	r_{p1p2}	-	0.47 ± 0.01	0.38 ± 0.01	0.36 ± 0.02
W12	r_{p1p2}		-	0.73 ± 0.01	0.62 ± 0.02
W15	r_{p1p2}			-	0.68 ± 0.01
AW3	r_{p1p2}				-
WW	r_{g1g2}	-	0.85 ± 0.05	0.83 ± 0.04	0.76 ± 0.06
W12	r_{g1g2}		-	0.69 ± 0.05	0.73 ± 0.07
W15	r_{g1g2}			-	0.76 ± 0.05
AW3	r_{g1g2}				-

Trait	Parameter	WW	W12	W15	AW3
WW	h^2_a	0.17 ± 0.02			
W12	h^2_a		0.22 ± 0.03		
W15	h^2_a			0.23 ± 0.02	
AW3	h^2_a				0.29 ± 0.04
WW	h^2_m	0.02 ± 0.01			
W15	h^2_m			0.01 ± 0.0	
WW	c^2_{mpe}	0.08 ± 0.01			
W12	c^2_{mpe}		0.00 ± 0.00		

σ_{p1p2} = Phenotypic covariance; σ_{a1a2} = direct additive covariance; σ^2_m = maternal additive variance; σ^2_{mpe} = maternal permanent environmental variance; σ_{e1e2} = environmental covariance; r_{p1p2} = phenotypic correlation; r_{g1g2} = genetic correlation; h^2_a = direct heritability; h^2_m = maternal heritability; c^2_{mpe} = maternal permanent environmental effect; WW = Weaning weight; W12 = body weight at 12 months of age; W15 = body weight at 15 months of age; AW3 = adult body weight at three years

4.5 Repeatability model

The different information criteria for the twelve repeatability models fitted for body weight are summarised in Tables 4.14 to 4.18. Log likelihood values were obtained from the ASReml output files, while the Akaike's Information Criterion (AIC) and the Bayesian Information Criterion (BIC) for the different models were calculated from the parameters presented in Table 4.16.

Table 4.14 The log likelihood values (LogL) for the different models evaluated

	M1	M2	M3	M4	M5	M6
With splines	-170525.12	-168937.92	-168931.47	-168919.58	-168930.24	-168917.05
Without splines	-133489.94	-132537.02	-132534.51	-132552.70	-132534.51	-132534.23

Table 4.15 LogL relative to the most suitable model (Most suitable model highlighted)

	M1	M2	M3	M4	M5	M6
With splines	75981.22	72806.82	72793.92	72770.14	72791.5	72765.1
Without splines	1910.86	5.02	0	36.38	0	-0.56

Table 4.16 Number of parameters (k) and total number of records (n) included in each model (with and without splines)

Parameter	M1	M2	M3	M4	M5	M6
n	59393	59393	59393	59393	59393	59393
k (with splines)	4	5	5	6	6	7
k (without splines)	3	4	4	5	5	6

Table 4.17 Akaike's Information Criterion (AIC) for the different models evaluated (Most suitable model highlighted)

	M1	M2	M3	M4	M5	M6
With splines	341058.24	337885.84	337872.94	337851.16	337872.48	337848.10
Without splines	266985.88	265082.04	265077.02	265115.40	265079.02	265080.46

Table 4.18 Bayesian Information Criterion (BIC) for the different models evaluated (Most suitable model highlighted)

	M1	M2	M3	M4	M5	M6
With splines	341069.33	337899.71	337886.81	337867.80	337889.12	337867.52
Without splines	266994.20	265093.13	265088.11	265129.27	265092.89	265097.10

From the LogL, AIC and BIC values given in Tables 4.14, 4.15, 4.17 and 4.18 it is evident that Model 3 without splines was the most appropriate model for estimation of genetic parameters for body weight for Merino sheep under a repeatability model.

(Co)variance components and genetic parameter estimates for body weight in the Grootfontein Merino stud estimated with various repeatability models, without fitting splines, are presented in Table 4.19. The corresponding values for models fitting splines are summarised in Table 4.20.

Table 4.19 (Co)variance component and genetic parameter estimates for body weight in Merino sheep estimated with various repeatability models, without fitting splines. (Most suitable model highlighted)

Parameter	**M1**	**M2**	**M3**	**M4**	**M5**	**M6**
σ^2_p	30.305	29.812	30.056	29.921	29.794	29.596
σ^2_a	11.021	7.812	7.918	9.352	7.616	9.099
σ^2_m			2.341	6.123	0.189	3.225
σ^2_{mpe}		0.216			3.452	3.931
σ_{am}				-4.747		-4.480
σ^2_{anim}	2.785	2.030	3.332	2.743	2.121	1.411
σ^2_e	16.500	16.418	16.466	16.449	16.416	16.410
h^2_a	0.36 ± 0.06	0.26 ± 0.06	0.26 ± 0.06	0.31 ± 0.08	0.26 ± 0.06	0.31 ± 0.08
h^2_m			0.08 ± 0.03	0.20 ± 0.06	0.01 ± 0.06	0.11 ± 0.06
c^2_{mpe}		0.12 ± 0.03			0.12 ± 0.03	0.13 ± 0.03
r_{am}				-0.63 ± 0.15		-0.83 ± 0.13
c^2_{anim}	0.09 ± 0.05	0.07 ± 0.05	0.11 ± 0.05	0.09 ± 0.06	0.07 ± 0.05	0.05 ± 0.06
t	0.45 ± 0.03	0.33 ± 0.04	0.37 ± 0.04	0.40 ± 0.05	0.33 ± 0.04	0.36 ± 0.05

σ^2_p = Phenotypic variance; σ^2_a = direct additive variance; σ^2_m = maternal additive variance; σ^2_{mpe} = maternal permanent environmental variance; σ_{am} = genetic covariance between the animal effects; σ^2_{anim} = animal permanent environmental variance; σ^2_e = environmental variance; h^2_a = direct additive heritability; h^2_m = maternal heritability; c^2_{mpe} = maternal permanent environmental effect; c^2_{anim} = animal permanent environmental effect; r_{am} = genetic correlation between the animal effects; t = repeatability

There is a slight influence on the values when splines are fitted as compared to when it is not. Direct heritabilities for all models fitting splines (Table 4.20) ranged from 0.31 to 0.41, while without splines (Table 4.19) it ranged from 0.26 to 0.36. Maternal heritability in models with splines ranged from 0.00 to 0.27 and without splines from 0.01 to 0.20. The direct-maternal genetic correlations in both Models 4 and 6 were higher in the models where splines were included.

