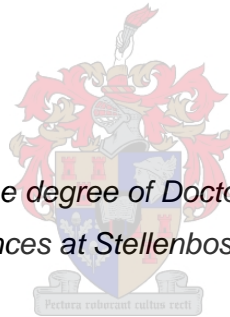# THE EVALUATION OF A SOUTH AFRICAN FINE WOOL GENETIC RESOURCE FLOCK

by

W.J. Olivier

Dissertation presented for the degree of Doctor of Philosophy in the Faculty of AgriSciences at Stellenbosch University

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April 2014

DECLARATION

By submitting this dissertation electronically, I declare that the entirety of the work contained therein is my own, original work, that I am the sole author thereof (save to the extent explicitly otherwise stated), that reproduction and publication thereof by Stellenbosch University will not infringe any third party rights and that I have not previously in its entirety or in part submitted it for obtaining any qualification.

Date: April 2014

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WJ Olivier

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PREFACE

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Olivier, W.J., Cloete, S.W.P., Snyman, M.A. & Van Wyk, J.B., 2014. Genetic relationships among lamb survival, birth coat score, birth, pre-weaning and weaning weight in a genetic fine wool Merino stud.In progress.

Olivier, W.J., Cloete, S.W.P., Snyman, M.A. & Van Wyk, J.B., 2014. Genetic parameters for subjective traits of a genetic fine wool Merino stud and correlations with production and reproduction traits.In progress.

Olivier, W.J., Cloete, S.W.P., Snyman, M.A., Van Wyk, J.B. & Gilmour, A.R., 2014.Genetic relationships among production traits measured at different ages in a fine wool Merino stud. In progress.

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Congress contributions:

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Olivier, W.J., Olivier, J.J., Cloete, S.W.P. & Van Wyk, J.B., 2006. Genetic analysis of the Cradock fine wool Merino stud. Proc. 8th WCGALP, Belo Horizonte, 13 -18 August.

Olivier, W.J., Olivier, J.J. & Greyling, A.C., 2008.Quantifying the relationship between birth coat score and wool traits in Merino sheep. 10th World Congress on Animal Production, Cape Town.

Olivier, W.J., 2006. Evaluation of the effect of selection for decreased fibre diameter on production and subjective traits. Proc. 42nd SASAS Congress, Bloemfontein, 3-6 April, 136.

Olivier, W.J., Cloete, S.W.P., Van Wyk, J.B. & Gilmour, A.R., 2011. Genetic relations among fibre diameter measures at different ages in a fine wool Merino stud. Proc. 44th SASAS Congress, Stellenbosch, 11 to 14 July.

Olivier, W.J. & Olivier, J.J., 2006. Evaluation of genetic fine wool animals under natural conditions in non-traditional fine wool producing areas, Proc. 42nd SASAS Congress, Bloemfontein, 3-6 April, 97.

Olivier, W.J., Olivier, J.J. & Greyling, A.C., 2006.Correlations of subjectively assessed traits of fine wool Merino sheep with production and reproduction traits. Proc. 42nd SASAS Congress, Bloemfontein, 3 - 6 April, 98.

Olivier, W.J., Snyman, M.A., Olivier, J.J. & Greyling, A.C., 2004.Genetic analysis of the production traits of the Cradock Fine Wool Merino Stud. Proc 2nd Joint Congress GSSA / SASAS, 103.

Olivier, W.J, Snyman, M.A., Olivier, J.J. & Greyling, A.C., 2004.Production and reproduction of adult ewes of the Cradock Fine Wool Merino Stud. Proc 2nd Joint Congress GSSA / SASAS, 102.

Olivier, W.J. & Greyling, A.C., 2009. Is selection for decreased fibre diameter in a Merino flock with overstrong wool viable? Proc. 43rd Cong. S. Afr. Soc. Anim. Sci. Alpine Heath 28 to 30 July 2009, 84.

Olivier, W.J., Cloete, S.W.P., Snyman, M.A. & Van Wyk, J.B., 2013. Genotype by environment interaction for fleece characteristics in Merino sheep. Proc. 46th Cong. S. Afr. Soc. Anim. Sci. Bloemfontein 23 to 26 June.

Olivier, W.J., Cloete, S.W.P., Van Wyk, J.B. & Gilmour, A.R., 2013. Genetic relationships among body weight, fleece weight and staple length measured at different ages in a fine wool Merino stud. Proc. 46th Cong. S. Afr. Soc. Anim. Sci. Bloemfontein 23 to 26 June.

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ABSTRACT

This study set out to determine (co)variance components for the important production, reproduction and conformation traits of a South African fine wool resource flock that was established at the request of the South African wool industry. A secondary aim was to assess progeny of these animals under pastoral conditions in areas where the production of fine wool is uncommon. The Cradock fine wool Merino stud was established in 1988 with ewes bought from producers with the finest clips in South Africa. Data collected from 1988 to 2010 were used to estimate the (co)variances for the genetic fine wool resource flock. The quantification of the interdependencies of fibre diameter (FD) with production, reproduction and subjective traits were the main objective of this study. It is evident from the results of this study that FD is a highly heritable (0.63 ± 0.03) trait, which can lead to marked genetic progress provided that there are adequate levels of phenotypic variation available during selection. Fibre diameter was unfavourably correlated with body weight (0.30 ± 0.05), clean fleece weight (0.24 ± 0.05) and reproduction (0.59 ± 0.18), which implies that selection for reduced FD can have a detrimental effect on all these traits. Despite these unfavourable genetic correlations genetic gain in the other economical important traits was achievable in the stud (-0.129 ± 0.033). These results were supported by the results obtained during the evaluation of progeny of this stud under pastoral conditions where the production and reproduction of the fine wool animals were comparable with medium wool animals. It can therefore be concluded that selection for reduced FD can be practiced without detrimental effects on the economically important traits and subsequently the profitability of the sheep enterprise, as long as breeders have a reasonable selection objective based on economic considerations.

OPSOMMING

Hierdie studie het dit ten doel gehad om (ko)variansie komponente vir die belangrike produksie, reproduksie en subjektiewe eienskappe in 'n Suid-Afrikaanse fyn wol hulpbronkudde, wat gevestig is op versoek van die Suid-Afrikaanse wolbedryf te bepaal. 'n Sekondêre doel was om die nageslag van hierdie diere onder veldtoestande te evalueer in gebiede waar die produksie van fynwol ongewoon is. Die Cradock fynwol Merino stoet is in 1988 gestig met die aankoop van ooie van produsente met die fynste skeersels in Suid-Afrika. Data wat ingesamel is vanaf 1988 tot 2010 is gebruik in die bepaling van (ko)variansie komponente vir hierdie genetiese fynwolkudde. Die kwatifisering van die interafhanklikheid van veseldikte (VD) met produksie, reproduksie en subjektiewe eienskappe was die hoofdoel van die studie. Dit is duidelik uit die resultate van die studie dat VD `n hoogs oorerflike (0.63 ± 0.03) eienskap is, wat tot vinnige vordering in VD kan lei indien genoegsame fenotipiese variasie beskikbaar is tydens seleksie. Veseldikte is ongunstig gekorreleer met liggaamsgewig (0.30 ± 0.05), skoonvaggewig (0.24 ± 0.05) en reproduksie (0.59 ± 0.18), wat beteken dat seleksie vir 'n verlaagde VD nadelige vordering in hierdie eienskappe tot gevolg kan hê. Ten spyte van hierdie ongunstige genetiese korrelasies was die genetiese vordering in die ekonomies belangrike eienskappe haalbaar in die kudde wat ondersoek is (-0.129 ± 0.033). Die laasgenoemde resultate word ondersteun deur die bevindinge dat die nageslag van hierdie stoet se produksie en reproduksie ooreengestem het met medium wol diere onder veldtoestande. Die gevolgtrekking wat gemaak kan word uit die studie is dat VD verlaag kan word sonder nadelige gevolge in die ekonomies belangrike eienskappe, asook die van `n skaapboerdery onderneming. Om dit te vermag moet telers `n aanvaarbare benadering tot seleksie, gegrond op ekonomiese beginsels, volg.

CHAPTER 1. GENERAL INTRODUCTION

Over the past two decades there was an increased consumer demand for fine-gauge and lightweight garments that can be worn across seasons and close to the skin. This demand created an opportunity for wool producers to produce such apparel wools (Atkins, 1995; Hatcher et al., 2010). Furthermore, the inherent natural moisture and thermal management attributes of wool is a significant advantage over cotton and synthetic fibres (Hatcher et al., 2010). However, wool as an apparel fibre was constrained by consumer resistance resulting from a wearer discomfort stemming from the prickle effect of wool garments. It is commonly acknowledged that more than 5% fibres above 30 μm results in an increase in the prickle effect (Gamsworthy et al., 1988).

According to Purvis (1995) the greater awareness by the breeders of wool sheep of the preferences and requirements of consumers for lightweight garments led to a new phase in genetic improvement programs for fine wool animals. The latter author further stated that these factors were encouraging breeders to base selection on economically important traits and resulted in a worldwide tendency to produce finer wool (below 19 μm).

This tendency, assisted by the price premium paid for finer fibres, has led to an increase in the number of breeders that diversified into the production of fine wool. However, Merinos in South Africa are not solely wool producers, but they also produce meat. Excellence in both wool and meat production is therefore required to ensure that this farming enterprise stays profitable. The growth and reproduction performance of sheep flocks generate 70% of the income on sheep farms in South Africa (Olivier, 1999). Although only 30% of income is derived from wool, selection to improve wool production still plays a major role on Merino farms.

The objective of wool producers between 1950 and 1960 was to increase the quantity of wool produced annually (Marx, 1981). This resulted in the reduction of the proportion of finer wool (<20 μm) from 69% in 1951/1955 to only 4% in 1976/1980. However, in the late 1980s there was an increased demand for finer wool in South Africa, as well as in Australia (Swan et al., 2008). This shift was driven by substantial price premiums for finer wool during this period. Therefore, the emphasis in wool production shifted towards the production of fine wool, rather than just the quantity of wool. The growing interest in fine wool production in Australia (Swan et al., 2008) and the price premiums for finer wool (Purvis & Piper, 1993; Cottle, 1994) concurred with developments in South Africa during the same period.

However, at this stage, there was little information available with regard to the production of fine wool (Olivier et al., 1989; Purvis & Piper, 1993; Swan et al., 2008) in South Africa and Australia. Furthermore, Olivier et al. (1989) stated that the Australian wool industry was better placed to react to the increased demand for fine wool as they had higher numbers of sheep, particularly genetic fine wool animals. It was therefore of the utmost importance that the situation was rectified as quickly as possible in South Africa. The wool industry of South Africa therefore requested the Grootfontein Agricultural Development Institute

to establish a genetic fine wool Merino flock. The establishment of this flock coincided with the establishment of the CSIRO fine wool project in Australia (Swan et al., 2008).

The change over years in the proportion wool finer than 20 μm in the South African clip is illustrated in Figure 1.1. Data from the weekly sale reports of Cape Wools pertaining to fibre diameter and quantity of wool produced were used to calculate the five-year averages from 1981 onwards. The data from 1951 to 1980 were obtained from Marx (1981) because the raw data were not available. The marked decrease in the proportion of fine wool from 69% in 1951/55 to 4% in 1976/80 is clearly visible in Figure 1.1. It must be noted that the response to the increased demand for the finer types of wool was initially slow due to the unavailability of genetic fine wool Merinos during the late 1980s and early 1990s (Olivier et al., 1989). The marked increase in the proportion of fine wool can directly be linked to the increase in available genetic fine wool animals. Genetic material from the Cradock fine wool Merino stud, as well as studs from breeders that had bred fine wool for generations had been widely used in the industry. The progeny of these sires were instrumental in the upswing in fine wool production from 1996 onwards.
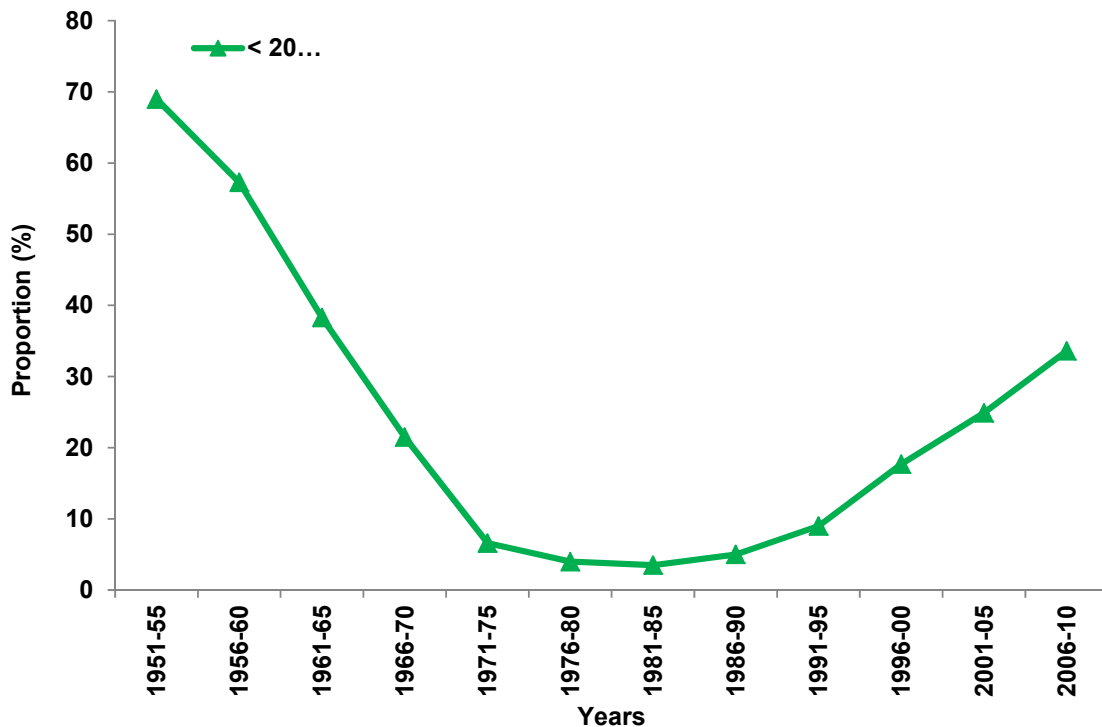
Figure 1.1 The proportion of wool finer than 20 μm in the South African clip from 1951 to 2010

Purvis (1995) and Swan et al. (2008) suggested that it is important to compare the inheritance and genetic relationships of fine wool Merino sheep with other Merino strains because this information is important when designing breeding programs and fine wool animals will be compared to animals from other strains in across-flock genetic evaluations to estimate breeding values in national improvement schemes (Purvis, 1995; Swan et al., 2008). The estimation of across-flock breeding values are important to Merino breeders as the application of these values during selection will increase the genetic gains in

economic merit of the traits included in the selection objective (Purvis & Piper, 1993).The same reasons could apply to the wool industry of South Africa.

Several authors in the past have assessed different Merino strains according to their production and reproduction potential. Fine wool animals consistently produced less but finer wool compared to the medium wool strains (Short & Carter, 1955; Dunlop, 1962; 1963; Jackson & Roberts, 1970;; Mortimer & Atkins, 1989; McGuirk, 2009), while there was also suggestions that reproduction of fine wool animals was poorer compared to medium wool strains (Mortimer et al., 1985; Kleemann et al., 2006). Moreover, Olivier et al. (1989) stated that there was a lack of information with regard to the production and reproduction potential of South African fine wool Merinos. Therefore it is of utmost importance to assess fine wool animals and to compare them to other Merino strains under South African conditions.

The shift towards fine wool production resulted in some breeders overemphasising fibre diameter in their selection programs to capitalise on the higher fine wool prices. In some cases fibre diameter was the only selection criterion and selection was practise without considering the indirect selection response in other traits of economic importance.

The existence of genetic relationships (correlations) between different traits implies that the expression of traits is interdependent. The indirect genetic responses in correlated traits depend on the nature and magnitude of the correlation between traits. These correlations can be either favourable or unfavourable. If a genetic correlation between two traits is favourable, the indirect selection response would be in the desired direction. However, it is unfavourable correlations that create the problems for animal scientists and the breeding industry as it could lead to undesirable changes in economically important traits.

As a backdrop to the thesis, a summary on the values reported in the literature on direct (h^2_a) and maternal (h^2_m) heritability, covariance between animal effects (r_{am}), animal (c^2_{anim}) and maternal (c^2_{mpe}) permanent environmental effects as well as litter effect (l^2) for body weight, objectively measure wool traits, reproduction traits and subjectively measured wool and conformation traits in sheep are presented in Tables 1.1 to 1.3. The genetic (r_g), phenotypic (r_p), maternal (r_m) and environmental (r_e) correlations (± s.e.) among objective and subjective wool and conformation traits reported in the literature are summarised in Tables 1.4 and 1.5.

Therefore, the planning and development of a breeding plan should be reasonable and include all traits of economic importance in a selection index. A specific trait can either be included in the selection objective or it can be monitored to prevent undesirable changes. It is important to quantify the inheritance and interdependencies of the economically important traits for South African fine wool Merino sheep under South African conditions to develop breeding plans. The overall selection progress may be compromised if these relationships are not considered when breeding strategies are defined. Purvis (1995) accordingly suggested that the context of the current enterprise cost and returns, as well as the long term production potential must be considered during strategies to genetically improve fine wool animals.