Table 4.20 (Co)variance component and genetic parameter estimates for body weight in Merino sheep estimated with various repeatability models, fitting splines

Parameter	**M1**	**M2**	**M3**	**M4**	**M5**	**M6**
σ^2_p	33.435	32.945	33.291	33.204	32.941	32.742
σ^2_a	13.736	10.124	10.236	13.153	10.051	12.890
σ^2_m			2.970	8.989	0.081	4.736
σ^2_{mpe}		4.285			4.240	4.900
σ_{am}				-7.669		-6.958
σ^2_{anim}	3.193	2.123	3.626	2.285	2.157	0.742
σ^2_e	16.506	16.413	16.457	16.447	16.412	16.412
Spline	0.333	0.333	0.333	0.333	0.333	0.333
h^2_a	0.41 ± 0.06	0.31 ± 0.06	0.31 ± 0.07	0.40 ± 0.09	0.31 ± 0.06	0.39 ± 0.09
h^2_m			0.09 ± 0.03	0.27 ± 0.10	0.00 ± 0.03	0.14 ± 0.06
c^2_{mpe}		0.13 ± 0.03			0.13 ± 0.03	0.15 ± 0.03
r_{am}				-0.70 ± 0.12		-0.89 ± 0.10
c^2_{anim}	0.10 ± 0.05	0.06 ± 0.05	0.11 ± 0.05	0.07 ± 0.07	0.07 ± 0.05	0.03 ± 0.06
t	0.51 ± 0.03	0.37 ± 0.04	0.42 ± 0.04	0.47 ± 0.05	0.38 ± 0.04	0.42 ± 0.05

σ^2_p = Phenotypic variance; σ^2_a = direct additive variance; σ^2_m = maternal additive variance; σ^2_{mpe} = maternal permanent environmental variance; σ_{am} = genetic covariance between the animal effects; σ^2_{anim} = animal permanent environmental variance; σ^2_e = environmental variance; h^2_a = direct additive heritability; h^2_m = maternal heritability; c^2_{mpe} = maternal permanent environmental effect; c^2_{anim} = animal permanent environmental effect; r_{am} = genetic correlation between the animal effects; t = repeatability

4.6 Random regression models

Several random regression models were fitted to the dataset including all body weights from birth to adult weight at six years of age. These included fitting direct as well maternal effects, fitting splines or omitting splines, and either fitting one or two age classes to account for heterogeneous residual variance. However, when the output values were processed to obtain variances, covariances and genetic parameters for the specific body weights at the different ages, it was obvious from the results that inaccurate estimates of variance components were calculated.

The variance components obtained from a model including direct genetic and maternal genetic effects, fitting a first order polynomial for each random effect, as well as fitting cubic splines for age of recording and fitting two age classes to account for heterogeneous variances are presented in Table 4.21 as an example. From

Table 4.21 it is obvious that the direct additive and phenotypic variances are too high. Residual variance on the other hand is comparable to those obtained with univariate and repeatability models, and even that for WW under the multivariate model in this study. Furthermore, the large increase in maternal variance with age is also contradictory to most reported literature. The reason for these wrong estimations is not known at this stage. The same results were found with data from the Carnarvon Afrino flock and the Cradock fine wool Merino flock when data from all animals (rams and ewes) from birth until 15 months of age were included in the analysis together with adult body weights on only ewes. When only data from ewes were included, the magnitude of the additive and phenotypic variance components decreased, but was still high. The results obtained with the random regression analyses in this study will therefore not be included and discussed. Further work on the model specification will be done to try and rectify the encountered problem.

Table 4.21 Variance components obtained from a random regression model including direct genetic and maternal genetic effects, fitting one polynomial per effect

	Month										
	1	**2**	**4**	**8**	**12**	**15**	**20**	**32**	**44**	**56**	**68**
σ^2_a	0.00	1.46	20.37	103.17	278.80	541.52	952.48	1908.39	3139.36	4747.31	5955.39
σ^2_m	0.40	0.89	3.18	12.97	29.70	46.80	83.99	217.52	413.56	672.11	993.17
σ^2_e	10.75	10.75	10.75	10.75	10.75	10.75	10.75	10.75	10.75	10.75	10.75
AC			21.37	21.37	21.37	21.37	21.37	21.37	21.37	21.37	21.37
σ^2_p	11.15	13.10	55.67	148.25	340.61	620.43	1068.58	2158.03	3585.04	5451.54	6980.68
h_a^2	0.00	0.11	0.37	0.70	0.82	0.87	0.89	0.88	0.88	0.87	0.82
h_m^2	0.04	0.07	0.06	0.09	0.09	0.08	0.08	0.10	0.12	0.12	0.14

σ^2_a = Direct additive variance; σ^2_m = maternal additive variance; σ^2_e = environmental variance; AC = age class; σ^2_p = phenotypic variance; h^2_a = direct additive heritability; h^2_m = maternal heritability;

4.7 Comparison of univariate, multivariate and repeatability models

Univariate and multivariate additive, phenotypic and residual variance components are depicted in Figure 4.1.

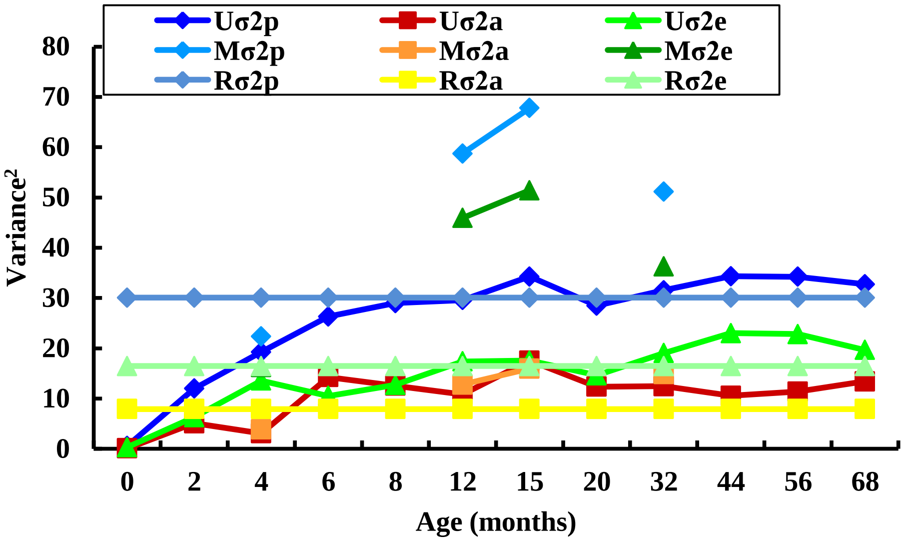

Figure 4.1 Comparison of univariate (U), multivariate (M) and repeatability (R) additive (σ^2_a), phenotypic (σ^2_p) and residual (σ^2_e) variance components

From Figure 4.1 it is evident that multivariate additive variance components are nearly the same as the univariate additive variance for a specific body weight, and it tended to increase with an increase of age of the animal. Repeatability additive variance components were in the same range as those of the univariate and multivariate values. The same was observed for the maternal components (Figure 4.2), where maternal genetic variance for WW was somewhat lower with the multivariate model, but maternal genetic variance for W15 was considerably lower with the multivariate model (0.419 vs. 2.693). The same applies for the maternal permanent environmental variance, which was 0.00 for W12 with the multivariate model, compared to 1.375 with the univariate model. Residual variance of W12, W15 and AW3 were much higher with the multivariate model than univariate residual variance components obtained for the corresponding body weights with univariate analyses (Figure 4.1). This consequently led to higher multivariate phenotypic variance components for these body weights as well.

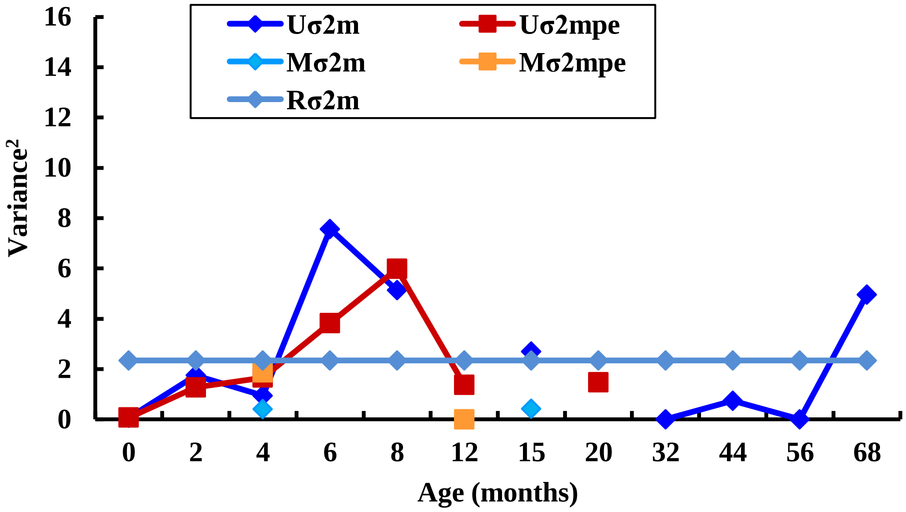

Figure 4.2 Comparison of univariate (U), multivariate (M) and repeatability (R) maternal (σ^2_m) and maternal permanent environmental (σ^2_{mpe}) variance components

Higher direct additive heritabilities were obtained with the univariate models for W12, W15 and AW3 compared to the multivariate model. Univariate h^2_a were 0.37 ± 0.05 (W12), 0.51 ± 0.04 (W15) and 0.40 ± 0.05 (AW3) compared to multivariate h^2_a of 0.22 ± 0.03 (W12), 0.23 ± 0.02 (W15) and 0.29 ± 0.04 (AW3). Direct additive heritability obtained with the repeatability model was 0.26 ± 0.06 for body weight, which was lower than most of the univariate h^2_a obtained for the different body weights.

With the multivariate model, direct genetic correlations of WW with W12, W15 and AW3 were 0.85 ± 0.05, 0.83 ± 0.04 and 0.76 ± 0.06 respectively. The genetic correlation estimated with bivariate models between WW and W12 (0.88 ± 0.05) was higher compared to the multivariate estimate, but lower than those between WW and W15 (0.72 ± 004) and between WW and AW3 (0.71± 0.09). Multivariate and bivariate r_g were comparable between W15 and AW3 (0.73 ± 0.07 – multivariate and 0.78 ± 0.05 – bivariate).

Phenotypic correlations estimated with the multivariate model for WW with W12, W15 and AW3 were 0.47 ± 0.01, 0.38 ± 0.01 and 0.36 ± 0.02 respectively. These r_p were lower than the r_p estimated with bivariate analyses between WW and W12, W15 and AW3 of 0.57 ± 0.01, 0.49 ± 0.01 and 0.59 ± 0.04 respectively. Phenotypic correlation for W12 and W15, AW3 and also for W15 and AW3 were respectively 0.73 ± 0.01, 0.62 ± 0.02 and 0.68 ± 0.01. Multivariate phenotypic correlations of W12 with W15 and AW3 and of W15 with AW3 are higher than bivariate r_p estimated for these traits.

It is difficult to compare repeatability model values with uni- or bi- or multivariate values, because the repeatability model yielded one heritability for body weight overall, whereas with uni- or bi- or multivariate models heritabilities were obtained for each of the different body weights.

4.8 Comparison of estimated breeding values (EBV)

Spearman rank correlations between EBVs obtained with univariate, multivariate and repeatability animal models for WW, W15 and AW3 are presented in Tables 4.22 to 4.24 for all animals in the pedigree file, animals with a 15-month body weight data record and for all sires respectively.