Table 1.1 Summary of literature values on direct (h^2_a) and maternal (h^2_m) heritability, covariance between animal effects (r_{am}), animal (c^2_{anim}) and maternal (c^2_{mpe}) permanent environmental effects as well as litter effect (l^2) for body weight and objectively measure wool traits in sheep

Trait	Breed	Age (months)	h^2_a ± s.e.	h^2_m ± s.e.	c^2_{mpe} ± s.e.	c^2_{pe} ± s.e.	l^2 ± s.e.	r_{am} ± s.e.	Reference
Greasy fleece weight									
	Fine wool Merino	10	0.40 ± 0.03	0.17 ± 0.03	-	-	-	-0.48 ± 0.10	(Asadi Zozi et al., 2005)
	Merino	16-18	0.35 ± 0.02	0.13 ± 0.01	-	-	-	-	(Brown et al., 2005)
	Rambouilet	12	0.08 ± 0.04	-	-	-	-	-	(Hanford et al., 2005)
	Turkish Merino	12	0.37 ± 0.02	-	-	-	-	-	(Ozcan et al., 2005)
	Wool breeds		0.38 ± 0.03	0.08 ± 0.01	0.15 ± 0.09	-	-	-	(Safari et al., 2005)
	Dual purpose		0.39 ± 0.02	0.02 ± 0.01	0.11 ± 0.02	-	-	-	(Safari et al., 2005)
	Menz sheep	12	0.39 ± 0.02	-	-	-	-	-	(Gizaw et al., 2006)
	Polypay	12	0.68 ± 0.03	-	-	-	-	-	(Hanford et al., 2006)
	Merino	14-17	0.46 ± 0.01	0.08 ± 0.01	0.00	0.03 ± 0.01	0.08 ± 0.01	-0.60 ± 0.02	(Safari et al., 2007b)
	Merino	15	0.36 ± 0.05	0.09 ± 0.03	0.05 ± 0.02			-0.65 ± 0.10	(Matebesi et al., 2009a)
Clean fleece weight									
	Fine wool Merino	10	0.36 ± 0.03	0.15 ± 0.03	-	-	-	-0.47 ± 0.10	(Asadi Zozi et al., 2005)
	Merino	18	0.28 ± 0.05	0.08 ± 0.02	-	-	-	-	(Cloete et al., 2005)
	Wool Breeds		0.36 ± 0.02	0.06 ± 0.01	0.21 ± 0.11	-	-	-	(Safari et al., 2005)
	Dual purpose		0.51 ± 0.07	-	-	-	-	-	(Safari et al., 2005)
	Dohne Merino	12-14	0.24 ± 0.01	-	-	-	-	-	(Swanepoel et al., 2005)
	Merino	14-18	0.44 ± 0.07	-	-	0.24 ± 0.07	-	-	(Naidoo & Cloete, 2006)
	Merino	15	0.54 ± 0.04			-	-	-	(Olivier et al., 2006a)
	Merino	15	0.40 ± 0.05	0.10 ± 0.03	0.05 ± 0.02	-	-	-0.70 ± 0.09	(Matebesi et al., 2009a)
Birth coat score									
	Merino		0.80 ± 0.10	-	-	-	-	-	(Morley (1955a)
	Merino		0.64	-	-	-	-	-	(Gregory (1982)
	Merino		0.66	-	-	-	-	-	(Ponzoni et al. (1996)
	Merino		0.70 ± 0.05	-	0.04 ± 0.02	-	-	-	(Cloete et al. (2003b)
	Merino		0.65 ± 0.02	-	-	-	-	-	(Kemper at al. (2003)
Birth weight									
	Merino		0.32 ± 0.08	-	-	-	-	-	(Lewer et al., 1994)
	Merino		0.23 ± 0.02	0.14 ± 0.02	0.12 ± 0.01	-	-	-0.40	(Mortimer & Atkins, 1995)
	Merino		0.29 ± 0.04	0.29 ± 0.09	0.00 ± 0.06	-	-	-0.42	(Vaez Torshizi et al., 1996)
	Merino		0.05 ± 0.04	0.29 ± 0.01	0.11 ± 0.03	-	-	-0.21	(Analla & Serradilla, 1998)
	Merino		0.35 ± 0.08	-	-	-	-	-	(Wuliji et al., 2001)
	Merino		0.19	0.25	0.10	-	-	-0.22	(Duguma et al., 2002b)
	Merino		0.18 ± 0.01	0.19 ± 0.01	0.07 ± 0.01	-	0.33 ± 0.01	-0.15 ± 0.01	(Safari et al., 2007b)

Table 1.1 Continue

Trait	Breed	Age (months)	h^2_a ± s.e.	h^2_m ± s.e.	c^2_{mpe} ± s.e.	c^2_{pe} ± s.e.	l^2 ± s.e.	r_{am} ± s.e.	Reference
Pre-weaning and weaning weight									
	Merino	3	0.37 ± 0.08	-	-	-	-	-	(Lewer et al., 1994)
	Merino	4-5	0.27 ± 0.03	0.11 ± 0.01	0.07 0.01	-	-	-0.20	(Mortimer & Atkins, 1995)
	Merino	3	0.27 ± 0.04	0.38 ± 0.07	0.03 ± 0.06	-	-	-0.60	(Vaez Torshizi et al., 1996)
	Merino	2	0.08 ± 0.04	0.16 ± 0.03	0.03 ± 0.02	-	-	-0.01	(Annalla & Serradilla, 1998)
	Merino	3	0.13 ± 0.05	0.04 ± 0.03	0.06 ± 0.02	-	-	0.07	(Annalla & Serradilla, 1998)
	Dohne Merino	3	0.06 ± 0.04	-	0.21 ± 0.04	-	-	-	(Cloete et al., 1998b)
	Merino	3	0.34 ± 0.08	0.16 ± 0.04	-	-	-	-	(Wuliji et al., 2001)
6 Month body weight									
	Merino	6	0.18 ± 0.04	0.10 ± 0.04	-	-	-	0.86 ± 0.30	(Snyman et al., 1996)
	Merino	6	0.44 ± 0.09	0.08 ± 0.04	-	-	-	-	(Wuliji et al., 2001)
	Merino	5	0.28 ± 0.08	0.04 ± 0.04	-	-	-	-	(Ingham et al., 2003)
12 and 15 Month body weight									
	Merino	15	0.39 ± 0.04	0.04 ± 0.03	0.00 ± 0.03	-	-	0.42	(Mortimer & Atkins, 1995)
	Merino	13	0.25 ± 0.10	-	-	-	-	-	(Woolaston et al., 1995
	Merino	16	0.29 ± 0.05	0.02 ± 0.09	0.00 ± 0.06			1.00	(Vaez Torshizi et al., 1996
	Merino	16	0.33 ± 0.09	-	-	-	-	-	(Brash et al., 1997
	Merino	16	0.32 ± 0.05	-	-	-	-	-	(Greeff & Karlsson, 1999
	Merino	14	0.13 ± 0.01	-	-	-	-	-	(Nagy et al., 1999
	Merino	15	0.37 ± 0.10	-	-	-	-	-	(Rose & Pepper, 1999
	Merino	16	0.49 ± 0.12	0.06 ± 0.05	-	-	-	-	(Wuliji et al., 2001
	Merino	12	0.33 ± 0.15	-	-	-	-	-	(Brown et al., 2002a
	Merino	16	0.52 ± 0.05	-	-	-	-	-	(Duguma et al., 2002a
	Merino	12	0.35 ± 0.02	-	-	-	-	-	(Clarke et al., 2003)
	Merino	15	0.49 ± 0.02	-	-	-	-	-	(Clarke et al., 2003)
	Merino	15	0.36 ± 0.02	0.05 ± 0.01	-	-			(Brown et al., 2005)
	Merino	15	0.38 ± 0.01	0.03 ± 0.01	0.00	-	0.06 ± 0.01	0.25 ± 0.08	(Safari et al., 2007a)
	Merino	15	0.38 ± 0.05	-	-	-	-	-	(Cloete et al., 2006)
	Merino	15	0.13 ± 0.01	0.02 ± 0.01	0.04 ± 0.02	-	-	0.42 ± 0.014	(Van Wyk et al., 2008)
	Merino	15	0.38 ± 0.05	0.05 ± 0.02	-	-	-	-0.28 ± 0.12	(Matebesi et al., 2009a)
	Merino	15	0.61 ± 0.06		-	-	-		(Brown et al., 2010)
Clean yield									
	Merino	15	0.46 ± 0.11	-	-	-	-	-	(Lewer et al., 1994)
	Merino	16	0.34 ± 0.08	-	-	-	-	-	(Brash et al., 1997)
	Merino	17	0.68 ± 0.02	-	-	-	-	-	(Cloete et al., 1998a)
	Dohne Merino	11	0.66 ± 0.05	-	-	-	-	-	(Cloete et al., 1998a)
	Merino	16	0.63 ± 0.02	-	-	-	-	-	(Cloete et al., 2002a)
	Ultrafine Merino	17	0.34 ± 0.02	-	0.11 ± 0.01	-	-	-	(Sherlock et al., 2003)
	Merino	15	0.65 ± 0.03	-	-	-	-	-	(Matebesi et al., 2009a)

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Table 1.1 Continue

Trait	Breed	Age (months)	h^2_a ± s.e.	h^2_m ± s.e.	c^2_{mpe} ± s.e.	c^2_{pe} ± s.e.	l^2 ± s.e.	r_{am} ± s.e.	Reference
Fibre diameter									
	Merino	15	0.57	-	-	-	-	-	(Safari et al., 2005)
	Merino	15	0.68 ± 0.05	0.05 ± 0.02	-	-	-	-0.43 ± 0.11	(Matebesi et al., 2009a)
	Merino	16	0.62 ± 0.03.	0.01 ± 0.01	-	-	-	-	(Brown et al., 2010)
Staple length									
	Merino	15	0.46	-	-	-	-	-	(Safari et al., 2005)
	Merino	15	0.39 ± 0.08	-	-	-	-	-	(Cloete et al., 2006)
	Merino	15	0.37 ± 0.03	-	-	-	-	-	
Standard deviation of fibre diameter									
	Merino	16	0.58	-	-	-	-	-	(Ponzoni et al., 1995)
	Merino	10	0.35	-	-	-	-	-	(Swan et al., 1995)
	Merino	10	0.50 ± 0.03	-	-	-	-	-	(Li et al., 1999)
	Merino	16	0.57 ± 0.08	-	-	-	-	-	(Hill, 2001)
	Merino		0.61 ± 0.03	-	-	-	-	-	(Matebesi et al., 2009a)
Coefficient of variation of fibre diameter									
	Merino	16	0.61	-	-	-	-	-	(Ponzoni et al., 1995)
	Merino	10	0.33	-	-	-	-	-	(Swan et al., 1995)
	Merino	16	0.60 ± 0.08	-	-	-	-	-	(Hill, 2001)
	Merino	10	0.60 ± 0.06	-	-	-	-	-	(Wuliji et al., 2001)
	Merino	18	0.37 ± 0.03	0.00 ± 0.00	-	-	-	-	(Brown et al., 2002a)
	Merino	15	0.52 ± 0.06	-	-	-	-	-	(Cloete et al., 2006)
	Merino	15	0.61 ± 0.04	-	-	-	-	-	(Matebesi et al., 2009a)
Crimp frequency									
	Merino	16	0.29	-	-	-	-	-	(Ponzoni et al., 1995)
	Merino	16	0.37 ± 0.10	-	-	-	-	-	(Taylor et al., 1997)
	Merino	16	0.54 ± 0.07	-	-	-	-	-	(Taylor et al., 1999)
	Merino	16	0.43 ± 0.05	-	-	-	-	-	(Hill, 2001)
	Merino	10	0.45 ± 0.11	-	-	-	-	-	(Wuliji et al., 2001)
Staple strength									
	Merino	15	0.23 ± 0.08	-	-	-	-	-	(Cloete et al. (2006)
	Merino	15	0.20 ± 0.05	-	-	-	-	-	(Matebesi et al., 2009a)
	Merino	14	0.39 ± 0.05	-	-	-	-	-	(Brown et al., 2010)

Table 1.2 Summary of literature values on direct (h^2_a) and maternal (h^2_m) heritability, covariance between animal effects (r_{am}), animal (c^2_{anim}) and maternal (c^2_{mpe}) permanent environmental effects as well as litter effect (l^2) for reproduction traits in sheep

Trait	Breed	Age (months)	h^2_a ± s.e.	h^2_m ± s.e.	c^2_{mpe} ± s.e.	c^2_{pe} ± s.e.	l^2 ± s.e.	r_{am} ± s.e.	Reference
Number of lambs born per lambing opportunity									
	Border Leicester		0.00 ± 0.01	-	-	0.06 ± 0.01	-	-	(Brash et al. 1994a)
	Dorset		0.06 ± 0.02	-	-	0.04 ± 0.02	-	-	(Brash et al., 1994c)
	Merino		0.05 ± 0.03	-	-	0.04 ± 0.25	-	-	(Woolaston et al., 1995)
	Merino		0.23 ± 0.05	-	-	-	-	-	(Olivier et al., 2001)
	Merino		0.19 ± 0.04	-	-	-	-	-	(Olivier et al., 2001)
	Dormer		0.06 ± 0.01	-	-	0.08 ± 0.01	-	-	(Van Wyk et al., 2003)
	Merino		0.10 ± 0.01	-	-	0.18 ± 0.01	-	-	(Vatankhah & Talebi, 2008)
	Merino		0.10 ± 0.01	-	-	-	-	-	(Zishiri et al., 2013)
Number of lambs weaned per lambing opportunity									
	Merino		0.04 ± 0.01	-	-	0.04 ± 0.01	-	-	(Brash et al., 1994d)
	Merino		0.04 ± 0.02	-	-	0.08 ± 0.03	-	-	(Fogarty et al., 1994)
	Merino		0.04 ± 0.01	-	-	0.09 ± 0.02	-	-	(Swan et al., 2001)
	Merino		0.17 ± 0.05	-	-	-	-	-	(Olivier et al., 2001)
	Merino		0.16 ± 0.04	-	-	-	-	-	(Olivier et al., 2001)
	Dormer		0.03 ± 0.01	-	-	0.07 ± 0.01	-	-	(Van Wyk et al., 2003)
	Merino		0.05 ± 0.01	0.00	0.00	0.10 ± 0.01	0.00	-	(Safari et al., 2007a)
	Merino		0.11	-	-	-	-	-	(Notter, 2008)
	Merino		0.10 ± 0.01	-	-	0.18 ± 0.01	-	-	(Vatankhah & Talebi, 2008)
	Merino		0.09 ± 0.01	-	-	-	-	-	(Zishiri et al., 2013)
Total weight of lamb weaned									
	Merino		0.19 ± 0.04	-	-	-	-	-	(Olivier et al., 2001)
	Merino		0.21 ± 0.05	-	-	-	-	-	(Olivier et al., 2001)
	Mixed		0.11	0.04		0.05	-	0.04	(Rosati et al., 2002)
	Dormer		0.05 ± 0.02	-	-	0.07 ± 0.02	-	-	(Van Wyk et al., 2003)
	Merino		0.15 ± 0.04	-	-	-	-	-	(Cloete et al., 2004)
	Merino		0.12 ± 0.01	-	-	0.01 ± 0.01	-	-	(Vatankhah & Talebi, 2008)
	Merino		0.12 ± 0.02	-	-	-	-	-	(Zishiri et al., 2013)

Table 1.3 Summary of literature values on direct (h^2_a) and maternal (h^2_m) heritability, covariance between animal effects (r_{am}), animal (c^2_{anim}) and maternal (c^2_{mpe}) permanent environmental effects as well as litter effect (l^2) for subjectively measured wool and conformation traits in sheep

Trait	Breed	Age (months)	h^2_a ± s.e.	h^2_m ± s.e.	c^2_{mpe} ± s.e.	c^2_{pe} ± s.e.	l^2 ± s.e.	r_{am} ± s.e.	Reference
Wool quality									
	Merino	12-14	0.27 ± 0.04	-	-	-	-	-	(Groenewald et al. (1999)
	Merino	15	0.31 ± 0.04	-	-	-	-	-	(Naidoo et al. (2004)
	Merino	15	0.49 ± 0.05	0.06 ± 0.02	-	-	-	-0.62 ± 0.09	(Matebesi et al. (2009b)
Evenness of the fleece									
	Merino	12-14	0.23 ± 0.04	-	-	-	-	-	(Groenewald et al. (1999)
	Merino	15	0.19 ± 0.03	-	-	-	-	-	(Naidoo et al. (2004)
	Merino	15	0.28 ± 0.04	0.03 ± 0.00	-	-	-	-0.70 ± 0.14	(Matebesi et al. (2009b)
Staple formation									
	Merino	12-14	0.09 ± 0.03	-	-	-	-	-	(Groenewald et al. (1999)
	Merino	15	0.13 ± 0.03	-	-	-	-	-	(Naidoo et al. (2004)
	Merino	15	0.21 ± 0.03	-	-	-	-	-	(Matebesi et al. (2009b)
Front quarter									
	Merino	12-14	0.21 ± 0.03	-	-	-	-	-	(Groenewald et al. (1999)
	Merino	15	0.15 ± 0.03	-	-	-	-	-	(Matebesi et al. (2009b)
Overall body conformation									
	Merino	12-14	0.31 ± 0.04	-	-	-	-	-	(Groenewald et al. (1999)
	Merino	15	0.55 ± 0.04	-	-	-	-	-	(Olivier et al., 2006)

Table 1.4 Literature values on the genetic (r_g), phenotypic (r_p), maternal (r_m) and environmental (r_e) correlations (± s.e.) among body weight and objective wool traits

Trait	r_g	r_m	r_p	r_e	Reference
Body weight X					
Greasy fleece weight	-0.21 ± 0.30	-	0.54 ± 0.02	-	(Brash et al. 1994a)
	0.13 ± 0.07	0.84 ± 0.12	0.37 ± 0.01	0.48 ± 0.12	(Matebesi et al., 2009a)
	0.48	-	0.39	-	(Di et al., 2011)
Clean fleece weight	0.37 ± 0.03	-	0.49 ± 0.01	-	(Cloete et al., 1998)
	0.26 ± 0.11	-	-	0.46 ± 0.03	(Cloete et al., 2006)
	0.06 ± 0.06	-	0.25 ± 0.02	-	(Olivier et al., 2006)
	0.14 ± 0.07	0.46 ± 0.12	0.48 ± 0.03	0.36 ± 0.03	(Matebesi et al., 2009a)
Fibre diameter	0.26 ± 0.02	-	0.21 ± 0.02	-	(Cloete et al., 1998)
	0.26 ± 0.08	-	-	0.18 ± 0.05	(Cloete et al., 2006)
	0.24 ± 0.06	-	0.11 ± 0.01	-	(Olivier et al., 2006)
	-0.01 ± 0.06	0.16 ± 0.17	0.14 ± 0.02	0.31 ± 0.04	(Matebesi et al., 2009a)
	0.03	-	0.07	0.08	(Di et al., 2011)
Clean Yield	0.16 ± 0.02	-	0.02 ± 0.02	-	(Cloete et al., 1998)
	0.08 ± 0.06	-	0.06 ± 0.020	0.06 ± 0.04	(Matebesi et al., 2009a)
Staple length	0.38 ± 0.03	-	0.21 ± 0.02	-	(Cloete et al., 1998)
	0.20 ± 0.06	-	0.13 ± 0.02	-	(Olivier et al., 2006)
	0.05 ± 0.12	-	0.10 ± 0.02	0.12 ± 0.04	(Matebesi et al., 2009a)
Coefficient of variation of fibre diameter	-0.13 ± 0.04	-	-0.13 ± 0.01	-	(Huisman & Brown, 2008)
	-0.15 ± 0.07	-	-0.16 ± 0.02	-0.18 ± 0.05	(Matebesi et al., 2009a)
	0.03	-	0.07	0.08	(Di et al., 2011)
Staple Strength	-0.06 ± 0.07	-	0.07 ± 0.01	-	(Huisman & Brown, 2008)
	0.09 ± 0.07	-	0.16 ± 0.02	0.22 ± 0.03	(Matebesi et al., 2009a)
Greasy fleece weight x					
Clean fleece weight	0.87 ± 0.03	-	0.90 ± 0.01	-	(Cloete et al., 2004)
	0.91	0.98	0.91	-	(Asadi Fozi et al., 2005)
	0.98 ± 0.01	-	0.93 ± 0.01	-	(Cloete et al., 2004)
	0.82 ± 0.01	-	0.81 ± 0.02	-	(Huisman & Brown, 2009)
	0.87 ± 0.02	0.86 ± 0.05	0.89 ± 0.00	0.91 ± 0.01	(Matebesi et al., 2009a)
Clean yield	-0.07 ± 0.10	-	-0.03 ± 0.03	0.00 ± 0.06	(Cloete et al., 2004)
	-0.09 ± 0.05	-	-0.06 ± 0.02	-0.06 ± 0.04	(Matebesi et al., 2009a)
Fibre diameter	0.27 ± 0.06	-	0.46 ± 0.02	-	(Cloete et al., 2006)
	0.18 ± 0.04	-	0.23 ± 0.01	-	(Huisman & Brown, 2009)
	0.08 ± 0.06	0.08 ± 0.02	0.21 ± 0.02	0.39 ± 0.04	(Matebesi et al., 2009a)
Staple length	0.45	-	-	0.21	(Hanford et al., 2005)
	0.65 ± 0.03	-	0.50 ± 0.02	-	(Gizaw et al., 2006)
	0.18 ± 0.06	-	0.26 ± 0.02	0.33 ± 0.03	(Matebesi et al., 2009a)