From Tables 4.22 to 4.24 it was evident that high correlations were obtained between the EBV rankings of WWU, W15U, WWM and W15M. Much lower correlations were obtained between WWU and AW3U, between W15U and AW3U, WWM and AW3U and W15M and AW3U. These correlations increased when AW3 was included in the multivariate analyses. Very high correlations were estimated among EBVs of the traits included in the multivariate model. Low correlations were obtained between the rankings of the repeatability model EBVs and the other EBVs.

Table 4.22 Spearman rank correlations between EBVs obtained with univariate, multivariate and repeatability animal models for WW, W15 and AW3 using all animals in the pedigree file

Trait	WWU	W15U	AW3U	WWM	W15M	AW3M	REP
WWU	-	0.65	0.25	0.86	0.72	0.73	0.24
W15U		-	0.23	0.77	0.87	0.76	0.22
AW3U			-	0.30	0.24	0.50	0.10
WWM				-	0.92	0.93	0.20
W15M					-	0.91	0.17
AW3M						-	0.17

WWU = Weaning weight univariate; W15U = 15-month body weight univariate; AW3U = 3-year adult body weight univariate; WWM = Weaning weight multivariate; W15M = 15-month body weight multivariate; AW3M = 3-year adult body weight multivariate; REP = Repeatability model; All correlations significant (P <0.001)

Table 4.23 Spearman rank correlations between EBVs obtained with univariate, multivariate and repeatability animal models for WW, W15 and AW3 using all animals with 15-month body weight data

Trait	WWU	W15U	AW3U	WWM	W15M	AW3M	REP
WWU	-	0.67	0.26	0.85	0.70	0.70	0.30
W15U		-	0.23	0.80	0.88	0.77	0.27
AW3U			-	0.32	0.25	0.52	0.12
WWM				-	0.92	0.92	0.26
W15M					-	0.91	0.23
AW3M						-	0.22

WWU = Weaning weight univariate; W15U = 15-month body weight univariate; AW3U = 3-year adult body weight univariate; WWM = Weaning weight multivariate; W15M = 15-month body weight multivariate; AW3M = 3-year adult body weight multivariate; REP = Repeatability model; All correlations significant ($P < 0.001$)

Table 4.24 Spearman rank correlations between EBVs obtained with univariate, multivariate and repeatability animal models for WW, W15 and AW3 using all sires

Trait	WWU	W15U	AW3U	WWM	W15M	AW3M	REP
WWU	-	0.66	0.26	0.84	0.67	0.67	-0.26
W15U		-	0.25	0.78	0.90	0.77	-0.29
AW3U			-	0.31	0.27	0.56	-0.05 ^{ns}
WWM				-	0.89	0.89	-0.25
W15M					-	0.88	-0.28
AW3M						-	-0.20

WWU = Weaning weight univariate; W15U = 15-month body weight univariate; AW3U = 3-year adult body weight univariate; WWM = Weaning weight multivariate; W15M = 15-month body weight multivariate; AW3M = 3-year adult body weight multivariate; REP = Repeatability model; All correlations significant ($P < 0.001$), except for ^{ns}

From the results on the Spearman rank correlations between EBVs obtained with univariate, multivariate and repeatability animal models for WW, W15 and AW3, it is clear that the correlations involving the multivariate model were the highest.

The number and proportion of common animals in the Top 10% and Top 1% lists when all animals in the pedigree were included are presented in Table 4.25 for EBVs estimated with different models for weaning weight, 15-month body weight and 3-year body weight. Corresponding values for animals with a 15-month body weight data record and all sires are summarised in Tables 4.26 and 4.27 respectively.

The highest percentage common animals in Tables 4.25 to 4.27 were present in the lists involving the univariate and multivariate models for the same traits, for example WWU and WWM or W15U and W15M. The lists involving the repeatability model EBVs had the least number of common animals. It is interesting to note that in both Tables 4.25 and 4.26 there was a higher percentage common animals in the Top 1% list than in the Top 10% list.

Table 4.25 The number and proportion of common animals in the Top 10% and Top 1% lists when all animals in the pedigree were included

Models	**Top 10% list (n = 1467)**		**Top 1% list (n = 147)**	
	Number	**%**	**Number**	**%**
WWU vs WWM	934	66.67	141	95.92
WWU vs REP	519	35.38	72	48.98
WWM vs REP	564	38.45	68	46.26
W15U vs W15M	955	65.10	144	97.96
W15U vs REP	535	36.47	65	44.22
W15M vs REP	563	38.38	67	45.58
AW3U vs AW3M	646	44.04	125	85.03
AW3U vs REP	243	16.56	29	19.73
AW3M vs REP	486	33.13	45	30.61

WWU = Weaning weight univariate; W15U = 15-month body weight univariate; AW3U = 3-year adult body weight univariate; WWM = Weaning weight multivariate; W15M = 15-month body weight multivariate; AW3M = 3-year adult body weight multivariate; REP = Repeatability model

Table 4.26 The number and proportion of common animals in the Top 10% and Top 1% lists when animals with a 15-month body weight data record were included

Models	**Top 10% list (n = 1069)**		**Top 1% list (n = 107)**	
	Number	**%**	**Number**	**%**
WWU vs WWM	658	61.55	101	94.39
WWU vs REP	385	36.01	53	49.53
WWM vs REP	391	36.58	44	41.12
W15U vs W15M	688	64.36	102	95.33
W15U vs REP	362	33.86	48	44.86
W15M vs REP	376	35.17	37	34.58
AW3U vs AW3M	468	43.78	93	86.92
AW3U vs REP	174	16.28	22	20.56
AW3M vs REP	333	31.15	27	25.23

WWU = Weaning weight univariate; W15U = 15-month body weight univariate; AW3U = 3-year adult body weight univariate; WWM = Weaning weight multivariate; W15M = 15-month body weight multivariate; AW3M = 3-year adult body weight multivariate; REP = Repeatability model

Table 4.27 The number and proportion of common animals in the Top 10% and Top 1% lists when all sires were included

Models	**Top 10% list (n = 27)**		**Top 1% list (n = 3)**	
	Number	**%**	**Number**	**%**
WWU vs WWM	18	66.67	2	66.67
WWU vs REP	6	22.22	1	33.33
WWM vs REP	11	40.74	1	33.33
W15U vs W15M	21	77.78	3	100.0
W15U vs REP	10	37.04	1	33.33
W15M vs REP	9	33.33	1	33.33
AW3U vs AW3M	15	55.56	3	100.0
AW3U vs REP	4	14.81	0	0.0
AW3M vs REP	9	33.33	0	0.0

WWU = Weaning weight univariate; W15U = 15-month body weight univariate; AW3U = 3-year adult body weight univariate; WWM = Weaning weight multivariate; W15M = 15-month body weight multivariate; AW3M = 3-year adult body weight multivariate; REP = Repeatability model

Descriptive statistics of the accuracies of the EBVs of all animals in the pedigree for WW, W15 and AW3 obtained with univariate, multivariate and repeatability animal models are presented in Table 4.28. From Table 4.28 it can be seen that EBV for REP (26.51%) and AW3U (40.90%) had the lowest mean accuracies. The highest mean accuracy was obtained for W15U (67.29%). The lowest minimum accuracy of 0.14% was recorded for REP and the highest maximum of 95.70 for W15U.

Table 4.28 Descriptive statistics of the accuracies (%) of the EBVs of all animals in the pedigree for WW, W15 and AW3 obtained with univariate, multivariate and repeatability animal models

Trait	Mean	Minimum	Maximum
WWU	56.77	34.78	91.96
W15U	67.29	12.28	95.70
AW3U	40.90	3.57	78.98
WWM	63.88	43.71	93.73
W15M	64.56	38.25	93.95
AW3M	57.99	30.44	86.27
REP	26.51	0.14	88.19

WWU = Weaning weight univariate; W15U = 15-month body weight univariate; AW3U = 3-year adult body weight univariate; WWM = Weaning weight multivariate; W15M = 15-month body weight multivariate; AW3M = 3-year adult body weight multivariate; REP = Repeatability model

Accuracy of EBVs for the sires on the Top 10% list obtained with univariate and multivariate models for WW, W15 and AW3 are presented in Table 4.29. It can be seen that except for W15, for each body weight EBV accuracy for the multivariate model was higher than for the univariate model. The highest accuracies was obtained for W15U (87.53%), W15M (84.62%) and WWM (83.67%).

Table 4.29 Accuracy of EBVs for the sires on the top 10% list obtained with univariate and multivariate models for WW, W15 and AW3

Sire	**Accuracy of EBV (%)**						
	WWU	**WWM**	**W15U**	**W15M**	**AW3U**	**AW3M**	**REP**
888020190	77.50	83.76	88.17	85.14	66.51	78.61	60.68
888020053	76.58	83.59	86.03	84.37	62.71	77.34	61.46
888020079	77.86	84.16	87.75	85.41	66.03	78.65	63.22
888030108	77.79	83.86	88.61	85.38	62.85	78.12	41.30
888000029	57.02	65.55	75.70	67.81	39.05	58.81	44.01
888960065	77.58	83.19	88.45	84.77	61.60	77.06	44.68
888050111	77.65	83.26	87.48	83.69	59.50	75.75	47.43
888960264	78.82	84.74	88.92	86.12	65.71	78.88	46.54
888940220	81.28	86.28	90.24	87.41	69.17	80.70	47.63
888060108	77.30	81.87	87.25	82.31	50.84	72.56	36.34
888930251	76.96	84.06	88.90	85.61	64.18	78.14	61.70
888030034	84.37	88.78	91.74	89.70	71.22	82.96	51.78
888940297	82.22	87.52	91.06	88.90	74.89	83.71	53.73
888960049	78.40	84.06	88.77	85.58	65.36	78.34	47.07
888030059	80.12	85.18	89.08	86.08	67.38	79.59	43.77
888080120	64.87	75.67	70.05	71.39	41.94	64.59	67.43
888950302	78.74	83.89	87.22	84.50	66.77	78.37	77.21
888020204	75.29	82.81	87.72	84.84	68.16	78.79	62.10
888910319	81.03	87.06	89.75	88.44	73.72	82.92	81.31
888930260	81.34	86.40	90.21	87.51	72.28	81.96	66.52
888970015	80.74	85.28	89.56	86.41	62.63	78.14	62.14
888960126	81.32	85.98	90.26	87.37	67.40	80.33	54.13
888000122	78.13	84.19	88.69	85.76	66.65	78.79	76.00
888050032	77.00	82.15	85.13	81.42	54.68	73.58	40.52
888060014	77.58	82.92	87.32	83.10	59.62	75.30	56.08
888910005	81.13	87.57	89.98	89.00	75.01	83.71	83.16
888010072	80.18	85.37	89.37	86.63	69.63	80.45	44.38
Average	**77.73**	**83.67**	**87.53**	**84.62**	**63.91**	**77.64**	**56.38**

WWU = Weaning weight univariate; W15U = 15-month body weight univariate; AW3U = 3-year adult body weight univariate; WWM = Weaning weight multivariate; W15M = 15-month body weight multivariate; AW3M = 3-year adult body weight multivariate; REP = Repeatability model

5. DISCUSSION

5.1 Introduction

It is important for any breeding program that the genetic and environmental components of variance for the traits under selection are known, so that accurate genetic parameters can be estimated for incorporation in genetic evaluation, selection schemes and especially genomic selection. For successful genomic selection implementation, it is imperative that accurate and reliable conventional estimated breeding values (EBV) for performance traits are available. The aim of this study was to identify the most appropriate model for estimation of breeding values for body weights recorded at different ages in Merino sheep for inclusion in a genomic selection program.