Table 1.4 Continue

Trait	r_g	r_m	r_p	r_e	Reference
Coefficient of variation of fibre diameter	0.12 ± 0.08	-	-0.09 ± 0.03	-	(Cloete et al., 2006)
	0.18 ± 0.04	-	0.07 ± 0.01	-	(Huisman & Brown, 2009)
	0.04 ± 0.06	-	0.02 ± 0.02	0.01 ± 0.04	(Matebesi et al., 2009a)
Staple strength	0.18 ± 0.12	-	0.29 ± 0.03	-	(Cloete et al., 2006)
	-0.07 ± 0.01	-	0.10 ± 0.02	0.18 ± 0.04	(Matebesi et al., 2009a)
Clean fleece weight X					
Clean yield	-0.19	-	0.30		(Naidoo & Cloete, 2006)
	0.33 ± 0.05	-	0.23 ± 0.02	0.18 ± 0.04	(Matebesi et al., 2009a)
Fibre diameter	0.15	-	-	-	(Swanepoel et al., 2005)
	0.36 ± 0.04	-	-	0.27 ± 0.03	(Cloete el al., 2005)
	0.35	-	-	0.42	(Cloete et al., 2006)
	0.35	-	-	0.42	(Naidoo & Cloete, 2006)
	0.17 ± 0.06	-	0.17 ± 0.02	-	(Olivier et al., 2006)
	0.14 ± 0.02	-	0.18 ± 0.00	-	(Van Wyk et al., 2006)
	0.20	-	0.25	-	(Olivier & Cloete, 2007)
	0.44 ± 0.03	-	0.22 ± 0.01	-	(Huisman & Brown, 2009)
	0.04 ± 0.06	0.19 ± 0.02	0.18 ± 0.02	0.36 ± 0.04	(Matebesi et al., 2009a)
Staple length	0.51 ± 0.05	-	0.36 ± 0.02	-	(Olivier et al., 2006)
	0.23	-	0.29	-	(Olivier & Cloete, 2007)
	0.29 ± 0.06	-	0.30 ± 0.02	0.34 ± 0.03	(Matebesi et al., 2009a)
Coefficient of variation of fibre diameter	0.14 ± 0.09	-	-	0.01 ± 0.03	(Cloete et al., 2006)
	0.13	-	-	-0.13	(Naidoo & Cloete, 2006)
	0.16 ± 0.04	-	0.21 ± 0.02	-	(Huisman & Brown, 2009)
	0.02 ± 0.06	-	-0.01 ± 0.02	-0.05 ± 0.04	(Matebesi et al., 2009a)
Staple strength	0.32 ± 0.13	-	-	0.32 ± 0.04	(Cloete et al., 2006)
	0.34	-	-	0.31	(Naidoo & Cloete, 2006)
	-0.12 ± 0.01	-	0.10 ± 0.02	0.21 ± 0.04	(Matebesi et al., 2009a)
Fibre diameter X					
Staple length	0.24	-	-	0.11	(Naidoo & Cloete, 2006)
	-0.02 ± 0.06	-	0.02 ± 0.02	-	(Olivier et al., 2006)
	0.16	-	0.22	-	(Olivier & Cloete, 2007)
	0.15 ± 0.05	-	0.19 ± 0.02	0.25 ± 0.00	(Matebesi et al., 2009a)
Staple strength	0.44 ± 0.11	-	-	0.26 ± 0.03	(Cloete et al., 2006)
	0.46	-	-	0.28	(Naidoo & Cloete, 2006)
	0.40 ± 0.09	-	0.29 ± 0.02	0.28 ± 0.05	(Matebesi et al., 2009a)
Clean yield	-0.06	-	-	0.21	(Naidoo & Cloete, 2006)
	-0.09 ± 0.04	-	-0.05 ± 0.02	0.02 ± 0.05	(Matebesi et al., 2009a)

Table 1.4 Continue

Trait	r_g	r_m	r_p	r_e	Reference
Coefficient of variation of fibre diameter	-0.12 ± 0.07	-	-	-0.11 ± 0.03	(Cloete et al., 2006)
	-0.11	-	-	-0.16	(Naidoo & Cloete, 2006)
	-	-	0.06	-	(Notter et al., 2007)
	-0.08 ± 0.05	-	-0.10 ± 0.02	-0.15 ± 0.06	(Matebesi et al., 2009a)
Clean yield X					
Staple length	-0.18	-		0.03	(Naidoo & Cloete, 2006)
	0.33 ± 0.05	-	0.22 ± 0.02	0.12 ± 0.04	(Matebesi et al., 2009a)
Staple strength	0.19	-		0.15	(Naidoo & Cloete, 2006)
	0.01 ± 0.10	-	0.08 ± 0.03	0.14 ± 0.05	(Matebesi et al., 2009a)
Coefficient of variation of fibre diameter	-0.11	-		-0.02	(Naidoo & Cloete, 2006)
	-0.04 ± 0.05	-	-0.12 ± 0.02	-0.25 ± 0.05	(Matebesi et al., 2009a)
Staple length X					
Staple strength	-0.42	-		-0.04	(Naidoo & Cloete, 2006)
	0.19 ± 0.12	-	0.14 ± 0.03	0.12 ± 0.04	(Matebesi et al., 2009a)
Coefficient of variation of fibre diameter	-0.38	-	-	-0.04	(Naidoo & Cloete, 2006)
	-	-	-0.06	-	(Notter et al., 2007)
	-0.11 ± 0.07	-	0.14 ± 0.02	0.18 ± 0.05	(Matebesi et al., 2009a)
Staple strength X					
Coefficient of variation of fibre diameter	-0.37	-	-	-0.16	(Naidoo & Cloete, 2006)
	-0.57 ± 0.09	-	-0.39 ± 0.02	-0.35 ± 0.05	(Matebesi et al., 2009a)

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Table 1.5 Literature values on the genetic (r_g), phenotypic (r_p), maternal (r_m) and environmental (r_e) correlations (± s.e.) among objectively and subjective wool and conformation traits

Trait	r_g	r_m	r_p	r_e	Reference
Wool Quality X					
Variation over fleece	0.43 ± 0.06		0.34 ± 0.02		(Olivier et al., 2006)
	0.49 ± 0.06	0.13 ± 0.28	0.43 ± 0.01	0.45 ± 0.02	(Matebesi et al., 2009b)
Staple formation	-0.46 ± 0.06		-0.26 ± 0.07		(Olivier et al., 2006)
	-0.45 ± 0.07		-0.23 ± 0.02	-0.16 ± 0.03	(Matebesi et al., 2009b)
Front quarter	0.04 ± 0.07		0.10 ± 0.02		(Olivier et al., 2006)
	-0.14 ± 0.07	0.02 ± 0.03	0.06 ± 0.02		(Matebesi et al., 2009b)
Overall body conformation	0.07 ± 0.04		0.08 ± 0.04		(Olivier et al., 2006)
Variation over fleece X					
Staple formation	-0.51 ± 0.07		0.20 ± 0.02		(Olivier et al., 2006)
	-0.49 ± 0.08		-0.19 ± 0.02	-0.10 ± 0.02	(Matebesi et al., 2009b)
Front quarter	-0.24 ± 0.04		-0.07 ± 0.04		(Olivier et al., 2006)
	0.10 ± 0.08		0.02 ± 0.02	0.05 ± 0.01	(Matebesi et al., 2009b)
Overall body conformation	-0.36 ± 0.04		-0.10 ± 0.04		(Olivier et al., 2006)
Front quarter X					
Overall body conformation	0.89 ± 0.02		0.72 ± 0.02		(Olivier et al., 2006)
Wool quality X					
Greasy fleece weight	0.10 ± 0.06	0.06 ± 0.13	0.05 ± 0.02	0.01 ± 0.03	(Matebesi et al., 2009c)
Clean fleece weight	0.40 ± 0.06		0.22 ± 0.02		(Olivier et al., 2006)
	0.18 ± 0.06	0.09 ± 0.013	0.09 ± 0.02	0.02 ± 0.03	(Matebesi et al., 2009c)
Fibre diameter	-0.47 ± 0.02		-0.33 ± 0.02		(Olivier et al., 2006)
	-0.32 ± 0.05	0.21 ± 0.22	-0.20 ± 0.02	-0.11 ± 0.04	(Matebesi et al., 2009c)
Staple length	0.31 ± 0.06		0.20 ± 0.02		(Olivier et al., 2006)
	-0.01 ± 0.08		0.01 ± 0.03	0.01 ± 0.03	(Matebesi et al., 2009c)
Front quarter X					
Greasy fleece weight	0.07 ± 0.11		0.12 ± 0.0	0.15 ± 0.03	(Matebesi et al., 2009c)
Clean fleece weight	-0.11 ± 0.06		0.05 ± 0.02		(Olivier et al., 2006)
	0.16 ± 0.11		0.14 ± 0.02	0.15 ± 0.03	(Matebesi et al., 2009c)
Fibre diameter	0.17 ± 0.06		0.12 ± 0.02		(Olivier et al., 2006)
	0.08 ± 0.08		0.10 ± 0.02	-0.13 ± 0.03	(Matebesi et al., 2009c)
Staple length	0.24 ± 0.09		0.15 ± 0.02		(Olivier et al., 2006)
	0.07 ± 0.10		0.10 ± 0.02	0.10 ± 0.03	(Matebesi et al., 2009c)

Table 1.5 Continue

Trait	r_g	r_m	r_p	r_e	Reference
Body weight X					
Wool quality	0.07 ± 0.07		0.02 ± 0.04		(Olivier et al., 2006)
	-0.01 ± 0.07	0.17 ± 0.17	0.04 ± 0.02	0.16 ± 0.02	(Matebesi et al., 2009c)
Front quarter	0.67 ± 0.04		0.46 ± 0.01		(Olivier et al., 2006)
	0.42 ± 0.09		0.29 ± 0.02	0.28 ± 0.03	(Matebesi et al., 2009c)
Overall body conformation	0.81 ± 0.06		0.60 ± 0.02		(Olivier et al., 2006)

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Most of the woolled sheep in South Africa are maintained under extensive farming conditions in the semi-arid and arid regions (Cloete & Olivier, 2010). Seasonal droughts regularly occur in these areas which subject the animals to nutritional stress. Furthermore, from Figure 1.1 it is evident that a large proportion of these animals for the last few decades were medium to strong wool types (>20 μm). These types of Merinos are considered by South African and Australian wool industries as a different and more robust Merino strain than fine wool animals (Mortimer et al., 1985).

It is important that the paucity in information with regard to fine wool production in South Africa be rectified. The effect of selection for a reduced fibre diameter on the other economically important traits thus needs to be investigated. The main objectives of this study are therefore to determine the phenotypic and genetic parameters of production, reproduction and subjective conformation traits in a genetic fine wool resource flock.

This study is divided into several subsections. Initially a historic background is provided for the resource flock (Chapter 2). The first research section (Chapter 3) deals with the estimation of genetic parameters and relationships of fibre diameter with growth and wool production traits from birth to performance testing age in progeny of the Cradock fine wool Merino stud (CMS) under optimum feeding conditions. Chapter 4 discusses genetic parameters for and relationships of fibre diameter with reproduction traits, while Chapter 5 reports genetic parameters for the survival rate of lambs. Chapter 6 reports on the inheritance of subjective conformation traits and genetic correlations of these traits with objective production and reproduction traits. The genetic parameters for and genetic correlations within production traits at different ages (predominately fibre diameter) at performance testing age with the expression of those traits in the adult ewe flock are discussed in Chapter 7. Chapters 8 and 9 discuss the comparison of genetic fine wool animals with medium woolled animals under natural grazing conditions while maintained in five divergent production environments. The results of the current study are combined with the current monetary value of meat and wool to calculate their contribution to the profitability of a wool sheep farming enterprise in Chapter 10. The conclusions arrived at during the study are reported in Chapter 11.

CHAPTER 2. HISTORY AND MANAGEMENT OF THE CRADOCK FINE WOOL MERINO STUD

BACKGROUND

In 1987 the wool industry in South Africa requested Grootfontein Agricultural Development Institute (GADI) to establish a research program that dealt with the production of fine wool (Olivier et al., 1989). The program was conducted in four phases, with each phase dealing with a different aspect of the program. The aim of the first phase of the program was to identify and purchase genetic fine wool animals to establish a genetic fine wool resource flock at the Cradock Experimental Station. The aim of the second phase was to expand and genetically improve the newly established flock and to upgrade the flock to the Cradock fine wool Merino stud (CMS).

The third phase dealt with the evaluation of these genetic fine wool animals. The evaluation phase was conducted simultaneously with the second phase of the program and was done in two parts. Firstly the production and reproduction potential of the CMS progeny was evaluated on irrigated pastures. Secondly the production and reproduction potential of progeny of CMS sires were evaluated under extensive farming conditions. The evaluation under extensive farming conditions was conducted from 1990 to 2000 on the Grootfontein Merino flock (Olivier & Roux, 2007) and from 2000 to 2005 on the farms of four Merino producers in the traditional medium wool areas of South Africa (Olivier & Olivier, 2007).

Due to the lack of genetic fine wool animals during the early 1990's, the aim of the fourth phase was to make genetic material from the CMS available to the South African wool industry. This was achieved through the dissemination of genetic material by the annual ram auction from 1990 onwards.

Phases 1 and 2 forms part of the history, routine management and selection of the flock and is described below. The outcomes of Phase 3 are reported in Chapters 3 to 7, while the outcomes of Phase 4 are reported in Chapters 8 and 9.

PHASE 1
A. IDENTIFICATION OF FINE WOOL EWES

The producers with the finest clips in South Africa according to auction results were identified by officials from the National Wool Growers' Association (NWGA). These producers were then contacted and requested to identify their 100 to 150 finest maiden replacement ewes. From these ewes, officials from GADI, the National Fleece Testing Centre and NWGA identified the finest 30 to 40 ewes of each producer through visual appraisal. A wool sample was collected from these ewes and the finest 10 to 30 ewes were selected from the participating producers based on objectively measured fibre diameter results. This resulted in a total of 356 ewes from 19 producers that were selected for further evaluation. These ewes were transported to GADI where they were kept in a feedlot for three months. This was done to determine the fibre diameter of each ewe under optimal feeding conditions. Final selection of the ewes was done at

the end of this three-month evaluation period. The body weight and fibre diameter of the ewes at the start and end of this three-month evaluation period are summarised in Table 2.1. Approximately 50% of the ewes were still finer than 20 µm after three months. These ewes were purchased from the producers and mated to four rams imported from Australia.

Table 2.1 Body weight and fibre diameter of ewes at the start and end of the evaluation period of three months

Trait	Start	End
Body weight (kg)	39.7	58.3
Fibre diameter (µm)	19.1	20.9

A further 294 ewes were purchased, using the same procedures, from the 19 producers, as well as from another 10 producers during the second round. The list of the producers from which ewes were purchased, the number of ewes from each producer and the fibre diameter profile of the ewes are summarized in Table 2.2. During a third round, another 48 ewes from three producers were purchased, bringing the total number purchased to 520 ewes from 32 breeders.

A group of 50 ewes from the Grootfontein Merino stud were selected to be used as a control line against this flock. The average fibre diameter of these ewes were 29 µm. These were managed the same as the fine wool ewes and mated to the same rams. Olivier et al. (1999), Olivier (2009) and Olivier & Greyling (2009) discussed the changes in the production and fibre diameter of this line.

B. SOURCING OUTSIDE BREEDING SIRES

The second part of obtaining genetic material was the purchase of genetic fine wool Merino rams. It was decided to import four fine wool Merino rams from Australia in 1988 for the start of the project. The wool industry of South Africa made funds available for officials from GADI to visit Australia with the main aim to select and purchase four breeding sires for the CMS. Several Australian fine wool Merino studs were visited. The information of the four rams purchased in Australia is presented in Table 2.3.

Since the establishment of the stud in 1988, only nine other rams from outside were used as sires in the stud. From 1992 to 1994 five of the finest rams in South Africa were introduced into the stud. In 1995 the semen of two fine wool Merino rams from the Nerstane Merino stud from Woolbrook, New South Wales Australia (See Photo 1) and in 2002 the semen of another two rams from The Grange Merino stud from Dongara, Western Australia were imported. The name or number of the ram, breeder, district or state and the year in which the ram was used as sire are presented in Table 2.4.

Table 2.2 The list of the producers, the number of ewes purchased and the fibre diameter profile (Wentzel, 1991)

Name	District	Number of ewes	Fibre diameter (± s.e.)	Coefficient of variation	Minimum	Maximum
D.H. Arnold	Cathcart	54	18.3 ± 0.2	9.5	14.3	23.6
A. Lombard	Adelaide	20	18.8 ± 0.3	7.9	16.5	22.1
Sumner Broers	Adelaide	13	18.5 ± 0.3	5.1	17.1	19.7
I.A. Davies	Adelaide	20	20.5 ± 0.3	7.1	18.1	23.9
G.P. Austin	Grahamstad	21	19.7 ± 0.3	5.3	17.8	21.4
W.R. Austin & Seuns	Grahamstad	14	18.3 ± 0.3	3.8	16.4	19.3
G.N. Painter	Adelaide	12	19.6 ± 0.3	2.1	18.7	20.1
Dr. J.W. van Niekerk	Machadodorp	15	16.0 ± 0.3	5.4	14.6	17.4
P.J. Uys	Bethal	10	19.8 ± 0.4	6.3	16.9	20.7
H.P. Hancke	Bethal	10	18.7 ± 0.4	5.3	16.8	20.3
H.P. Hancke	Bethal	16	19.6 ± 0.3	6.7	17.6	21.2
J.D. Hancke	Bethal	15	18.1 ± 0.3	3.6	16.7	19.1
J.R. Buhrmann	Ermelo	9	17.6 ± 0.4	2.6	16.7	18.0
G.W. Buhrmann	Ermelo	18	20.3 ± 0.3	5.0	18.2	21.5
J.R. Buhrmann	Sheepmoor	18	19.9 ± 0.3	6.2	17.8	21.5
J.W. Ziervogel	Amersfoort	19	19.0 ± 0.3	4.0	17.7	20.5
J.C. Venter	Volksrust	28	18.9 ± 0.2	5.9	15.6	20.8
N.W. Turner & Seuns	Middleton	21	19.3 ± 0.3	6.9	15.3	21.3
Oorlogspoort Boerdery	Noupoort	20	21.5 ± 0.3	5.0	19.3	23.2
O.T.K. Merinostoet	Bethal	11	20.0 ± 0.4	2.6	19.3	20.9
C.J. Uys	Bredasdorp	8	21.9 ± 0.4	2.4	21.2	22.7
G. van Dyk	Napier	10	21.6 ± 0.4	6.8	18.9	24.2
P. Wessels	Napier	10	20.6 ± 0.4	4.8	18.9	21.6
H.J. Human	Riviersonderend	10	20.3 ± 0.4	4.0	18.4	21.4
G.J. van Deventer	Swellendam	10	20.3 ± 0.4	2.5	19.5	21.1
J.J. van Deventer	Swellendam	10	19.8 ± 0.4	2.7	18.6	20.5
A. du T. Streicher	Swellendam	10	20.0 ± 0.4	2.8	19.2	20.9
F. du Toit	Swellendam	10	21.5 ± 0.4	3.5	20.4	22.4
P.E. Steenkamp	Heidelberg	10	20.9 ± 0.4	2.6	19.8	21.7
Dr. A.I. van Niekerk	Kenhardt	20	21.0 ± 0.3	4.6	18.9	22.6

Table 2.3 The information of the first four breeding sires imported from Australia in 1988

Stud	State	Ram ID	Fibre diameter
Glenleigh Merino stud	New South Wales	7-1525	17.1
Siera Park Merino stud	Victoria	87-086	17.6
Siera Park Merino stud	Victoria	87-078	17.4
Grathlyn Merino stud	New South Wales	7-2220	17.8

Table 2.4 The name or number of the ram, breeder, district or state and the year in which the ram was used as sire

Year	Ram	Breeder	District / State
1992	75005 / Topper	Oorlogspoort	Middelburg
1992	75006 / Bitterfyn	Oorlogspoort	Middelburg
1993	75007 / Tiptop	Oorlogspoort	Middelburg
1994	75008 / Tino	Austin & Sons	Grahamstown
1994	75009 / Seppi	Austin & Sons	Grahamstown
1995	N225	Nerstane	New South Wales, Australia
1995	N697	Nerstane	New South Wales, Australia
2002	968052	The Grange	Western Australia.
2002	998345	The Grange	Western Australia.