5.2 Descriptive statistics and non-genetic factors

The body weight of the ewes increased from 26.1 kg at weaning to 55.4 kg at 3 years of age, after which it remained constant at approximately 56 kg. The overall CVs (coefficient of variations) for body weight of the ewes (12.6% to 24.5%) and rams (16.8% to 25.1%) recorded in this study fall within the range of 6.0% to 28.0% reported in literature (Cloete et al., 2007; Van Wyk et al., 2008; Matebesi et al., 2009; Olivier, 2014). In this study there was no specific trend with age, regarding the coefficient of variation for both ewes and rams. A decreasing CV with an increase in age was reported in literature (Cloete et al., 2007; Van Wyk et al., 2008; Matebesi et al., 2009; Olivier, 2014). The limited data of various body weights (W6, W8, W12, AW5, AW6 and AW7) might have influenced the trend.

Regarding the non-genetic effects included in this study, the year/season of birth had a significant effect on birth weight. Similar results were reported in literature (Thiruvenkadan et al., 2008; Bely & Haile, 2009; Thiruvenkadan et al., 2009). The significant influence of sex on the weight of lambs in this study, where male lambs were heavier than the females, also corresponded with reports in literature (Van Wyk et al., 1993; Snyman et al., 1995a; Thiruvenkadan et al., 2008). Van Wyk et al. (1993) and Qwabe (2011) reported that the age of the dam had a significant influence on early growth traits as older ewes gave birth to lambs that are heavier than lambs of younger ewes. Corresponding results were obtained in this study.

5.3 Genetic parameter estimates using linear models

Genetic parameters were estimated with the most suitable model obtained for each trait under univariate analysis. A combination of LogL, AIC and BIC information criteria were used to determine the most suitable model for each trait. As AIC and BIC included the number of parameters in the model, and BIC furthermore included the number of observations in the data set, these two criteria improved the accuracy of determining the most suitable model. The models with the highest LogL and lowest AIC and BIC values were selected. For BW to W15, selecting the most suitable model was straightforward. However, choosing the best model for some of the adult body weights was more difficult. For 3-year (AW3) and 5-year (AW5) adult body weights there was no difference between Model 2 and Model 3, either in information criteria of genetic parameters. With both models, the maternal component had a 0.000 variance. Both these models were better than Model 1. Model 3 was chosen for further analyses and discussion of variances and genetic parameters.

5.3.1 Birth weight

In previously published literature h^2_a values estimated for birth weight with linear animal models for Merino sheep ranged from 0.05 to 0.35 (Lewer et al., 1994; Mortimer & Atkins, 1995; Vaez Torshizi et al., 1996; Analla & Serradilla, 1998; Wuliji et al., 2001; Duguma et al., 2002b; Cloete et al., 2003; Safari et al., 2007a). The h^2_a estimate of 0.20 obtained in this study falls within the range of 0.04 to 0.45 (Safari et al., 2005; Safari et al., 2007a; Ceyhan et al., 2009; Cloete et al. 2009; Jafari & Hashemi, 2014) reported in literature for all wool types of sheep breeds.

The h^2_m of 0.11 estimated for birth weight in this study is lower than the range of 0.28 to 0.37 reported in literature (Mortimer & Atkins, 1998; Vaez Torshizi et al., 1996; Analla & Serradilla, 1998; Wuliji et al., 2001; Duguma et al., 2002b; Cloete et al., 2003; Safari et al., 2007). Olivier (2014) reported a value of 0.21 for birth weight in Merino sheep estimated with linear animal models.

The c^2_{mpe} estimated for birth weight (0.12) was within the range of 0.00 to 0.17 reported in the literature for Merino sheep (Mortimer & Atkins, 1998, Vaez Torshizi et al., 1996, Analla & Serradilla, 1998; Duguma et al., 2002b; Cloete et al., 2003b). Olivier et al. (2014) estimated h^2_a, h^2_m and c^2_{mpe} of 0.21, 0.21 and 0.14 respectively with a linear animal model for the Cradock fine wool Merino stud. The r_{am} for birth weight in this study was lower than the value of -0.46 reported by Olivier (2014), but falls within the range reported in literature of -0.40 to -0.15 (Mortimer & Atkins, 1995; Vaez Torshizi et al., 1996; Analla & Serradilla, 1998; Duguma et al., 2002b) on Merino sheep.

5.3.2 Body weight at 42 days of age

The h^2_a estimate of W42 (pre-weaning) of 0.42 estimated in this study is above the range reported in the literature for Merino pre-weaning weights (2 to 5 months of age), which ranged from 0.08 to 0.37 (Lewer et al., 1994; Swan & Hickson, 1994; Mortimer & Atkins, 1995; Vaez Torshizi et al., 1996; Analla & Serradilla, 1998; Greeff & Karlsson, 1998; Nagy et al., 1999).

The h^2_m of 0.15 estimated for W42 in this study falls within the range (0.11 to 0.38) reported in literature (Swan & Hickson, 1994; Mortimer & Atkins, 1995; Vaez Torshizi et al., 1996; Analla & Serradilla, 1998; Olivier, 2014). The literature c^2_{mpe} values ranged from 0.01 to 0.07 (Swan & Hickson, 1994; Mortimer & Atkins, 1995; Vaez Torshizi et al., 1996; Analla & Serradilla, 1998; Olivier, 2014). However, the estimate obtained in this study was slightly higher at 0.10. The relatively high values obtained for h^2_a and c^2_{mpe} in this study might have been influenced by the lower number of records available for W42.

5.3.3 Weaning weight

Estimates for heritability reported in the literature for weaning weight for Merino sheep ranged from 0.06 to 0.34 (Snyman et al., 1996; Analla & Serradilla, 1998; Cloete et al., 2001; Wuliji et al., 2001; Duguma et al., 2002b; Cloete et al., 2003; Safari et al., 2007a; Olivier, 2014). The h^2_a for weaning weight estimated in this study falls within this range. The h^2_m estimated in this study was comparable to the lower end of the values reported for weaning weight in Merino sheep that ranged from 0.05 to 0.30 (Snyman et al., 1996; Analla & Serradilla, 1998; Cloete et al., 2001; Wuliji et al., 2001; Duguma et al., 2002b; Cloete et al., 2003; Safari et al., 2007a; Olivier, 2014). The estimate for c^2_{mpe} of weaning weight in this study of 0.09 is comparable to the values reported in the literature that ranged from 0.05 to 0.08 (Snyman et al., 1996; Duguma et al., 2002b; Cloete et al., 2003; Safari et al., 2007a; Olivier, 2014). Although weaning weight is lowly heritable and is influenced by maternal effects it can be considered as a selection criterion for growth in Merino sheep and can result in a shorter sheep production cycle.