Photo 1. The Nerstane ram N697

PHASES 1 TO 3

A. FLOCK MANAGEMENT

The first group of ewes were artificially inseminated (AI) with fresh semen of the four Australian rams during October 1988 and they lambed during March 1989. During March 1989, the second group of ewes purchased, were inseminated intra-vaginally with fresh semen from the four Australian rams. The size of the ewe flock that was mated annually from 1990 was approximately 350 ewes. The ewes were annually mated for 34 days during autumn (March to April). The control line ewes were inseminated with semen of the same rams used on the fine wool ewes. The ewes in oestrus were identified with teaser rams and inseminated twice at 8 to 16 hour intervals. From 1988 to 2010 the ewes were inseminated with fresh semen and in 1995 and 2002 a group of the ewes were laparoscopically inseminated with semen imported from Australia. Since 2011 the ewes were mated to individual rams in small paddocks.

The first own-bred rams were used as breeding sires during the 1991 breeding season. The allocation of breeding sires was done in such a manner to ensure that dams were not mated to their sons and that sibs were not mated. Since only 13 migrant sires were introduced to the stud over a period of 14 years, care was taken to ensure that the allocation of ewes to sires would minimise inbreeding. Approximately 10 rams (± 35 ewes / sire) were used annually as breeding sires and at least two rams were carried across to a second breeding season since 2003 to create sire genetic ties across years.

The stud was kept on irrigated pastures at the Cradock Experimental Station station (32º 13' S, 25º 41' E, elevation 847 m) near Cradock in the Eastern Cape Province. The average annual rainfall is 366 mm, with 15% occurring in spring, 32% in summer, 43% in autumn and 10% in winter. The average minimum temperature (July) is 8,1 °C and the average maximum temperature (January) is 23,5 °C. Frost occurs from mid-April to mid-September. The pastures consisted of a mixture of lucerne, ryegrass and clovers planted in small paddocks. The flock was maintained on the pastures throughout the year and lucerne hay was supplied on an *ad libitum* basis to all animals.

Lambs were born in spring, identified and tagged at birth, while birth weight as well as sex, birth status and the identity of the dam were recorded. Pedigree information could be derived from the dam identities recorded. Lambs were weaned at approximately 100 days of age (Chapter 3). After weaning the sexes were separated and maintained in different flocks. At 6 months of age the lambs were shorn and a fleece sample was taken for fibre diameter analysis. The progeny were visually appraised at approximately 14 months of age after which the animals were shorn (8 months wool growth). Body weight and fleece traits were recorded at this stage. All ram and ewe progeny were retained until an age of 16 months when final selection on estimated breeding values for the economically important traits was done. The animal health program followed in the stud are summarised in Appendix A. The adult ewes were annually shorn in February before mating in March. The following detailed production and reproduction data were recorded on the experimental flock:

On the ewe flock:
- Reproductive performance of ewes
- Body weight at mating
- Fleece weight at each shearing
- Full wool sample analysis at each shearing including tensile strength

On the progeny:
- Sire and dam identification
- Birth date, birth status, sex and birth coat score
- Birth weight
- Birth remarks such as dead at birth or died after birth
- Weaning date, status
- Body weight at 42 days, 100 - 120 days (weaning)
- Body weight at 6 and 12 months of age
- Fibre diameter at 6 months and 12 months of age
- Body weight and fleece weight at 14 months of age
- Full wool sample analysis at 14 months of age, including tensile strength
- Linear scoring of fleece and conformation traits at the age of 14 months (See Chapter 6 for trait definitions)

B. SELECTION OBJECTIVES

The main selection objectives for the first few years in the Cradock fine wool Merino stud was to increase body weight and conformation, maintain fleece weight and maintain or decrease fibre diameter. This selection objective was motivated by the perception that the body weight and conformation of the initial animals sourced from industry was not acceptable as stud animals. The emphasis on body weight and conformation is motivated by the importance of meat to the income derived from sheep flocks in South Africa. Replacement animals were from the onset of the stud selected on estimated breeding values for the traits included in the selection objective.

The selection objective in the stud was changed in 1996 to place more pressure on the reduction of fibre diameter and less emphasis on body weight and conformation. This change was possible as the body weight and conformation of the progeny were at an acceptable level for fine wool stud animals in South Africa. The selection objective from the 1996 to 2003 breeding season was therefore to decrease fibre diameter, maintain body weight and clean fleece weight. The pressure on fibre diameter was further increased by annually culling adult ewes with a fibre diameter exceeding 21 μm.

In 1999 it was decided to add staple length and reproduction (defined as total weight of lamb weaned) in the selection objective. The aim was to increase both these traits. Adult ewes were also annually culled on their reproductive performance before the onset of the next mating season. Selection was based on the profitability selection index (R/ small stock unit) developed by Herselman (2004) from 2004. Rams

with the highest profitability values with acceptable breeding values for fibre diameter, body weight, clean fleece weight, staple length and total weight of lamb weaned were selected as breeding sires.

With this information as background, the following chapters reports data recorded on the flock since its establishment. Results concentrated upon includes genetic parameters on various traits of economic and industry importance, the usage of fine wool animals in traditionally strong and medium wool areas and the estimation of genotype x environment interactions. Finally, genetic information is combined with economic information to assess the implications of various levels of recording in the South African sheep industry.

CHAPTER 3. GENETIC PARAMETERS FOR PRODUCTION TRAITS OF A GENETIC FINE WOOL MERINO STUD

INTRODUCTION

The profitability of sheep enterprises in South Africa depends on the production (meat and wool production) and reproduction potential of the flock. Reproduction and growth have the biggest influence on profitability as more than 70% of the income of sheep flocks is generated from meat production (Olivier, 1999). Although income from wool only amounts to about 30%, selection for wool traits still plays a major role on Merino farms in South Africa. The direction of improvement in wool traits is largely market driven in South Africa.

Prior to the late 1980s, the quantity of wool produced was seen as the most important breeding objective in woolled sheep (Marx, 1981). There was a subsequent shift in the emphasis from wool quantity to the production of finer wool. This change was driven by the higher consumer demand for finer wool types that resulted in increased price premiums for finer wool. Wool producers thus included fibre diameter in their selection programs to reduce the fibre diameter of their wool clip to receive these higher wool prices.

In some instances, producers put all the emphasis in their breeding plans on reducing fibre diameter, irrespective of the effect that it might have on the growth, wool production, reproduction and subjectively assessed wool and conformation traits. Given the genetic relationship among reproduction, live weight and wool traits (Olivier, 1999). it is clear that selection should not only be based on one of these trait groups, but on all of them to ensure that production and reproduction will be at an optimum level. It is important to have a good knowledge of the respective variance components and accurate genetic parameters to design effective breeding programmes.

It is furthermore important to understand the correlations and subsequent indirect responses that may accrue based on different traits included in the selection program. The selection progress will be hampered if these relationships are not considered when breeding strategies are defined.

The aim of this study was therefore to estimate genetic parameters for body weights at different ages and wool production traits in a genetic fine wool Merino stud and to quantify the relationships between these traits. It is argued that this will lead to an increase in the knowledge base for genetic parameters in South Africa Merino sheep and especially in fine wool animals.

MATERIALS AND METHODS

The Cradock Fine Wool Merino Stud was established at the Cradock Experimental station (32º 13' S, 25º 41' E, elevation 847 m) in 1988 on request from the Wool industry of South Africa. Five hundred and

twenty ewes were bought from 32 Merino breeders with the finest clips throughout South Africa (Chapter 2; Olivier et al., 1989; Olivier et al., 2006a).

The stud was kept on irrigated pastures at the Cradock Experimental Station, near Cradock in the Eastern Cape Province. The pastures consisted of a mixture of lucerne, ryegrass and clovers planted in small paddocks. The ewes were artificially inseminated during March to April each year for a six-week mating period. Teaser rams were used to identify the ewes that were in oestrus. See Chapter 2, for a detailed description of the history and management of this stud.

As the initial progeny born in the project were small with below average body conformation, the selection objectives were originally to increase body weight, maintain fleece weight and to maintain or decrease fibre diameter. Therefore, most of the selection pressure was on body weight. In 1996 it was decided that the desired body weight and conformation was achieved and the emphasis was moved to reduce fibre diameter. The selection objectives were then changed to increase body weight, maintain fleece weight and reduce fibre diameter. These are still the selection objectives at present. Since 2002, increasing staple length was also included as part of the selection objectives. The adult ewes were also subjected to selection for reduced fibre diameter, as all ewes with a fibre diameter above 21.5 µm were culled annually.

Data collected on 8 368 ram and ewe progeny born within this stud from 1988 to 2010 were used for the analysis of the body weights and wool characteristics. The body weights included in the analysis, were birth weight (BirthW), body weights at 42 days of age (pre-weaning; PWW), weaning (WW), 6 months of age (BW6), 12 months of age (BW12) and 15 months of age (performance testing age; BW15). The wool production traits included in the analyses, were fibre diameter at 6 (FD6) and 12 (FD12) months of age, as well as the following wool production traits recorded at 15 months of age: greasy fleece weight (GFW), clean fleece weight (CFW), fibre diameter (FD), staple length (SL), clean yield (CY), number of crimps per 25 mm (Crimp), standard deviation of fibre diameter (SDFD), coefficient of variation of fibre diameter (CVFD), wrinkle score (Wrinkle), comfort factor (CF) and staple strength (SS). Birth coat score (BirthC) was also included in the analysis. The latter score ranged from 1 to 4, with 1 being more woolly and 4 being more hairy (Chapter 5). The deviation from the Duerden standard (Duer), is the actual fibre diameter divided by the estimated fibre diameter according to the number of crimps per 25.4 mm based on the Duerden standard (Duerden, 1929). The latter author compiled a table that linked the spinning count to fibre diameter and number of crimps. This value is expressed as a deviation from 100, with under crimped wool having fewer crimps relative to the measured FD and over crimped wool having more crimps in relation to FD. The deviation from Duerden standard was also included in the analysis.

The Proc MEANS-procedure of SAS (SAS, 2009) was used to obtain the descriptive statistics of the data set. The least-squares means and standard errors for the body weights and wool characteristics were obtained with the Proc GLM-procedure of SAS, and significance levels for the non-genetic effects were obtained with the PDIFF-option under the Proc GLM-procedure of SAS (SAS, 2009). Only effects and interactions that had a significant effect ($P<0.01$) on a specific trait, were included in the final operational model.

The estimation of the genetic parameters was done with ASREML (Gilmour et al., 2009) by fitting single-trait animal models. These models included different combinations of the direct additive, maternal additive and maternal permanent environment effects, as well as the covariation between the direct and maternal additive effects. These different combinations led to the following six models in matrix notation:

$$\mathbf{y} = X\mathbf{b} + Z_1\mathbf{a} + \mathbf{e} \tag{1}$$

$$\mathbf{y} = X\mathbf{b} + Z_1\mathbf{a} + Z_3\mathbf{mpe} + \mathbf{e} \tag{2}$$

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

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

$$\mathbf{y} = X\mathbf{b} + Z_1\mathbf{a} + Z_2\mathbf{m} + Z_3\mathbf{mpe} + \mathbf{e}; \text{ with cov(a,m)} = 0 \tag{5}$$

$$\mathbf{y} = X\mathbf{b} + Z_1\mathbf{a} + Z_2\mathbf{m} + Z_3\mathbf{mpe} + \mathbf{e}; \text{ with cov(a,m)} = A\sigma_{am} \tag{6}$$

where $\mathbf{y}$ is a vector of observed traits of animals; $\mathbf{b}$, $\mathbf{a}$, $\mathbf{m}$ and $\mathbf{mpe}$ are vectors of fixed effects, direct additive effects, maternal additive effects and maternal permanent environmental effects respectively; X, Z_1, Z_2 and Z_3 are incidence matrices respectively relating fixed effects, direct additive effects, maternal additive effects and maternal permanent environmental effects to $\mathbf{y}$; $\mathbf{e}$ is the vector of residuals; A is the numerator relationship matrix, and σ_{am} is the covariance between direct additive and maternal additive 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 is an identity matrix, σ^2_a, σ^2_m, σ^2_{mpe} and σ^2_e are the direct additive variance, maternal additive 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 of the log likelihood, as well as the parameters.

The determination of the most suitable model to estimate (co)variance components for each trait was done with the log likelihood ratio tests. The inclusion of a random effect was considered to be significant when the log likelihood value improved significantly compared to a model where the effect was not included. This improvement was determined when the statistic $-2(\log L_2 - \log L_1)$ was greater than values of the chi-square distribution of $\alpha = 0.05$ (3.84) at one degree of freedom (Swalve, 1993). This was done to determine the most suitable model for each trait with the least possible number of random effects included.

The genetic, environmental, phenotypic and maternal correlations between the different traits were estimated using two-trait models with ASREML (Gilmour et al., 2009). The (co)variance component values obtained with the single-trait models was used as starting values for the two-trait models using best model for each trait. Breeding values were averaged within birth years and used to obtain genetic trends. Average annual estimated breeding values were regressed on the year of birth to get an indication of the annual gain that was achieved. Three separate linear regressions were fitted, viz. from 1988 to

1995, 1996 to 2003 and from 2004 to 2010, to describe the three distinct periods, during which different selection objectives were applied (Chapter 2).

RESULTS AND DISCUSSION

The non-genetic effects that had a significant influence on the different traits are summarised in Table 3.1. They were year of birth (1988 to 2010 for most traits; 2000 to 2010 for SS), sex (male/female), birth status (single/multiple) for BirthW and BirthC or rearing status for other traits (single/multiple) and age of dam in years (2 to 6+). Several two-factor interactions between the non-genetic effects, as well as age of the animal for a specific trait as a linear regression, were also tested for significance. It is evident from Table 3.1 that year of birth had a significant (P<0.05) effect on all the traits, while sex did not affect Duer. Only the two-way interaction between year of birth and sex is included in Table 3.1, as none off the other interactions had a significant effect on any of the traits.

Table 3.1 The significance level of the different non-genetic effects, two-way interaction and age of the animal for the respective traits

Trait	Year of birth	Sex	Bstat /RS	Dam age	Year* Sex	Animal Age
BirthW	*	*	*	*	*	-
BirthC	*	*	*	*	*	-
PWW	*	*	*	*	*	*
WW	*	*	*	*	*	*
BW6	*	*	*	ns	*	*
FD6	*	*	*	*	*	*
BW12	*	*	*	ns	*	*
FD12	*	*	*	*	*	*
BW15	*	*	*	*	*	*
GFW	*	*	*	*	*	*
CFW	*	*	*	*	*	*
FD	*	*	*	*	*	*
SL	*	*	ns	ns	*	ns
CY	*	*	*	ns	*	ns
Crimp	*	*	ns	*	*	ns
Duer	*	ns	*	ns	*	ns
SDFD	*	*	ns	*	*	ns
CVFD	*	*	ns	*	*	ns
Wrinkle	*	*	*	*	*	ns
CF	*	*	ns	*	ns	ns
SS	*	*	*	*	*	ns

* P < 0.05; ns - non significant; Bstat – birth status for BirthW and BirthC; RS - rearing status for all other traits; BirthC – birth coat score; Body weight: BirhtW – birth; PWW – pre-weaning (42 days of age); WW – weaning; BW6 –6 months of age; BW12 –12 months of age; BW15 –15 months of age; fibre diameter: FD6 –6 months of age; FD12 –12 months of age; FD – 15 months of age; GFW – greasy fleece weight; CFW – clean fleece weight; SL – staple length; CY – clean yield; Crimp – number of crimps per 25 mm; Duer – Duerden; SDFD – standard deviation of fibre diameter; CVFD - coefficient of variation of fibre diameter; Wrinkle – wrinkle score; CF – comfort factor; SS – staple strength

Descriptive statistics for birth coat score, the different body weights and objective wool characteristics are summarised in Table 3.2. The total number of records available for analysis ranged from 3434 to 8368 for

SS and BirthW respectively. The coefficient of variation (CV) for body weights ranged from 18.7% (BirthW) to 22.3% (PWW). The CV for the wool traits ranged from 0.7% (CF) to 29.3% (CFW). The CV of the body weights fell within the range of values reported in the literature (Groenewald et al., 1999; Brown et al., 2005; Safari et al., 2005; Miraei-Ashtiane et al., 2007; Olivier & Cloete, 2007; Van Wyk et al., 2008; Matebesi et al., 2009a) that ranged from 6.0% to 28.0%.

Table 3.2 The number of records, number of sires, number of dams, mean and coefficient of variation (CV) of the different body weights, birth coat score and wool traits

Trait	Nr of records	Nr of sires	Nr of dams	Mean	CV (%)
BirthC	7201	144	1521	1.8	44.3
BirthW (kg)	8367	151	1808	4.5	18.7
PWW (kg)	7684	151	1772	16.6	22.3
WW (kg)	7514	151	1759	27.2	18.8
BW6 (kg)	7348	151	1752	35.8	20.9
BW12 (kg)	7120	151	1743	55.3	19.7
BW15 (kg)	6919	151	1728	60.9	19.2
FD6 (µm)	7451	151	1755	17.2	7.9
FD12 (µm)	7091	151	1739	18.3	9.0
GFW (kg)	6891	151	1726	5.7	28.4
CFW (kg)	6891	151	1726	4.6	29.3
FD (µm)	6916	151	1728	18.6	9.0
SL (mm)	6738	151	1728	104.6	16.4
CY (%)	6891	151	1726	68.7	9.0
Crimp	6905	151	1727	14.1	15.5
Duer	6905	151	1727	96.1	10.6
SDFD (µm)	5461	137	1295	3.1	13.6
CVFD (%)	5461	137	1295	17.0	12.1
Wrinkle	6905	151	1727	7.6	27.3
CF (%)	5461	137	1295	99.6	0.7
SS (N/Ktex)	3434	86	862	42.1	26.4

BirthC – birth coat score; Body weight: BirhtW – birth; PWW – pre-weaning (42 days of age); WW – weaning; BW6 –6 months of age; BW12 –12 months of age; BW15 –15 months of age; fibre diameter: FD6 –6 months of age; FD12 –12 months of age; FD – 15 months of age; GFW – greasy fleece weight; CFW – clean fleece weight; SL – staple length; CY – clean yield; Crimp – number of crimps per 25 mm; Duer – Duerden; SDFD – standard deviation of fibre diameter; CVFD - coefficient of variation of fibre diameter; Wrinkle – wrinkle score; CF – comfort factor; SS – staple strength

Fleece weight (GFW and CFW) and SL had similar CV's than the respective ranges of 16.2% to 28.3%, 16.2% to 42.0% and 11.9% to 20.9% reported in the literature (Groenewald et al., 1999; Naidoo et al., 2004; Brown et al., 2005; Safari et al., 2005; Hanford et al., 2006; Olivier & Cloete, 2007; Notter et al., 2007; Van Wyk et al., 2008; Matebesi et al., 2009a; Valera et al., 2009; Greeff et al., 2013).