5.3.4 Body weight at 6 and 8 months of age

The h^2_a (0.54) and h^2_m (0.28) estimated for W6 in this study were higher than the estimates reported in literature which ranged from 0.18 to 0.44 and 0.04 to 0.12, respectively (Snyman et al., 1996; Wuliji et al., 2001; Ingham et al., 2003; Olivier, 2014) on Merino sheep. The values estimated for h^2_a, h^2_m and c^2_{mpe} for W8 were 0.43, 0.18 and 0.21 respectively with a r_{am} of -0.93. Limited results are available for this age in previously published literature. Snyman et al. (1995) reported values for h^2_a (0.59) and h^2_m (0.10) on W8 of Afrino sheep.

The maternal variance in this study did not show a specific trend, which is not in line with the normal maternal variance trend of decreasing with an increase in age. The limited number of records for W6 and W8 might have influenced this result. This could also be the reason why no definite trend in maternal heritability values was found, when taking into account the relatively high maternal heritabilities estimated for W6 (0.28 ± 0.17) and W8 (0.18 ± 0.08). Snyman et al. (1995) reported a trend of decreasing maternal heritability with an increase in age for body weight in Afrino sheep

The high parameter values obtained for W6 and W8 in this study is in contrast with many literature reports, where the maternal effect tended to be higher for birth weight and weaning weight than weights recorded at a later stage in life (Safari *et al.*, 2007b; Olivier, 2014), which might have been influenced by limited and incompleteness of the data for W6 and W8.

5.3.5 Body weight at 12 to 16 months of age

The range of h^2_a estimates reported in the literature for body weights between 12 to 16 months of age for Merino sheep were 0.13 to 0.61 (Mortimer & Atkins, 1995; Woolaston et al., 1995; Brash et al., 1997; Greeff & Karlsson, 1999; Nagy et al., 1999; Rose &Pepper, 1999; Brown et al., 2005; Brown et al., 2010). The heritability values estimated in this study for W12 and W15 were within the reported range at 0.37 and 0.51 respectively.

In this study the h^2_m estimate for W15 was 0.08. This falls within the range of h^2_m values (0.04 to 0.15) reported in literature (Vaez Torshizi et al., 1996; Ingham et al., 2003; Safari et al., 2005; Van Wyk et al., 2008; Matebesi et al., 2009a, Olivier, 2014). Snyman (1996) reported a lower value of 0.04 for body weight at 18 months in Merino sheep.

5.3.6 Adult body weights

The h^2_a estimates for all the adult weights in this study ranged from 0.31 to 0.43 and fell within the range of 0.31 to 0.57 (Fogarty, 1995; Safari et al., 2005) reported in literature on Merino sheep.

The positive genetic correlation between weights at 12 to 15 months with adult weights is high. This indicates that selection for 14 months body weight will directly increase adult weight, which will lead to a higher maintenance requirement of the adult ewes and as a result less animals could be kept on the farm. Selection for increased 14 months body weight will also increase birth weight, which could lead to dystocia if birth weights get too heavy. The simultaneous increase in weaning and 6- to 8-month body weight, however, will mean that the lambs will reach market stage at an earlier age. This will have an overall positive effect on the enterprise, as the earlier lambs are marketed, the more ewes could be kept on the farm.

5.4 Genetic parameters estimated using a repeatability model

As with the univariate models, a combination of LogL, AIC and BIC information criteria were used to determine the most suitable model for each trait. The models with the highest LogL and lowest AIC and BIC values were selected. In this study the repeatability model without fitting splines was the most suitable model for estimating the (co)variance components and genetic parameters for body weight. The repeatability of body weight from birth weight to 68 months of age estimated with the most suitable model (M3) was 0.37, which is higher than the range of 0.19 to 0.26 reported in a study on three newly developed Canadian breeds (Hansen & Shrestha, 2002) and on the Cradock fine wool Merino stud (Olivier, 2014). The value in this study was however, lower than the range of 0.46 to 0.75 reported in several other studies (Morley, 1951; Katada & Takeda., 1959; Young et al., 1960; Beattie, 1961; Turner & Young, 1969; Mortimer, 1987; Said et al., 1999; Hatcher & Atkins, 2000; Cloete et al., 2004; Hatcher et al., 2005; Wolc et al., 2011; Boujenane et al., 2013).

The repeatability for body weight in this study is moderate and can be an indicator of the accuracy of the estimates of genetic parameters for use in genetic improvement programs. Birwe (2006) stated that if the repeatability estimate is high, it implies the variability in measurements is mostly genetically influenced while low estimates indicate high environmental influence on the measurements.

Direct heritability for body weights using the most suitable repeatability model for this study was 0.26 ± 0.06. Direct heritability estimated on Cradock Fine Wool Merino stud by (Olivier, 2014) was low at 0.17. Maternal heritability calculated in this study was 0.08 ± 0.08 which is high compared to 0.02 ± 0.02 for the Cradock Fine Wool Merino stud (Olivier, 2014). No other references were found with the same data structure where repeatability and heritability were estimated with a repeatability model as in the current study for sheep.

5.5 Random regression model estimations

Random regression models were fitted including direct as well maternal effects, including splines or omitting splines, and either fitting one or two age classes to account for heterogeneous residual variance. From the results of the random regression analyses it was obvious that the direct additive and phenotypic variances were too high. Residual variance on the other hand was comparable to those obtained with univariate and repeatability models, and also comparable to WW under the multivariate model in this study. Furthermore, the large increase in maternal variance with age was contradictory to most previously reported literature. The reason for these unexpected estimations is not known at this stage. Further work on the model specification will be performed to try and correct the problem.