The CV's for FD6, FD12 and FD were below 10%, which is in accordance with the values reported in the literature (Groenewald et al., 1999; Brown et al., 2005; Safari et al., 2005; Olivier & Cloete, 2007; Van Wyk et al., 2008; Matebesi et al., 2009a; Valera et al., 2009; Greeff et al., 2013). The range (12.2% to 16.6%) of CV's for CVFD reported in the literature (Safari et al., 2005; Notter et al., 2007; Safari et al., 2007a; Matebesi et al., 2009a; Greeff et al., 2013) is similar to the values of the current study.

Staple strength, which is a trait that has an appreciable influence on the income derived from wool production, had a very high CV, which falls within the range of 19.3% to 36.4% reported in the literature (Naidoo et al., 2004; Safari et al., 2005; Notter et al., 2007; Matebesi et al., 2009a; Greeff et al., 2013). The CV for CY was similar to the values reported in the literature (Brown et al., 2005; Safari et al., 2005; Van Wyk et al., 2008; Safari et al., 2007a; Matebesi et al., 2009a; Greeff et al., 2013).

Comfort factor, which is an indication of the number of fibres below 30 μm, has a very low CV. The lack of variation in this trait is because the maximum boundary for this trait is 100% and subsequently the large proportion of the animals in a flock that have a measurement of 100%. This will particularly be the case for fine woolled animals. This argument is further supported by the mean of the trait that was close to 100%. The distribution for this trait would therefore also be skew. This CV is in accordance with values of below 2% reported in the literature (Pollott & Greeff, 2004; Lupton et al., 2007; Greeff et al., 2013).

Ponzoni et al. (1995), Taylor et al. (1997), Taylor et al. (1999), Hill (2001), Wuliji et al. (2001) and Valera et al. (2009) reported that the variation in number of crimps per 25 mm ranged from 11.0% to 19.0%. These reports were comparable with the results of the present study, where the CV for the number of crimps per 25 mm was 12.0%. No comparable information on the CV of Duer was found in the literature. The variation in Wrinkle obtained in this study is on the lower end of the range of values reported in the literature ranging from 24.7 to 41.7 (Cloete et al., 1998a; Groenewald et al., 1999; Matebesi et al., 2009a; Brown et al., 2010).

The Log likelihood values for body weight at different ages, birth coat score and wool weights and characteristics are presented in Table 3.3 as a deviation from the most suitable model. The most suitable model for BirthW and PWW included the direct additive effect (σ^2_a), maternal additive effect (σ^2_m), the covariation between the direct and maternal additive effects (σ_{am}) and the maternal permanent environmental effect (σ^2_{mpe}). The final operational models for BirthC and WW included the direct additive effect (σ^2_a), maternal additive effect (σ^2_m) and the maternal permanent environmental effect (σ^2_{mpe}). The direct additive effect (σ^2_a) and maternal additive effect (σ^2_m) were the only random effects that had a significant influence (P<0.05) on the final operational model for the body weight traits from 6 months onwards.

The most suitable operational model for GFW, CFW, and FD at all ages; Crimp and Wrinkle included both the direct additive effect and the maternal additive effect. The direct additive effect was the only random influence on SL, CY, Duer, SDFD, CVFD and CF. For SS the direct additive effect and the maternal permanent environmental effect had a significant influence.

Table 3.3 Log Likelihood deviations from the most suitable model for body weight at different ages, birth coat score and wool traits

Trait	σ^2_a	$\sigma^2_a + \sigma^2_{mpe}$	$\sigma^2_a + \sigma^2_m$	$\sigma^2_a + \sigma^2_m + \sigma_{am}$	$\sigma^2_a + \sigma^2_m + \sigma^2_{mpe}$	$\sigma^2_a + \sigma^2_m + \sigma^2_{mpe} + \sigma_{am}$
BirthC	67.90	11.20	11.16	7.30	**0.00**	-3.72
BirthW	631.56	76.42	65.02	47.34	13.62	**0.00**
PWW	264.20	42.40	26.60	23.00	3.40	**0.00**
WW	253.06	28.40	29.30	29.26	**0.00**	-0.12
BW6	95.16	13.16	**0.00**	-0.04	-3.04	-3.06
BW12	23.56	12.10	**0.00**	-2.66	-0.32	-2.68
BW15	24.94	14.96	**0.00**	-0.10	-0.02	-0.10
FD6	16.04	8.14	**0.00**	-1.28	-0.90	-3.58
FD12	19.40	7.52	**0.00**	-1.36	-0.56	-2.96
GFW	41.68	34.50	**0.00**	-0.50	0.00	-0.50
CFW	25.32	20.84	**0.00**	-0.60	0.00	-0.60
FD	17.96	8.28	**0.00**	-2.80	-1.36	-3.48
SL	**0.00**	-0.64	0.00	-0.14	-0.64	-0.14
CY	**0.00**	12.22	0.90	0.76	0.90	0.76
Crimp	9.60	7.30	**0.00**	-0.08	0.00	-0.08
Duer	**0.00**	-2.94	-1.68	-2.98	-3.10	NC
SDFD	**0.00**	0.00	0.00	-0.60	0.00	0.00
CVFD	**0.00**	0.00	0.00	-0.54	0.00	-0.54
Wrinkle	8.26	6.78	**0.00**	-0.44	0.00	-0.44
CF	**0.00**	0.00	0.00	NC	NC	NC
SS	9.16	**0.00**	9.02	7.60	6.00	4.80

NC – the analysis did not converge; BirthC – birth coat score; Body weight: BirhtW – birth; PWW – pre-weaning (42 days of age); WW – weaning; BW6 –6 months of age; BW12 –12 months of age; BW15 –15 months of age; fibre diameter: FD6 –6 months of age; FD12 –12 months of age; FD – 15 months of age; GFW – greasy fleece weight; CFW – clean fleece weight; SL – staple length; CY – clean yield; Crimp – number of crimps per 25 mm; Duer – Duerden; SDFD – standard deviation of fibre diameter; CVFD - coefficient of variation of fibre diameter; Wrinkle – wrinkle score; CF – comfort factor; SS – staple strength

The direct additive heritability (h^2_a), maternal heritability (h^2_m), the genetic correlation between the animal effects (r_{am}) and the maternal permanent environmental effect (c^2_{mpe}) for BirthC, body weights at different ages and wool traits are summarised in Table 3.4. The h^2_a, h^2_m and c^2_{mpe} estimated in this study for BirthC were 0.36, 0.04 and 0.04 respectively. The h^2_a for BirthC, defined as a threshold trait, obtained with Gibbs Sampling (0.54; Chapter 5) was higher than the h^2_a estimate for BirthC on the same dataset used in this study. The h^2_a estimated in Chapter 5 is similar to the reported estimates in the literature for BirthC ranging from 0.55 to 0.70 (Morley, 1955a; Gregory, 1982; Davis, 1987; Ponzoni et al., 1996; Cloete et al., 2003b; Kemper at al., 2003) and is notably higher than the present estimate of 0.36.

The c^2_{mpe} estimated in this study (0.04) for BirthC is in the same order as the value reported by Cloete et al. (2003b). With Gibbs Sampling (Chapter 5) a h^2_m of 0.11 was estimated, which is higher than the value of 0.04 estimated in this study. No other comparable literature with regard to the h^2_m of birth coat score was found.

Table 3.4 Direct additive heritability (h^2_a), maternal heritability (h^2_m), genetic correlation between the animal effects (r_{am}) and the maternal permanent environmental effect (c^2_{mpe}) for BirthC, body weights and wool traits (± s.e.)

Trait	h^2_a	h^2_m	r_{am}	c^2_{mpe}
BirthC	0.36 ± 0.03	0.04 ± 0.01	-	0.04 ± 0.02
BirthW	0.21 ± 0.04	0.21 ± 0.04	-0.46 ± 0.09	0.14 ± 0.02
PWW	0.15 ± 0.03	0.13 ± 0.03	-0.31 ± 0.14	0.09 ± 0.02
WW	0.09 ± 0.02	0.10 ± 0.02	-	0.12 ± 0.02
BW6	0.26 ± 0.03	0.12 ± 0.02	-	-
BW12	0.47 ± 0.03	0.04 ± 0.01	-	-
BW15	0.49 ± 0.03	0.05 ± 0.01	-	-
FD6	0.37 ± 0.03	0.05 ± 0.01	-	-
FD12	0.72 ± 0.02	0.01 ± 0.01	-	-
GFW	0.54 ± 0.03	0.06 ± 0.01	-	-
CFW	0.55 ± 0.03	0.05 ± 0.01	-	-
FD	0.63 ± 0.03	0.02 ± 0.01	-	-
SL	0.41 ± 0.03	-	-	-
CY	0.62 ± 0.03	-	-	-
Crimp	0.43 ± 0.03	0.03 ± 0.01	-	-
Duer	0.50 ± 0.03	-	-	-
SDFD	0.56 ± 0.03	-	-	-
CVFD	0.52 ± 0.03	-	-	-
Wrinkle	0.54 ± 0.03	0.03 ± 0.01	-	-
CF	0.81 ± 0.02	-	-	-
SS	0.26 ± 0.04	-	-	0.04 ± 0.01

"-" – not fitted; BirthC – birth coat score; Body weight: BirhtW – birth; PWW – pre-weaning (42 days of age); WW – weaning; BW6 –6 months of age; BW12 –12 months of age; BW15 –15 months of age; fibre diameter: FD6 –6 months of age; FD12 –12 months of age; FD – 15 months of age; GFW – greasy fleece weight; CFW – clean fleece weight; SL – staple length; CY – clean yield; Crimp – number of crimps per 25 mm; Duer – Duerden; SDFD – standard deviation of fibre diameter; CVFD - coefficient of variation of fibre diameter; Wrinkle – wrinkle score; CF – comfort factor; SS – staple strength

The h^2_a estimates for body weights ranged from 0.10 (WW) to 0.54 (BW15) and the h^2_m estimates ranged from 0.06 (BW15) to 0.29 (BirthW). The r_{am} was negative and amounted to -0.47 for BirthW and -0.39 for PWW. Furthermore, the influence of the maternal additive effect (σ^2_m) on the body weights decreased with an increase of age. At the same time the influence of the direct additive effect (σ^2_a) increased when animals get older. The same tendency was observed in other studies done with random regression models (Lewis & Brotherstone, 2002; Fischer et al., 2004; Molina et al., 2007; Wolc et al., 2011; Chapter 7).

Heritability estimates for BirthW for all wool type sheep breeds reported in the literature ranged from 0.04 to 0.41 (Safari et al., 2005; Safari et al., 2007b; Ceyhan et al., 2009). The current estimate for BirthW (0.21 in Table 3.4) falls within this range, as well as the range reported specifically for Merino sheep that 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., 2003a; Safari et al., 2007b).

The h^2_m estimated in this study of 0.21 (Table 3.4) for BirthW are lower than the range (0.28 to 0.37) reported in the literature by Mortimer & Atkins (1995), Vaez Torshizi et al. (1996), Analla & Serradilla (1998), Wuliji et al. (2001), Duguma et al. (2002b), Cloete et al. (2003b) and Safari et al. (2007b) for Merino sheep. The reported range of c^2_{mpe} for BirthW in the literature is 0.00 to 0.17 (Mortimer & Atkins, 1995, Vaez Torshizi et al., 1996, Analla & Serradilla, 1998; Cloete et al., 1998b; Duguma et al., 2002b; Cloete et al., 2003a) for Merino and Dohne Merino sheep, which is similar to the value of 0.04 estimated in this study (Table 3.5), as well as the value estimated with Gibbs Sampling (Chapter 5).The correlation between the animal and maternal effects (r_{am}) was found to be moderately negative (-0.46) for BirthW, which was just outside the upper boundary of the values reported in the literature that ranged from -0.21 to -0.42 (Mortimer & Atkins, 1995; Vaez Torshizi et al., 1996; Analla & Serradilla, 1998; Duguma et al., 2002b) for Merino sheep.

The h^2_a estimates cited in the literature for pre-weaning and weaning weights of Merino sheep ranged from 0.16 to 0.35 (Lewer et al., 1994; Wuliji et al., 2001; Safari et al., 2005). The current estimate of 0.15 for PWW was similar to the lower end of this range, while the estimate of 0.09 for WW was slightly lower than the reported range. The h^2_a estimated with Gibbs Sampling on the same dataset, was similar to the results of this study (Chapter 5). The c^2_{mpe} estimates of 0.09 and 0.12 corresponded with the range (0.11 to 0.17) reported in the literature (Annalla & Serradilla, 1998; Cloete et al., 1998b; Safari et al., 2005), but were slightly higher than the corresponding Gibbs Sampling estimates (Chapter 5).

The h^2_m of PWW is consistent with the range (0.14 to 0.29) reported in the literature for pre- and weaning weight (Mortimer & Atkins, 1995; Annalla & Serradilla, 1998; Safari et al., 2005). However, the h^2_m estimate for WW (0.10) is slightly lower than the reported range. The r_{am} of -0.31 estimated for PWW in this study falls within the range of values reported in the literature that ranged from -0.21 to -0.42 (Vaez Torshizi et al., 1996; Annalla & Serradilla, 1998; Safari et al., 2005).

The marked increase in the h^2_a from WW to BW6 (Table 3.4) is the result of the re-partitioning of the maternal permanent environmental effect, which was excluded in the BW6 analysis, to the direct and maternal additive effects. The h^2_a estimate of 0.26 for BW6 falls within the range (0.18 to 0.44) reported in the literature for body weights at the same age (Snyman et al., 1996; Wuliji et al., 2001; Ingham et al., 2003).

The range of h^2_a estimates reported in the literature for body weights between 12 to 16 months of age for Merino sheep are 0.13 to 0.56 (Mortimer & Atkins, 1995; Ponzoni et al., 1995; Woolaston et al., 1995; Vaez Torshizi et al., 1996; Brash et al., 1997; Greeff & Karlsson, 1998, 1999; Nagy et al., 1999; Rose &Pepper, 1999; Wuliji et al., 2001; Brown et al., 2002a; Duguma et al., 2002a; Lee et al., 2002b; Clarke et al., 2003; Brown et al., 2005; Safari et al., 2005; Cloete et al., 2006; Van Wyk et al., 2008; Matebesi et al., 2009a; Brown et al., 2010). The corresponding values estimated in this study for BW12 and BW15 were within the upper end of the reported range (Table 3.4).

Estimates for h^2_m obtained in this study for BW12 (0.04) and BW15 (0.05) were at the lower end of the range of h^2_m values (0.04 to 0.15) reported in the literature (Vaez Torshizi et al., 1996; Ingham et al., 2003; Safari et al., 2005; Van Wyk et al., 2008; Matebesi et al., 2009a).

The h^2_a estimates for GFW and CFW obtained in this study were in the same order and was also higher than most of the values reported in the literature for Merino sheep (Safari et al., 2005). Matebesi et al. (2009a) reported values of 0.38 and 0.36 for GFW and CFW respectively for South African Merino sheep. These estimates are lower than the values obtained in this study, as well as the estimates reported by Olivier et al. (2006) on the same flock. The contribution of the maternal additive variance on fleece weight traits estimated in this study, as well as in the literature were consistently below 10% of the total phenotypic variation (Safari et al., 2005; Olivier et al., 2006a; Safari et al., 2007a; Matebesi et al., 2009a).

The h^2_a estimate for CY in this study (see Table 3.4) was at the higher of the end of the range (0.34 to 0.72) of estimates reported in the literature (Lewer et al., 1994; Ponzoni et al., 1995; Brash et al., 1997; Cloete et al., 1998a; Cloete et al., 2002a; Safari et al., 2007a; Matebesi et al., 2009a). Sherlock et al. (2003) estimated a much lower h^2_a (0.34) for an ultrafine wool Merino flock when c^2_{mpe} (0.11) were included in the model.

Fibre diameter is one of the most important traits in any wool sheep enterprise, as is the heritability of FD, as it has an effect on the selection progress. Heritability estimates reported in the literature for FD are high and the average of values reported by Safari et al. (2005) was 0.57. This is consistent with the values obtained in this study for FD (Table 3.4), as well as other estimates reported for South African Merino sheep of 0.52 (Cloete et al., 2006), 055 (Olivier & Cloete, 2007) and 0.68 (Matebesi et al., 2009a). However, the h^2_a for FD6 (0.37) was appreciably lower than literature estimates, while the h^2_a for FD12 (0.72) was on the higher end of the range of comparable estimates (Safari et al., 2005; Olivier & Cloete, 2007; Safari et al., 2007a; Matebesi et al., 2009a; Brown et al., 2010).

In most of the studies in the literature the direct additive effect was included as the only random effect. Where the maternal additive effect was included, the h^2_m estimates were close to zero. This is similar to the estimates obtained in this study for FD that ranged from 0.01 for FD12 to 0.05 for FD6. In contrast, Sherlock et al. (2003) estimated a c^2_{mpe} of 0.26, with a h^2_a of 0.42 in an ultrafine wool Merino flock. It is thus evident from the current study, as well as the literature that expression of fibre diameter is mainly determined by direct additive gene effects.

The h^2_a estimates reported in the literature (Safari et al., 2005; Cloete et al., 2006) for SL were in agreement with the estimate reported in Table 3.4 for this study. However, the estimate of the current study was higher than the estimate reported by Olivier & Cloete (2007; 0.26), but similar to the value of 0.37 reported by Matebesi et al. (2009a) for South African Merino sheep. SDFD and CVFD h^2_a estimates of 0.56 and 0.52 respectively were within the range of 0.37 to 0.74 reported in the literature (Ponzoni et al., 1995; Swan et al., 1995; Li et al., 1999; Hill, 2001; Wuliji et al., 2001; Brown et al., 2002a; Lee et al., 2002b; Cloete et al., 2006; Matebesi et al., 2009a).

All the studies in the literature that reported on crimp frequency included only the direct additive effect. These results are in contrast with the present study where the maternal additive effect was also included in the final model. Nevertheless, the h^2_a estimated in this study was consistent with the values reported in the literature (Ponzoni et al., 1995; Taylor et al., 1997; Taylor et al., 1999; Hill, 2001; Wuliji et al., 2001), possibly as a result of the modest contribution of h^2_m.

The wrinkle score h^2_a estimate obtained in this study was higher than the values estimated by Groenewald et al. (1999) and Cloete et al. (1998a), but it was similar to the estimate obtained by Cloete et al. (2006) for South African Merino sheep. Furthermore, the latter studies did not include a maternal effect in the estimation. In contrast to these studies, Brown et al. (2010) estimated a lower h^2_a than the current study, while their estimate for h^2_m was similar.

As previously indicated, SS is a very important trait for wool farmers that are not normally measured due to cost implications. The h^2_a of the current study was lower than the value reported by Herselman et al. (2006) for the same flock and Matebesi et al. (2009a) for another South African Merino flock. The difference between the present study and the previous study by Herselman et al. (2006) on the same flock can be related to more data that accrued as is also reflected by a lower standard error for the present estimates. The present h^2_a estimate of 0.26 for SS was somewhat below those of Pollot & Greeff (2004) and Brown et al. (2010), as well as the average SS from a number of literature sources derived by Safari et al. (2005). However, Cloete et al. (2006) and Greeff et al. (2013) reported h^2_a estimates of 0.23 and 0.25 respectively that were quite similar to the current estimate.

The estimates reported in the literature for comfort factor ranged from 0.30 to 0.55 (Pollott & Greeff, 2004; Notter et al., 2007; Greeff et al., 2013). These estimates were lower than the estimate of 0.81 obtained in this study (Table 3.4). This might be the result of much less variation in comfort factor in this study when compared to the results reported in the literature. The average CF in this study was almost 100% (Table 3.2), which means that the overwhelming majority of animals of the Cradock fine wool Merino stud had no fibres coarser than 30 µm.

The genetic (r_g), maternal (r_m), environmental (r_e) and phenotypic (r_p) correlations among the body weights at different ages and birth coat score (± s.e.) are summarised in Table 3.5. It is evident from this table that all the correlations among the body weights were significant (correlations reached levels of double their corresponding s.e.). In contrast, the genetic correlations between BirthC and the different body weights were close to zero and not significant. The r_m between BirthC and the body weights were low to moderate and ranged from 0.10 (BW12) to 0.42 (BirthW), with a tendency to decrease with age. These estimates are consistent with values reported by Cloete et al. (2003) and in Chapter 5 for body weights from birth to weaning. No other comparable correlations were found in the literature.

Table 3.5 Genetic, maternal, environmental and phenotypic correlations among the body weights at different ages and birth coat score (± s.e.)

Trait	BirthW	PWW	WW	BW6	BW12	BW15
Additive genetic correlations						
BirthC	-0.03 ± 0.09	0.00 ± 0.11	0.02 ± 0.11	0.11 ± 0.09	-0.01 ± 0.07	-0.08 ± 0.07
BirthW		0.54 ± 0.09	0.37 ± 0.01	0.26 ± 0.10	0.24 ± 0.08	0.24 ± 0.08
PWW			0.79 ± 0.06	0.62 ± 0.07	0.65 ± 0.06	0.64 ± 0.07
WW				0.91 ± 0.03	0.83 ± 0.04	0.81 ± 0.04
BW6					0.91 ± 0.02	0.87 ± 0.02
BW12						0.98 ± 0.01
Maternal genetic correlations						
BirthC	0.42 ± 0.16	0.24 ± 0.19	0.13 ± 0.19	0.15 ± 0.16	0.10 ± 0.22	0.18 ± 0.22
BirthW		0.67 ± 0.07	0.59 ± 0.08	0.51 ± 0.08	0.61 ± 0.11	0.53 ± 0.10
PWW			0.99 ± 0.01	0.96 ± 0.03	0.93 ± 0.06	0.92 ± 0.07
WW				0.98 ± 0.01	0.99 ± 0.03	1.00 ± 0.04
BW6					0.97 ± 0.04	0.92 ± 0.05
BW12						0.98 ± 0.02
Environmental correlations						
BirthC	0.08 ± 0.03	0.04 ± 0.02	0.03 ± 0.02	-0.02 ± 0.03	0.00 ± 0.03	0.02 ± 0.03
BirthW		0.46 ± 0.02	0.36 ± 0.02	0.3 ± 0.02	0.32 ± 0.03	0.29 ± 0.03
PWW			0.77 ± 0.01	0.64 ± 0.01	0.45 ± 0.02	0.41 ± 0.02
WW				0.79 ± 0.01	0.55 ± 0.02	0.50 ± 0.02
BW6					0.62 ± 0.02	0.54 ± 0.02
BW12						0.77 ± 0.01
Phenotypic correlations						
BirthC	0.07 ± 0.02	0.04 ± 0.02	0.03 ± 0.02	0.03 ± 0.02	0.00 ± 0.02	-0.02 ± 0.02
BirthW		0.48 ± 0.01	0.37 ± 0.01	0.31 ± 0.01	0.29 ± 0.01	0.28 ± 0.01
PWW			0.80 ± 0.01	0.67 ± 0.01	0.51 ± 0.01	0.47 ± 0.01
WW				0.82 ± 0.00	0.63 ± 0.01	0.58 ± 0.01
BW6					0.75 ± 0.01	0.68 ± 0.01
BW12						0.88 ± 0.00

"-" – not fitted; BirthC – birth coat score; Body weight: BirhtW – birth; PWW – pre-weaning (42 days of age); WW – weaning; BW6 –6 months of age; BW12 –12 months of age; BW15 –15 months of age

The genetic correlations between birth weight and pre-weaning weight were higher than the correlations between birth weight and post weaning body weights (Table 3.5). These correlations were within the range of values reported in the literature (Lewer et al., 1994; Nasholm & Danell, 1996; Yazdi et al., 1997; Neser et al., 2001; Wuliji et al., 2001; Duguma et al., 2002a; Abegaz et al., 2005; Safari et al., 2005; Huisman & Brown, 2008). The genetic correlations among weaning weight and post weaning body weights ranged from 0.81 to 0.98 and were in the same order as the values reported in the literature (Brash et al., 1994b, 1994c; Lewer et al., 1994; Al-Shorepy & Notter, 1996; Snyman et al., 1998c; Abegaz et al., 2005; Safari et al., 2005; Huisman & Brown, 2008).

It is evident from this table that adjacent weights had the highest r_g and that these correlations decreased as the time lapse between the records increased. The r_p and r_e followed the same pattern as the r_g but the estimates were lower in magnitude. The r_m between maternal effects of BirthW and the other body weights ranged from 0.53 to 0.67, which was much lower than the corresponding range (0.92 to 1.00) among the other body weights. These correlations were within the range (0.22 to 0.96) reported by Wuliji et al. (2001), Vaez Torshizi et al. (1996), Abegaz et al. (2005) and Huisman & Brown (2008). The lowest

of these correlations in the literature, were also between birth weight and older weights, which is similar to the estimates of the current study.

The genetic (r_g), maternal (r_m), environmental (r_e) and phenotypic (r_p) correlations among the wool characteristics (± s.e.) are summarised in Tables 3.6 to 3.9. It is evident from these tables that almost all r_g, r_p, and r_e among traits were significant, while relatively few of the r_m were significant. The r_g between FD recorded at different ages ranged from 0.89 to 0.96, while the r_m between FD12 and FD amounted to 0.87. These r_g is in agreement with values reported by Ponzoni et al. (1995), Brash et al. (1997) and Hill (2001). No corresponding r_m estimates between fibre diameters at different ages was found in the literature.

Table 3.6 Genetic, maternal, environmental and phenotypic correlations among FD6, FD12, GFW, CFW, FD, SL and CY (± s.e.)

Trait	FD12	GFW	CFW	FD	SL	CY
	Additive genetic correlations					
FD6	0.91 ± 0.02	0.11 ± 0.06	0.10 ± 0.06	0.89 ± 0.03	0.06 ± 0.06	0.06 ± 0.05
FD12		0.24 ± 0.04	0.18 ± 0.04	0.96 ± 0.01	0.06 ± 0.05	-0.02 ± 0.04
GFW			0.89 ± 0.01	0.31 ± 0.05	0.35 ± 0.05	0.13 ± 0.05
CFW				0.24 ± 0.05	0.48 ± 0.05	0.49 ± 0.04
FD					0.08 ± 0.05	0.03 ± 0.04
SL						0.44 ± 0.04
	Maternal genetic correlations					
FD6	0.16 ± 0.24	0.06 ± 0.17	0.08 ± 0.20	0.19 ± 0.23	-	-
FD12		0.04 ± 0.26	0.04 ± 0.28	0.87 ± 0.03	-	-
GFW			0.82 ± 0.05	-0.20 ± 0.25	-	-
CFW				-0.13 ± 0.26	-	-
	Environmental correlations					
FD6	0.25 ± 0.03	0.14 ± 0.03	0.12 ± 0.03	0.23 ± 0.03	0.04 ± 0.03	-0.07 ± 0.03
FD12		0.25 ± 0.04	0.19 ± 0.04	0.58 ± 0.03	0.07 ± 0.04	-0.08 ± 0.04
GFW			0.86 ± 0.01	0.20 ± 0.04	0.17 ± 0.03	0.05 ± 0.04
CFW				0.17 ± 0.04	0.23 ± 0.03	0.28 ± 0.03
FD					0.07 ± 0.03	-0.10 ± 0.04
SL						0.16 ± 0.03
	Phenotpic correlations					
FD6	0.57 ± 0.01	0.12 ± 0.02	0.11 ± 0.02	0.54 ± 0.01	0.05 ± 0.02	0.00 ± 0.02
FD12		0.23 ± 0.02	0.18 ± 0.02	0.86 ± 0.01	0.06 ± 0.02	-0.04 ± 0.02
GFW			0.87 ± 0.01	0.25 ± 0.02	0.25 ± 0.02	0.10 ± 0.02
CFW				0.20 ± 0.02	0.34 ± 0.01	0.40 ± 0.01
FD					0.07 ± 0.02	-0.02 ± 0.02
SL						0.30 ± 0.02

"-" – not fitted; Fibre diameter: FD6 –6 months of age; FD12 –12 months of age; FD – 15 months of age; GFW – greasy fleece weight; CFW – clean fleece weight; SL – staple length; CY – clean yield

The correlations between GFW and CFW were very high. This was expected, as CFW is a function of GFW. The derived estimates were consistent with comparable estimates in the literature (Safari et al., 2005; Huisman & Brown, 2009; Matebesi et al., 2009a). The relationships of CY with GFW and CFW were quite different in magnitude as these correlations were low (0.05 to 0.13) and moderate (0.28 to 0.49) respectively. The correlations between SL and the fleece weights were moderate ranging from 0.17 to 0.48. These estimates were in accordance with the results of Huisman & Brown (2009) and Matebesi et al. (2009a).

The r_g of FD with GWF and CFW were low to moderate and unfavourable (i.e. positive). However, these correlations were lower than estimates published by Huisman & Brown (2009), but higher than the previous estimates reported by Olivier & Cloete (2007) and Matebesi et al. (2009a) for South African Merino sheep but were within the range (0.14 to 0.51) of estimates cited by Safari et al. (2005).

Table 3.7 Genetic, maternal, environmental and phenotypic correlations between FD6, FD12, GFW, CFW, FD, SL and CY and Crimp, Duer, SDFD, CVFD and Wrinkle (± s.e.)

Trait	Crimp	Duer	SDFD	CVFD	Wrinkle
Additive genetic correlations					
FD6	-0.01 ± 0.07	0.67 ± 0.05	0.56 ± 0.07	-0.09 ± 0.07	0.04 ± 0.06
FD12	-0.04 ± 0.05	0.78 ± 0.02	0.49 ± 0.06	-0.26 ± 0.05	0.11 ± 0.05
GFW	-0.49 ± 0.05	-0.20 ± 0.05	0.35 ± 0.07	0.21 ± 0.06	0.54 ± 0.04
CFW	-0.60 ± 0.04	-0.32 ± 0.05	0.31 ± 0.08	0.14 ± 0.06	0.40 ± 0.05
FD	-0.11 ± 0.05	0.72 ± 0.03	0.54 ± 0.06	-0.13 ± 0.06	0.18 ± 0.05
SL	-0.66 ± 0.04	-0.44 ± 0.05	-0.02 ± 0.09	-0.05 ± 0.06	-0.42 ± 0.05
CY	-0.45 ± 0.04	-0.31 ± 0.05	-0.05 ± 0.08	-0.13 ± 0.06	-0.09 ± 0.05
Maternal genetic correlations					
FD6	-0.46 ± 0.24	-	-	-	-0.49 ± 0.22
FD12	-0.76 ± 0.34	-	-	-	-0.56 ± 0.42
GFW	-0.89 ± 0.16	-	-	-	0.51 ± 0.18
CFW	-0.87 ± 0.16	-	-	-	0.58 ± 0.19
FD	-0.54 ± 0.31	-	-	-	-0.59 ± 0.36
Environmental correlations					
FD6	0.04 ± 0.03	0.18 ± 0.03	0.17 ± 0.03	-0.01 ± 0.03	0.07 ± 0.03
FD12	0.09 ± 0.04	0.39 ± 0.03	0.19 ± 0.05	-0.04 ± 0.05	0.18 ± 0.04
GFW	0.02 ± 0.03	0.17 ± 0.03	0.02 ± 0.05	-0.10 ± 0.04	0.23 ± 0.04
CFW	0.01 ± 0.03	0.14 ± 0.03	0.01 ± 0.05	-0.08 ± 0.04	0.16 ± 0.04
FD	0.06 ± 0.03	0.63 ± 0.02	0.24 ± 0.04	-0.10 ± 0.04	0.12 ± 0.04
SL	0.05 ± 0.03	0.10 ± 0.03	-0.04 ± 0.03	-0.09 ± 0.02	0.06 ± 0.03
CY	-0.04 ± 0.03	-0.07 ± 0.03	-0.09 ± 0.04	-0.08 ± 0.04	-0.11 ± 0.04
Phenotypic correlations					
FD6	0.00 ± 0.02	0.38 ± 0.02	0.32 ± 0.02	-0.05 ± 0.02	0.03 ± 0.02
FD12	0.00 ± 0.02	0.62 ± 0.01	0.35 ± 0.02	-0.17 ± 0.02	0.12 ± 0.02
GFW	-0.26 ± 0.02	-0.02 ± 0.02	0.18 ± 0.02	0.06 ± 0.02	0.41 ± 0.01
CFW	-0.32 ± 0.01	-0.10 ± 0.02	0.16 ± 0.02	0.04 ± 0.02	0.31 ± 0.02
FD	-0.05 ± 0.02	0.67 ± 0.01	0.39 ± 0.02	-0.12 ± 0.02	0.14 ± 0.02
SL	-0.26 ± 0.01	-0.15 ± 0.02	-0.03 ± 0.02	-0.12 ± 0.03	-0.17 ± 0.02
CY	-0.26 ± 0.02	-0.20 ± 0.02	-0.07 ± 0.02	-0.10 ± 0.02	-0.09 ± 0.02

"-" – not fitted; Fibre diameter: FD6 –6 months of age; FD12 –12 months of age; FD – 15 months of age; GFW – greasy fleece weight; CFW – clean fleece weight; SL – staple length; CY – clean yield; Crimp – number of crimps per 25 mm; Duer – Duerden; SDFD – standard deviation of fibre diameter; CVFD - coefficient of variation of fibre diameter; Wrinkle – wrinkle score; CF – comfort factor; SS – staple strength

The correlations among FD and SL and CY were low and insignificant. These estimates were within the values reported in the literature that ranged from -0.18 to 0.37 (Lewer et al., 1994; Swan et al., 1995; Purvis & Swan, 1997; Cloete et al. 1998b; Wuliji et al., 1998; Cloete et al., 2002a).

Positive r_g estimates were derived between FD and Duer, SDFD, Wrinkle and SS, while the corresponding estimates with Crimp, CVFD and CF were negative. Similar results were reported in the literature (Swan et al., 1995; Brash et al., 1997; Greeff & Karlsson, 1999; Hill, 2001; Cloete et al., 2006; Huisman & Brown, 2009; Matebesi et al., 2009a). The unfavourable correlation between FD and CVFD

makes it imperative that the CVFD of animals are monitored or CVFD is included in selection objectives when reducing FD is a priority. This will ensure that CVFD and SS are not affected adversely.

The r_g of GFW and CFW with SDFD and CVFD (Table 3.8) are unfavourable (positively correlated), which were similar to the relationship of fleece weight with FD. These estimates were within the range (-0.10 to 0.34) reported in the literature (Swan et al., 1995; Brash et al., 1997; Greeff & Karlsson, 1999; Hill, 2001; Brown et al., 2002b; Huisman & Brown, 2009; Matebesi et al., 2009a). These estimates were in contrast to the highly favourable correlation of -0.85 estimated by Di et al. (2011) for Chinese superfine wool Merino sheep. The r_g estimated between SDFD and FD was favourable (moderate positive) and the r_g between CVFD and FD was low, but also favourable. The estimate between SDFD and FD concurred with the values reported in the literature that ranged from 0.44 to 0.64 (Swan et al., 1995; Hill, 2001; Matebesi et al., 2009a; Di et al., 2011). The r_g estimates reported in the literature between CVFD and FD ranged from -0.27 to 0.24 (Swan et al., 1995; Brash et al., 1997; Purvis & Swan, 1997; Greeff & Karlsson, 1998, 1999; Hill, 2001; Brown et al., 2002b; Cloete et al., 2002a; Lee et al., 2002b; Huisman & Brown, 2009; Matebesi et al., 2009a) and the estimate of the current study were within this range. Di et al. (2011) reported a r_g between CVFD and FD that was highly favourable and much lower than the values reported in the literature.

Table 3.8 Genetic, maternal, environmental and phenotypic correlations between FD6, FD12, GFW, CFW, FD, SL and CY and CF and SS (± s.e.)

Trait	CF	SS
Additive genetic correlations		
FD6	-0.65 ± 0.05	0.44 ± 0.09
FD12	-0.64 ± 0.05	0.61 ± 0.06
GFW	-0.32 ± 0.06	0.24 ± 0.09
CFW	-0.23 ± 0.06	0.27 ± 0.09
FD	-0.66 ± 0.05	0.51 ± 0.07
SL	-0.01 ± 0.07	0.06 ± 0.10
CY	0.02 ± 0.06	0.39 ± 0.08
Environmental correlations		
FD6	-0.12 ± 0.04	0.11 ± 0.03
FD12	-0.20 ± 0.05	0.21 ± 0.04
GFW	-0.01 ± 0.05	0.24 ± 0.04
CFW	-0.01 ± 0.05	0.15 ± 0.04
FD	-0.66 ± 0.05	0.19 ± 0.04
SL	0.04 ± 0.04	0.15 ± 0.03
CY	0.08 ± 0.05	0.09 ± 0.04
Phenotypic correlations		
FD6	-0.37 ± 0.02	0.21 ± 0.02
FD12	-0.46 ± 0.02	0.36 ± 0.02
GFW	-0.20 ± 0.02	0.21 ± 0.02
CFW	-0.14 ± 0.02	0.18 ± 0.02
FD	-0.48 ± 0.02	0.30 ± 0.02
SL	0.01 ± 0.02	0.12 ± 0.02
CY	0.04 ± 0.02	0.21 ± 0.02

Fibre diameter: FD6 –6 months of age; FD12 –12 months of age; FD – 15 months of age; GFW – greasy fleece weight; CFW – clean fleece weight; SL – staple length; CY – clean yield; CF – comfort factor; SS – staple strength

The r_g estimates between Wrinkle and GFW and CFW were unfavourable. These estimates were in agreement with the range (0.19 to 0.39) reported in the literature (Matebesi et al., 2009c; Mortimer et al., 2009). However, FD and SL were favourably correlated with Wrinkle. Mortimer et al. (2009) reported low, but favourable correlations between wrinkle score and FD, while their r_g between wrinkle score and SL was unfavourable.

The genetic relationships of SS with GFW and CFW (Table 3.8) were moderately favourable, as well as between SS and SL. However, it is important to note that r_g between SS and FD, which is the two factors with the biggest influence on the price of wool, was unfavourable. The same tendency was observed for FD6 and FD12 with SS. The r_g estimates between SS and fleece weights in the current study concurred with the estimates reported by Wuliji et al. (1998) and Hill (2001), but were higher than the values reported by Greeff & Karlsson (1999) and Huisman & Brown (2009). Swan et al. (1995) and Matebesi et al. (2009a) reported unfavourable (negative) r_g between SS and fleece traits. The unfavourable r_g estimated in the current study between SS and FD was in agreement with the values reported in the literature (Swan et al., 1995; Wuliji et al., 1998; Greeff & Karlsson, 1999; Huisman & Brown, 2009; Matebesi et al., 2009a).

Table 3.9 Genetic, maternal, environmental and phenotypic correlations among Crimp, Duer, SDFD, CVDD, Wrinkle, CF and SS (± s.e.)