However, the general trend of the results from this study were similar to results obtained on the Cradock Fine Wool Merino stud (Olivier, 2014) and other studies by Lewis & Brotherstone (2002), Fischer et al. (2004), Molina et al. (2007), Kariuki et al. (2010) and Wolc et al. (2011) of h^2_a increasing with age. In this study the h^2_a increased until 20 months of age, after which it remained constant. Olivier (2014) emphasized that the higher h^2_a in body weight at older ages might be the result of increased expression of genes with direct additive effects which is accompanied by a decline in the variance of the other random effects at later ages (Fischer et al., 2004; Kesbi et al., 2008). This would mean that the direct additive genetic variance becomes a larger portion of the phenotypic variance resulting in a higher h^2_a.

5.6 Estimated breeding values and model selection

The estimated breeding values (EBVs) for Merino sheep obtained with different statistical procedures for body weights were compared in this study. These EBVs showed large variation for the traits included (WW, W15 and AW3). Effectiveness of different statistical procedures was judged by using various criteria like Spearman rank correlations, number and proportion of common animals in the Top 10% and Top 1% lists. For judging criteria the Spearman ranking correlation was used to estimate the correlations between the ranks of the estimated breeding values for WW, W15 and AW3 where the statistical procedure yielding the highest correlation was chosen. Regarding the number and proportion of common animals in the Top 10% and Top 1% lists, the procedure chosen was the one that gave the highest percentage of common animals for EBVs estimated for weaning weight, 15-month body weight and 3-year body weight. In this study, the multivariate model was considered as the most efficient method as it yielded the most accurate EBVs followed by the univariate and repeatability models respectively.

In the study by Jeichitra et al. (2015) on Mecheri sheep, EBVs for body weight (birth, 3, 6, 9 and 12 months of age) obtained with least-squares (LS), best linear unbiased prediction (BLUP) and derivative free restricted maximum likelihood (DfReml) were compared. The DfReml method seemed to be the most efficient (lower error variance) and accurate (higher coefficient of determination) method. Krejcova et al. (2007) obtained EBVs for average daily gain on Czech Pied bulls (Simmental type) using random regression models with Legendre polynomials of the 2nd, 3rd and 4th degree (RR2, RR3 and RR4) and compared these with a multi-trait model (MTM) used as a reference model. The authors reported that RR3 and RR4 had higher rank correlations with MTM in comparison to model RR2 and the number of common animals in the 1% and 10% top-lists showed that models RR3 and RR4 are to be preferred over RR2 when it comes to the estimation of breeding values. Literature reports on comparison of EBVs of body weights with different statistical models are limited.

5.7 Conclusion

Comparison of estimated breeding values for body weights obtained with univariate, multivariate and repeatability models revealed that the multivariate model was the most efficient method. For the implementation of genomic selection, the most accurate estimated breeding values should be estimated with multivariate models. Estimated breeding values will be obtained from weaning weight where direct, maternal and maternal permanent environment effects will be included. The direct and maternal effects and genetic covariance between the animal effects will be included for 15 month body weight, while for 3-year body weight only direct and maternal effects will be included.

6. CONCLUSIONS

This is the first study of its kind on South African Merino sheep where estimated breeding values (EBVs) for body weights obtained with different statistical procedures were compared. It is important that EBVs for performance traits should be estimated as accurately as possible. This can only be achieved by fitting the most appropriate model, which accounts for all known non-genetic effects, as well as correctly partitioning the genetic variance into its various sources.

The direct heritability of body weight increased with an increase in age until 15 months of age, where after it reached a plateau. Maternal heritabilities were generally low, while the permanent environmental effects were high. The genetic correlations between the animal effects were negative for those weights for which this effect was included. The limited records available for 6- and 8-month body weights probably caused the high standard errors for the parameters estimated for these weights. The environmental correlations from BW up to W15 tended to decrease with an increase in age.

The repeatability model including direct and maternal genetic effects, without splines, was the most appropriate repeatability model for estimation of genetic parameters for body weight. There was a slight increase on the values when splines were fitted as compared to when they were not.

Random regression models were fitted including direct as well as maternal effects, including splines or omitting splines, and either fitting one or two age classes to account for heterogeneous residual variance. From the results of the random regression analyses it was obvious that the direct additive and phenotypic variances were too high. Residual variance on the other hand was comparable to those obtained with univariate and repeatability models, and also comparable to WW under the multivariate model in this study. Furthermore, the large increase in maternal variance with age was contradictory to most previously reported literature. The reason for these unexpected estimations is not known at this stage.

The accuracy of the estimated breeding values were determined using Spearman rank correlations, number and proportion of common animals in the Top 10% and Top 1% lists. Very high Spearman rank correlations were estimated among EBVs of the weights included in the multivariate model. Low correlations were obtained between the rankings of the repeatability model EBVs and the other EBVs. The highest number and proportion of common animals in the Top 1% lists were obtained for WW and W15 between the uni- and multivariate models. The most complete data sets were available for these two weights, which could have contributed to more accurate EBVs being estimated for these weights.

It is recommended that the data to be used in a study like this must be as comprehensive and complete as possible. Proof of the limitations encountered when using incomplete data sets, is evident in the body weight at 6 and 8 months of age where estimates obtained were too high when compared to reported literature values and these also did not show any specific trend. It was also evident with the adult body weights where the bivariate models did not converge when maternal effects were included, most probably also due to a limited number of records. This indicates that data must be as complete as possible, as genomic selection is dependent on accurate estimates and large numbers of phenotypic records should be available.

The comparison of estimated breeding values for body weights obtained with univariate, multivariate and repeatability models revealed that the multivariate model was the most efficient method due to the high accuracies obtained with this procedure.

These results will be implemented when estimating breeding values for body weights for the animals in the Merino reference population during the development phase of a suitable SNP key (prediction equation) to be used in genomic selection for body weight in South African Merino sheep. Furthermore, the EBV estimated for the animals for body weight in this study will be used to identify suitable animals for genotyping to be used in a genome wide association study, involving the identification of possible genetic markers associated with reproduction and body weight in different sheep flocks.

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