Trait	Duer	SDFD	CVFD	Wrinkle	CF	SS
	Additive genetic correlations					
Crimp	0.61 ± 0.03	-0.25 ± 0.08	-0.26 ± 0.06	0.09 ± 0.06	0.13 ± 0.06	0.27 ± 0.09
Duer		0.30 ± 0.08	-0.27 ± 0.06	0.12 ± 0.05	-0.37 ± 0.06	0.61 ± 0.07
SDFD			0.83 ± 0.02	0.40 ± 0.08	-0.84 ± 0.02	-0.39 ± 0.08
CVFD				0.25 ± 0.06	-0.56 ± 0.05	-0.66 ± 0.06
Wrinkle					-0.31 ± 0.06	0.28 ± 0.09
CF						-0.04 ± 0.10
	Maternal genetic correlations					
Crimp				-0.45 ± 0.29	-	-
	Environmental correlations					
Crimp	0.77 ± 0.01	-0.02 ± 0.04	-0.02 ± 0.03	0.01 ± 0.03	-0.01 ± 0.04	-0.02 ± 0.04
Duer		0.12 ± 0.04	-0.08 ± 0.03	0.12 ± 0.03	-0.14 ± 0.04	0.10 ± 0.04
SDFD			0.90 ± 0.01	0.02 ± 0.04	-0.18 ± 0.06	-0.08 ± 0.04
CVFD				0.01 ± 0.04	-0.16 ± 0.05	-0.20 ± 0.03
Wrinkle					0.03 ± 0.05	0.00 ± 0.04
CF						-0.16 ± 0.06
	Phenotypic correlations					
Crimp	0.69 ± 0.01	-0.12 ± 0.02	-0.13 ± 0.02	0.04 ± 0.02	0.07 ± 0.02	0.08 ± 0.02
Duer		0.2 ± 0.02	-0.18 ± 0.02	0.12 ± 0.02	-0.27 ± 0.02	0.29 ± 0.02
SDFD			0.86 ± 0.01	0.20 ± 0.02	-0.61 ± 0.01	-0.20 ± 0.02
CVFD				0.13 ± 0.02	-0.38 ± 0.02	-0.37 ± 0.02
Wrinkle					-0.17 ± 0.02	0.11 ± 0.02
CF						-0.07 ± 0.03

Crimp – number of crimps per 25 mm; Duer – Duerden; SDFD – standard deviation of fibre diameter; CVFD - coefficient of variation of fibre diameter; Wrinkle – wrinkle score; CF – comfort factor; SS – staple strength

Correlations between Crimp and Duer, as well as between SDFD and CVFD were moderate to high (Table 3.9). This outcome can be expected, as Duer and CVFD are functions of Crimp and SDFD.

Correlations reported in the literature between SDFD and CVFD ranged from 0.76 to 0.83 (Swan et al., 1995; Hill, 2001). However, no corresponding correlations were found in the literature for Crimp and Duer.

SS is positively related to Crimp and Duer, but negatively correlated to SDFD and CVFD (Table 3.10). The latter estimates were consistent with estimates (-0.35 to -0.58) published in the literature (Swan et al. 1995; Greeff & Karlsson, 1998, 1999; Hill 2001). Phenotypic correlations were similar in sign to the corresponding r_g, but smaller in magnitude.

The genetic, maternal, environmental and phenotypic correlations between body weights, BirthC and wool traits are summarised from Tables 3.10 to 3.12. The genetic correlations between fleece weight and BirthW and PWW were lowly favourable and were in the same order as estimates reported by Brash et al. (1994b) and Wuliji et al. (1998). The r_g estimates between BW15 and GFW and CFW were close to zero and not significant. These estimates were lower than the values reported in the literature (Lewer et al., 1994; Brash et al., 1997; Snyman et al., 1998c; Rose & Pepper, 1999; Greeff & Karlsson, 1999; Matebesi et al., 2009a; Di et al., 2011).

Body weights at different ages, excluding birth weight, were moderately and unfavourably correlated with fibre diameter at different ages (Table 3.10). These estimates were within the range of corresponding correlations reported in the literature (Brash et al., 1994a; Lewer et al., 1994; Purvis & Swan, 1997; Cloete et al., 1998a; Snyman et al., 1998c; Safari et al., 2005; Huisman & Brown, 2008; Matebesi et al., 2009a). The phenotypic correlations between the body weights, fleece weight and fibre diameters were low to moderate and ranged from -0.05 to 0.35.

BirthC was lowly and positively correlated to all the wool traits (Table 3.11), which implies that the more hairy type of lamb tended to produce more wool with coarser and longer staples. These r_g estimated in this study was slightly higher than the estimates reported by Ponzoni et al. (1996) and Kemper et al. (2003) between BirthC, fleece weight and FD. The corresponding r_m with FD were also moderate negative, while the r_m with fleece weight were positive.

The r_g estimates between BirthC and SDFD and CVFD were lowly to moderately positive (Table 3.11). The estimate between BirthC and CVFD of the current study concurred with the estimate reported by Kemper et al. (2003), but was lower than the corresponding estimate reported by Ponzoni et al. (1996). The r_g estimates among BW12, BW15, SDFD and CVFD were favourable (negatively correlated). The estimates of the current study were higher than the range (0.02 to -0.25) reported in the literature (Brash et al., 1997; Purvis & Swan, 1997; Greeff & Karlsson, 1998, 1999; Brown et al., 2002a, 2002b; Cloete et al., 2002a; Lee et al., 2002b; Huisman & Brown, 2008; Matebesi et al., 2009a; Di et al., 2011). Body weight at 12 and 15 months of age were favourably correlated with Wrinkle score. These estimates were in contrast to the unfavourable correlations between body weight and wrinkle score reported by Matebesi et al. (2009c) and Mortimer et al. (2009).

Table 3.5 Genetic, maternal, environmental and phenotypic correlations between body weights and BirthC and FD6, FD12, GFW, CFW, FD and SL (± s.e.)

Trait	FD6	FD12	GFW	CFW	FD	SL
Additive genetic correlations						
BirthC	0.14 ± 0.07	0.20 ± 0.06	0.23 ± 0.07	0.20 ± 0.07	0.15 ± 0.06	0.22 ± 0.07
BirthW	0.07 ± 0.09	0.05 ± 0.07	0.24 ± 0.08	0.21 ± 0.08	0.12 ± 0.07	0.09 ± 0.08
PWW	0.26 ± 0.10	0.27 ± 0.08	0.25 ± 0.09	0.21 ± 0.09	0.30 ± 0.09	-0.02 ± 0.10
WW	0.28 ± 0.11	0.42 ± 0.08	0.13 ± 0.10	0.03 ± 0.10	0.42 ± 0.08	0.06 ± 0.11
BW6	0.23 ± 0.08	0.44 ± 0.06	0.15 ± 0.07	0.13 ± 0.07	0.46 ± 0.06	0.10 ± 0.08
BW12	0.15 ± 0.07	0.34 ± 0.05	0.13 ± 0.06	0.09 ± 0.06	0.36 ± 0.05	0.13 ± 0.06
BW15	0.16 ± 0.07	0.28 ± 0.05	0.03 ± 0.06	0.03 ± 0.06	0.30 ± 0.05	0.10 ± 0.06
Maternal genetic correlations						
BirthC	-0.26 ± 0.23	-0.22 ± 0.3	0.36 ± 0.17	0.35 ± 0.20	-0.15 ± 0.29	-
BirthW	-0.26 ± 0.12	-0.54 ± 0.16	0.79 ± 0.08	0.87 ± 0.08	-0.48 ± 0.17	-
PWW	-0.12 ± 0.17	-0.51 ± 0.23	0.73 ± 0.10	0.77 ± 0.11	-0.51 ± 0.25	-
WW	0.11 ± 0.16	-0.36 ± 0.25	0.74 ± 0.11	0.81 ± 0.12	-0.38 ± 0.25	-
BW6	-0.05 ± 0.14	-0.42 ± 0.23	0.59 ± 0.10	0.61 ± 0.12	-0.51 ± 0.22	-
BW12	-0.17 ± 0.21	-0.30 ± 0.29	0.87 ± 0.11	0.97 ± 0.11	-0.54 ± 0.30	-
BW15	-0.09 ± 0.20	-0.34 ± 0.3	0.68 ± 0.13	0.72 ± 0.14	-0.50 ± 0.30	-
Environmental correlations						
BirthC	0.06 ± 0.03	-0.02 ± 0.04	0.06 ± 0.03	0.07 ± 0.03	0.02 ± 0.04	-0.03 ± 0.03
BirthW	0.00 ± 0.03	-0.08 ± 0.04	0.29 ± 0.03	0.30 ± 0.03	-0.10 ± 0.03	0.00 ± 0.03
PWW	0.14 ± 0.02	-0.02 ± 0.03	0.35 ± 0.03	0.36 ± 0.03	-0.06 ± 0.03	0.05 ± 0.02
WW	0.18 ± 0.02	0.00 ± 0.04	0.41 ± 0.03	0.42 ± 0.03	-0.05 ± 0.03	0.06 ± 0.02
BW6	0.15 ± 0.03	0.11 ± 0.04	0.46 ± 0.03	0.44 ± 0.03	0.01 ± 0.03	0.10 ± 0.03
BW12	0.15 ± 0.03	0.26 ± 0.04	0.56 ± 0.03	0.56 ± 0.03	0.14 ± 0.04	0.13 ± 0.03
BW15	0.10 ± 0.03	0.16 ± 0.04	0.53 ± 0.03	0.54 ± 0.03	0.14 ± 0.04	0.15 ± 0.03
Phenotypic correlations						
BirthC	0.07 ± 0.02	0.09 ± 0.02	0.11 ± 0.02	0.09 ± 0.02	0.07 ± 0.02	0.07 ± 0.02
BirthW	-0.01 ± 0.02	-0.04 ± 0.02	0.30 ± 0.02	0.30 ± 0.02	-0.03 ± 0.02	0.03 ± 0.01
PWW	0.14 ± 0.01	0.05 ± 0.02	0.31 ± 0.01	0.30 ± 0.02	0.04 ± 0.02	0.03 ± 0.01
WW	0.18 ± 0.01	0.12 ± 0.02	0.31 ± 0.01	0.29 ± 0.02	0.09 ± 0.02	0.05 ± 0.01
BW6	0.16 ± 0.02	0.22 ± 0.02	0.34 ± 0.02	0.32 ± 0.02	0.17 ± 0.02	0.09 ± 0.02
BW12	0.14 ± 0.02	0.28 ± 0.02	0.36 ± 0.02	0.35 ± 0.02	0.24 ± 0.02	0.13 ± 0.02
BW15	0.12 ± 0.02	0.22 ± 0.02	0.28 ± 0.02	0.29 ± 0.02	0.21 ± 0.02	0.12 ± 0.02

"-" – not fitted; BirthC – birth coat score; Body weight: BirhtW – birth; PWW – pre-weaning (42 days of age); WW – weaning; BW6 – 6 months of age; BW12 – 12 months of age; BW15 – 15 months of age; fibre diameter: FD6 – 6 months of age; FD12 – 12 months of age; FD – 15 months of age; GFW – greasy fleece weight; CFW – clean fleece weight; SL – staple length

Table 3.6 Genetic, maternal, environmental and phenotypic correlations between body weights and BirthC and CY, Crimp, Duer, SDFD, CVFD and Wrinkle (± s.e.)

Trait	CY	Crimp	Duer	SDFD	CVFD	Wrinkle
	Additive genetic correlations					
BirthC	-0.11 ± 0.06	-0.17 ± 0.07	-0.06 ± 0.06	0.30 ± 0.09	0.20 ± 0.07	0.12 ± 0.07
BirthW	0.13 ± 0.07	-0.11 ± 0.08	-0.14 ± 0.07	0.06 ± 0.10	0.00 ± 0.08	0.17 ± 0.08
PWW	0.04 ± 0.09	0.06 ± 0.10	0.23 ± 0.09	-0.02 ± 0.12	-0.19 ± 0.10	0.00 ± 0.10
WW	-0.09 ± 0.09	-0.04 ± 0.10	0.24 ± 0.09	-0.05 ± 0.13	-0.31 ± 0.09	-0.16 ± 0.10
BW6	-0.03 ± 0.07	0.01 ± 0.08	0.26 ± 0.07	-0.08 ± 0.10	-0.36 ± 0.07	-0.20 ± 0.08
BW12	-0.04 ± 0.05	0.06 ± 0.06	0.26 ± 0.06	-0.24 ± 0.08	-0.40 ± 0.06	-0.29 ± 0.06
BW15	-0.04 ± 0.05	0.00 ± 0.06	0.19 ± 0.06	-0.26 ± 0.08	-0.40 ± 0.06	-0.32 ± 0.06
	Maternal genetic correlations					
BirthC	-	-0.05 ± 0.26	-	-	-	-0.58 ± 0.27
BirthW	-	-0.37 ± 0.15	-	-	-	0.53 ± 0.15
PWW	-	-0.14 ± 0.19	-	-	-	0.24 ± 0.19
WW	-	-0.22 ± 0.20	-	-	-	0.08 ± 0.20
BW6	-	-0.34 ± 0.17	-	-	-	0.10 ± 0.17
BW12	-	-0.6 ± 0.24	-	-	-	0.28 ± 0.23
BW15	-	-0.27 ± 0.23	-	-	-	0.26 ± 0.23
	Environmental correlations					
BirthC	0.08 ± 0.03	0.01 ± 0.03	0.03 ± 0.03	0.13 ± 0.04	0.13 ± 0.03	0.02 ± 0.03
BirthW	0.12 ± 0.03	-0.03 ± 0.03	-0.06 ± 0.03	-0.01 ± 0.03	0.03 ± 0.03	0.10 ± 0.03
PWW	0.14 ± 0.03	-0.02 ± 0.02	-0.04 ± 0.03	-0.03 ± 0.03	-0.01 ± 0.03	0.15 ± 0.03
WW	0.14 ± 0.03	0.03 ± 0.03	0.02 ± 0.03	-0.05 ± 0.03	-0.04 ± 0.03	0.13 ± 0.03
BW6	0.12 ± 0.03	0.08 ± 0.03	0.09 ± 0.03	-0.07 ± 0.03	-0.09 ± 0.03	0.13 ± 0.03
BW12	0.08 ± 0.04	0.04 ± 0.03	0.13 ± 0.03	0.02 ± 0.04	-0.11 ± 0.04	0.21 ± 0.04
BW15	0.10 ± 0.04	0.06 ± 0.03	0.14 ± 0.03	0.02 ± 0.04	-0.07 ± 0.04	0.21 ± 0.04
	Phenotypic correlations					
BirthC	-0.01 ± 0.02	-0.06 ± 0.02	-0.01 ± 0.02	0.19 ± 0.02	0.15 ± 0.02	0.04 ± 0.02
BirthW	0.10 ± 0.02	-0.08 ± 0.02	-0.07 ± 0.02	0.01 ± 0.02	0.02 ± 0.02	0.14 ± 0.02
PWW	0.08 ± 0.02	0.00 ± 0.02	0.04 ± 0.02	-0.02 ± 0.02	-0.06 ± 0.02	0.09 ± 0.02
WW	0.05 ± 0.02	0.00 ± 0.02	0.07 ± 0.02	-0.04 ± 0.02	-0.10 ± 0.02	0.03 ± 0.02
BW6	0.04 ± 0.02	0.03 ± 0.02	0.14 ± 0.02	-0.07 ± 0.02	-0.18 ± 0.02	0.00 ± 0.02
BW12	0.01 ± 0.02	0.03 ± 0.02	0.19 ± 0.02	-0.10 ± 0.02	-0.25 ± 0.02	-0.04 ± 0.02
BW15	0.02 ± 0.02	0.02 ± 0.02	0.16 ± 0.02	-0.11 ± 0.02	-0.23 ± 0.02	-0.06 ± 0.02

"-" – not fitted; BirthC – birth coat score; Body weight: BirhtW – birth; PWW – pre-weaning (42 days of age); WW – weaning; BW6 –6 months of age; BW12 –12 months of age; BW15 –15 months of age; CY – clean yield; Crimp – number of crimps per 25 mm; Duer – Duerden; SDFD – standard deviation of fibre diameter; CVFD - coefficient of variation of fibre diameter; Wrinkle – wrinkle score

Body weight at 12 and 15 months of age were favourably correlated with SS (Table 3.12). These correlations were within the range of -0.31 to 0.50 reported in the literature. These correlations varied a lot between different studies, as well as between different body weights and SS within the same flock (Greeff & Karlsson, 1998, 1999; Huisman & Brown, 2008; Matebesi et al., 2009a).

The influence that fibre diameter has in the current market in South Africa, as well as the rest of the wool producing world, makes it imperative that relationships that FD will have with other economically important traits be quantified. It is evident from the results of this study that there are traits favourably related to FD, meaning that selection for FD will improve these traits indirectly. However, the important relationships are the unfavourable correlations, as selection for FD can have an adverse effect on these traits.

Table 3.72 Genetic, maternal, environmental and phenotypic correlations between body weights and BirthC and CF and SS (± s.e.)

Trait	CF	SS
Additive genetic correlations		
BirthC	-0.46 ± 0.07	-0.04 ± 0.10
BirthW	-0.16 ± 0.08	-0.06 ± 0.11
PWW	0.01 ± 0.11	0.12 ± 0.14
WW	-0.19 ± 0.11	0.02 ± 0.14
BW6	-0.20 ± 0.08	0.15 ± 0.11
BW12	-0.11 ± 0.07	0.27 ± 0.09
BW15	-0.03 ± 0.07	0.20 ± 0.09
Environmental correlations		
BirthC	0.02 ± 0.04	0.02 ± 0.03
BirthW	0.09 ± 0.04	0.04 ± 0.03
PWW	0.02 ± 0.04	0.09 ± 0.03
WW	0.09 ± 0.04	0.10 ± 0.03
BW6	0.08 ± 0.04	0.13 ± 0.03
BW12	0.02 ± 0.05	0.21 ± 0.04
BW15	-0.01 ± 0.05	0.18 ± 0.04
Phenotypic correlations		
BirthC	-0.21 ± 0.02	0.00 ± 0.02
BirthW	-0.02 ± 0.02	0.01 ± 0.02
PWW	0.01 ± 0.02	0.08 ± 0.02
WW	-0.01 ± 0.02	0.07 ± 0.02
BW6	-0.05 ± 0.02	0.12 ± 0.02
BW12	-0.05 ± 0.02	0.22 ± 0.02
BW15	-0.02 ± 0.02	0.17 ± 0.02

BirthC – birth coat score; Body weight: BirhtW – birth; PWW – pre-weaning (42 days of age); WW – weaning; BW6 – 6 months of age; BW12 – 12 months of age; BW15 – 15 months of age; CF – comfort factor; SS – staple strength

Fibre diameter had the highest h^2_a estimate of the economically important traits, which implies that genetic progress is possible at a faster rate compared to the other traits. However, the lack of phenotypic variance (low CV; Table 3.2) within this stud will hamper the progress that can be made within this stud. The effect of the high h^2_a will be more apparent when genetic fine woolled sires are used to genetically upgrade a flock with a divergent fibre diameter structure. This is supported by Olivier et al. (1999), who indicated that it is possible to reduce the fibre diameter of a strong wool (26 µm) Merino flock with 0.5 µm per annum, by upgrading with genetic fine wool sires. This is an important factor because there is still a large proportion of Merino wool in South Africa that is above 20 µm (Chapter 1).

The Merino sheep breed in South Africa are not only a fibre producing breed, but it also makes a large contribution to meat production in South Africa, as it is the largest sheep breed. Selection for fibre diameter should therefore not be over emphasised, but the broader picture of the production environment must be considered, and this is where the unfavourable correlations will play an important role.

The two main selection objectives of South African Merino producers are to increase body weight and to reduce fibre diameter. However, the genetic correlation between these two traits is unfavourable. This implies that selections based on only one of these two traits will adversely affect the other trait. When FD is reduced the BW of an animal will also be reduced, which will have a direct effect on the profitability of

the sheep enterprise. This is supported by the results of studies that are in agreement with the current study's results (Safari et al., 2005; Huisman & Brown, 2009; Matebesi et al., 2009).

The antagonistic relationship between FD and fleece weight and SL implies that uncontrolled selection for FD would lead to animals producing less wool and shorter wool. This will have a negative effect on the benefit of reducing FD, as a reduced SL will result in to lower realised prices for wool. Reduced fleece weight, on the other hand, will have a negative effect on the income derived from wool production, as less wool will be available to be sold. The existence of this unfavourable relationship between fleece weight and FD is supported by several authors (Safari et al., 2005; Olivier & Cloete, 2007; Huisman & Brown, 2009; Matebesi et al., 2009).

However, it is important to note that, when the selection objective included criteria based on the economically important traits that desirable changes can be achieved (Figure 3.1) when animals are selected on estimate breeding values, despite the unfavourable genetic correlations. The results of Olivier et al. (1995) support this, while Cloete et al. (2013) indicated that single-trait selection on FD will result in detrimental changes in unfavourably correlated traits.

The slight unfavourable correlation between FD and CVFD implies that reducing FD will tend to an increase in CVFD and subsequently a less uniform staple. The importance of monitoring or including CVFD in selection plans, is further accentuated by the high favourable correlation between CVFD and SS. Decreasing the CVFD of animals will result in more uniform staples with a narrower fibre distribution, which in turn will benefit SS. This correlation is in agreement with results reported in the literature (Swan et al., 1995; Greeff & Karlsson, 1998, 1999; Hill, 2001). As the measurement of SS is expensive and not practiced by wool producers in South Africa, some producers have implemented the use of this relationship as an indirect selection method for SS.

The importance of using CVFD as an indirect selection criterion together with FD, is accentuated by the unfavourable correlation between FD and SS. Selection for decreased FD will lead to a reduced staple strength, that will have a direct effect on the income derived from wool production, as tender wool (<30 N/Ktex) is discriminated against. The genetic correlations between BW15 and CVFD and SS are low to moderately favourable. This suggests that selection for increased body weight will not have a negative effect on these two traits, but will rather aid in the genetic improvement of these two traits.

It is noteworthy to take the favourable correlation between BW15 and Wrinkle into consideration. The trend in the wool industry of South Africa is to discriminate against animals that have too much wrinkles. This discrimination is supported by findings of Scholtz et al. (2010) and Greeff et al. (2013) that different wrinkles scores recorded over the body are unfavourably correlated with breech strike. However, it is important to note that both fleece weight and FD are unfavourably correlated with Wrinkle. Thus, this implies that Wrinkle will increase if selection for these traits is practiced without considering wrinkle score.

The moderate low favourable genetic correlations between BirthC and FD, as well as BirthC and fleece weight suggest that the woollier type of lamb will tend to produce more and finer wool compared to the

hairier type of lamb. Furthermore, the woollier lambs will also tend to have a lower CVFD and subsequently more uniform staples. BirthC might therefore be used at an early age as an independent culling level to aid producers in identifying the finer portion of the lamb crop.

These unfavourable correlations of FD with BW, fleece weight and SL, as well as reproduction (Chapter 4) have led to the development of a selection model for Merino sheep (Herselman, 2004; Herselman & Olivier, 2010). The aim of the selection index that is derived from the model is to calculate the weight of each of the economically important traits from the direct contribution to the profitability of a sheep enterprise. This selection tool will therefore aid producers in identifying animals with the correct combination of these traits to increase the profitability of the enterprise.

The genetic trends in body weight at 15 months of age (BW15), clean fleece weight (CFW) and fibre diameter (FD) are summarised in Table 3.13 and illustrated in Figure 3.1. These regression coefficients were obtained for the three distinct selection objective stages described in Chapter 2. During the first stage selection resulted in a 0.9% increase per annum in BW15 and a 1.4% per annum for CFW. However, no significant change in FD was observed. During stage 2 the emphasis on the reduction of FD resulted in a 0.67% decrease in FD. BW15 and CFW still increased during this period, but at a lower rate. The implementation of the profitability index for Merino sheep in 2004 lead to a similar increase in BW15 than in Stage 1, but the change per annum in CFW was the same as during Stage 2. During this stage, FD15 decrease at a slower rate than during Stage 2, but still at a faster rate than during Stage 1.

Cloete et al. (2013) reported a decrease of 0.19 ± 0.02 μm per annum in FD of a fine wool flock where the only selection objective was to decrease FD, while maintaining BW. The latter authors further reported unfavourable changes in CFW and SS, while only a slight increase was noted in live weight. Olivier et al. (1995) indicated that the selection for overall excellence based on conformation resulted in increases of 0.41% in BW, 0.45% in CFW and 0.12% in FD per annum. This selection objective was changed in the latter study to select animals on estimated breeding values for increasing BW and reducing FD. This policy resulted in a three-fold increase in the genetic change per annum for BW while the regression ($\pm$s.e.) for FD was negative at 0.157 ± 0.030 μm per annum (Olivier et al., 1995). No response was observed in CFW during this period.

Table 3.8 The genetic trends in body weight at 15 months of age (BW15), clean fleece weight (CFW) and fibre diameter (FD15)

Stage	Trend line information	BW15 (kg)	CFW (kg)	FD15 (µm)
	Mean	61.05	4.32	19.16
Stage 1	Regression coefficient	0.560 ± 0.066	0.062 ± 0.009	-0.010 ± 0.014
(1988 to 1995)	Change per annum (%)	0.918	1.428	-0.055
Stage 2	Regression coefficient	0.317 ± 0.109	0.021 ± 0.024	-0.129 ± 0.033
(1996 to 2003)	Change per annum (%)	0.520	0.486	-0.671
Stage 3	Regression coefficient	0.569 ± 0.084	0.019 ± 0.022	-0.051 ± 0.045
(2004 to 2010)	Change per annum (%)	0.932	0.439	-0.264
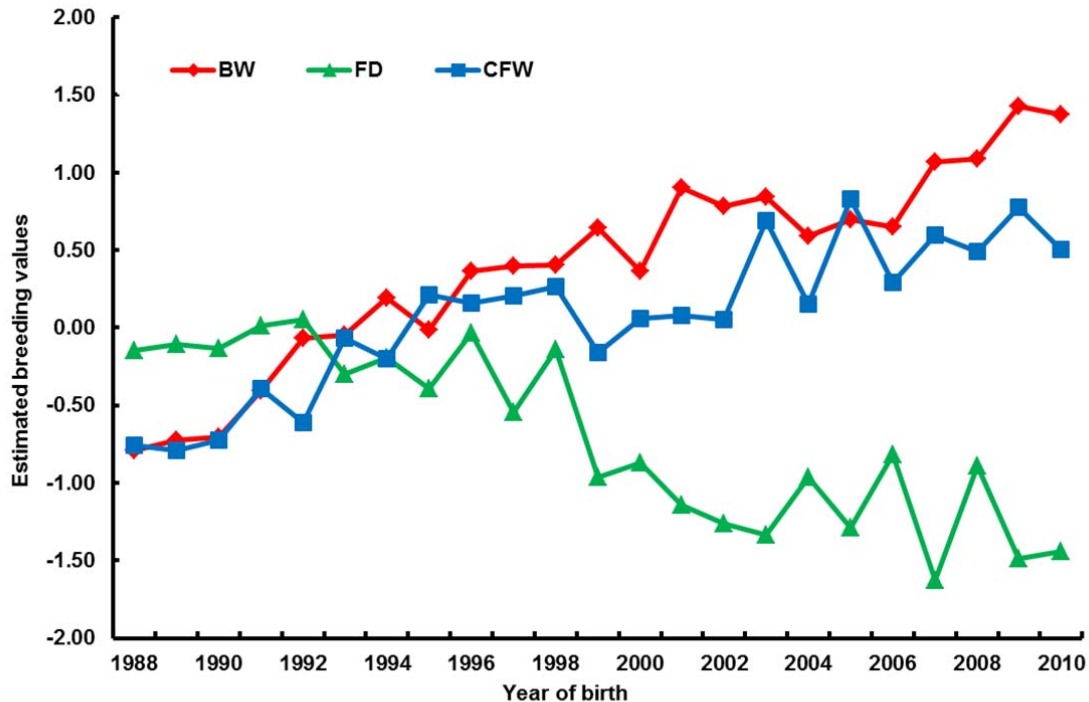
Figure 3.1 Genetic trends in body weight at 15 months of age (BW15), clean fleece weight (CFW) and fibre diameter (FD) expressed relative to the standard deviation of each trait to allow comparison on an equitable basis

CONCLUSIONS

The results from this study correspond with the parameter estimates reported in the literature for all traits considered. The moderate to high heritability estimates linked to sufficient phenotypic variation of all the economically important traits, confirm that these traits can be included in well-designed selection programs to improve the production of fine wool Merino sheep.

It can be concluded that selection for reduced fibre diameter can have an immediate and large effect on reducing the fibre diameter of a flock, as a result of the high h^2_a. However, this effect will be hampered if there is little phenotypic variance to exploit in the selection process. The relative importance of fibre diameter on the realisable income derived from wool production has led to a lot of emphasis being placed on the selection for reduced fibre diameter. In some instances, it is the only trait that is included in the breeding plans of wool producers. However, if this selection is done injudiciously, it can adversely affect the other economically important traits as a result of the unfavourable correlations between these traits. This means that decreasing fibre diameter can lead to a decrease in body and fleece weight, as well as shorter and less uniform staples with a lower staple strength.

CHAPTER 4. GENETIC PARAMETERS FOR REPRODUCTION TRAITS AND THEIR RELATIONSHIPS WITH PRODUCTION TRAITS IN A GENETIC FINE WOOL MERINO STUD

INTRODUCTION

The economic viability of sheep enterprises in South Africa under different environments and production systems largely depends on the reproduction potential of the adult ewe flock. Firstly, the reproduction potential is directly linked to the 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). Secondly, an improvement in reproduction will influence selection intensity as a result of more animals being available for selection.

It is therefore important to quantify the impact that genetic improvement can have on reproduction potential. The main trait that influences reproduction potential is ewe productivity, which can be defined as the total weight of lamb weaned per lambing opportunity (TWW) (Snowder & Fogarty, 2009). Total weight of lamb weaned is a composite trait that is influenced by several components and selection can be done on each of these components in order to improve the reproduction potential (Falconer & Mackay, 1996, Olivier et al., 2001). Mothering ability, milk production of the ewe, ovulation rate, twinning rate, embryo survival, age at puberty, fertility, lamb survival and lamb growth, are some of the components that influence ewe productivity (Lee & Atkins, 1994; Snowder & Fogarty, 2009).

Selection for increased production through the use of TWW is the ultimate goal in any sheep flock. However, the fact that this is a composite trait is very complex and is only expressed later in the life of a ewe complicates the selection progress. This has led to the use of component traits to improve TWW, rather than direct selection (Olivier et al., 2001). Furthermore, by following this route one or more of the component traits can be emphasised. Snyman et al. (1998c) stated that it would be short sighted of breeders to over emphasise litter size without taking the weaning weight of the lambs into consideration. This is especially true when selection is done in a high fertile flock in harsh production environments (Snyman et al., 1998c; Olivier et al., 2001).

However, despite the importance of reproduction under local conditions, it is important to note that it is not the only economically important trait that is included in woolled sheep selection programs worldwide. The relationships that exist between reproduction and growth traits (body weight) and objectively measured wool traits need to be considered when selection is practiced on woolled sheep. The inclusion of reproduction in selection programs is still to a large extent being ignored by the average wool producer, mainly because it is difficult to measure and it is perceived that progress is likely to be slower than in the other economically important traits. Selection for increased body weight is used by producers as an indirect selection criterion for reproduction due to the favourable genetic correlations of live weight with

reproduction (Safari et al., 2005). The increased mature weight and hence maintenance requirements stemming from such selection, however, needs consideration.

The quantification of the reproduction potential of fine woolled animals is even more important due to the unfavourable correlation between reproduction and fibre diameter (Safari et al., 2005). Kuchel & Lindsay (1999) reported that fine wool Merinos is reputed to be poor mothers when compared to Merino Peppin strains. It was also found that superfine wool Merinos had a higher post-natal mortality rate up to four weeks. The latter finding was related to the poor mothering ability of the superfine wool ewes and secondly it was indicated that the smaller size of these ewes and their smaller lambs were also contributing factors.

Furthermore, Swan et al. (2001) stated that there is anecdotal evidence that fine wool Merinos is reputed to be poorer reproducers compared to other Merino strains. This is also the popular believe in South Africa and is supported by findings from a study done by Mortimer et al. (1985) that there was a substantial difference in number of lambs weaned between fine wool strains (0.55) and medium wool Peppin (0.80) bloodlines. In contrast to this, Swan et al. (2001) and Olivier & Olivier (2007) found that the reproduction of fine wool animals is comparable with other Merino strains.

Accurate genetic parameters are prerequisites for purposeful selection in livestock. It is therefore important that animal breeders continually re-evaluate these parameters. This will aid livestock producers in the improvement of selection practices and the accuracy of selection. This is even more important for reproduction traits of sheep, which is lowly heritable and impossible to measure at an early age (Olivier et al., 1998). The aim of this study was therefore to estimate genetic parameters for reproduction of a fine wool Merino stud and to quantify the relationships between reproduction, body weight and the objectively measured wool traits.

MATERIALS AND METHODS

The Cradock Fine Wool Merino Stud originated from 520 ewes bought from 32 Merino breeders with the finest clips throughout South Africa in 1988 (Chapter 2; Olivier et al., 1989; Olivier et al., 2006a).

This stud was kept on irrigated pastures at the Cradock Experimental Station near Cradock in the Eastern Cape Province during data collection. The pastures consisted of a mixture of lucerne, ryegrass and clovers planted in small paddocks. The ewe flock was artificially inseminated during March to April every year for a six week mating period. Teaser rams were used to identify the ewes that were in oestrus. A more detailed description of the history, management and selection of this stud is given in Chapter 2.

Reproduction data collected on 1 775 ewes born in this stud from 1988 to 2010, were used for the analysis of reproduction traits. The reproduction traits considered in the analysis were number of lambs born per lambing opportunity (NLB), number of lambs weaned per lambing opportunity (NLW), total weight of lamb weaned per lambing opportunity (TWW), number of lambs born over three lambing opportunities (NLB3), number of lambs weaned over three lambing opportunities (NLW3), the total weight

of lamb weaned over three lambing opportunities (TWW3) and total weight of lamb weaned per ewe per lambing opportunity (TWW-L).

The Proc MEANS-procedure of SAS (SAS, 2009) was used to obtain the descriptive statistics of the data set. The significance levels for the non-genetic fixed effects (Repeated records animal model: year of lambing and age of animal at lambing; single record animal model: year of birth) were obtained with the PDIFF-option under the Proc GLM-procedure of SAS (SAS, 2009). Only effects and interactions that had a significant effect (P<0.01) on a specific trait, were included in the final operational model.

The estimation of the genetic parameters among NLB, NLW and TWW was done with ASREML (2009) by fitting a repeatability model. The estimation of the genetic parameters for NLB3, NLW3, TWW3 and TWW-L to be used in the estimation of correlations was done with ASREML (Gilmour et al., 2009) by fitting single-trait animal models. These models included different combinations of the direct additive, maternal additive and maternal permanent environmental effects, as well as the covariation between the direct and maternal additive effects. These different combinations lead to the following seven models for the repeatability analysis:

$$\mathbf{y} = X\mathbf{b} + Z_1\mathbf{a} + \mathbf{e} \tag{1}$$

$$\mathbf{y} = X\mathbf{b} + Z_1\mathbf{a} + Z_4\mathbf{pe} + \mathbf{e} \tag{2}$$

$$\mathbf{y} = X\mathbf{b} + Z_1\mathbf{a} + Z_3\mathbf{mpe} + Z_4\mathbf{pe} + \mathbf{e} \tag{3}$$

$$\mathbf{y} = X\mathbf{b} + Z_1\mathbf{a} + Z_2\mathbf{m} + Z_4\mathbf{pe} + \mathbf{e}; \text{ with cov(a,m)} = 0 \tag{4}$$

$$\mathbf{y} = X\mathbf{b} + Z_1\mathbf{a} + Z_2\mathbf{m} + Z_4\mathbf{pe} + \mathbf{e}; \text{ with cov(a,m)} = A\sigma_{am} \tag{5}$$

$$\mathbf{y} = X\mathbf{b} + Z_1\mathbf{a} + Z_2\mathbf{m} + Z_3\mathbf{mpe} + Z_4\mathbf{pe} + \mathbf{e}; \text{ with cov(a,m)} = 0 \tag{6}$$

$$\mathbf{y} = X\mathbf{b} + Z_1\mathbf{a} + Z_2\mathbf{m} + Z_3\mathbf{mpe} + Z_4\mathbf{pe} + \mathbf{e}; \text{ with cov(a,m)} = A\sigma_{am} \tag{7}$$

The six different model combinations for the single record analysis:

$$\mathbf{y} = X\mathbf{b} + Z_1\mathbf{a} + \mathbf{e} \tag{1}$$

$$\mathbf{y} = X\mathbf{b} + Z_1\mathbf{a} + Z_3\mathbf{mpe} + \mathbf{e} \tag{2}$$

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

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

$$\mathbf{y} = X\mathbf{b} + Z_1\mathbf{a} + Z_2\mathbf{m} + Z_3\mathbf{mpe} + \mathbf{e}; \text{ with cov(a,m)} = 0 \tag{5}$$

$$\mathbf{y} = X\mathbf{b} + Z_1\mathbf{a} + Z_2\mathbf{m} + Z_3\mathbf{mpe} + \mathbf{e}; \text{ with cov(a,m)} = A\sigma_{am} \tag{6}$$

where $\mathbf{y}$ is a vector of the observed traits for animals; $\mathbf{b}$, $\mathbf{a}$, $\mathbf{m}$, $\mathbf{mpe}$ and $\mathbf{pe}$ are vectors of fixed effects, direct additive effects, maternal additive effects, maternal permanent environmental effects and ewe permanent environmental effects (include only in the repeatability models) respectively; X, Z_1, Z_2, Z_3 and Z_4 are incidence matrices respectively relating fixed effects, direct additive effects, maternal additive effects, maternal permanent environmental effects and ewe permanent environmental effects to $\mathbf{y}$; $\mathbf{e}$ is the vector of residuals; A is a numerator relationship matrix, and σ_{am} is the covariance between direct additive and maternal additive effects.

It was assumed that $V(a) = A\sigma^2_a; V(m) = A\sigma^2_m; V(mpe) = I\sigma^2_{mpe}; V(pe) = I\sigma^2_{pe}; V(e) = I\sigma^2_e$, where I is an identity matrix, σ^2_a, σ^2_m, σ^2_{mpe}, σ^2_{pe} and σ^2_e are the direct additive variance, maternal additive variance, maternal permanent environmental variance, ewe 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, $\sigma_{am,}$ σ^2_{mpe}, σ^2_{pe} and σ^2_e, were derived at convergence for the repeatability analysis, while σ^2_p were the sum of σ^2_a, σ^2_m, $\sigma_{am,}$ σ^2_{mpe} and σ^2_e, were derived at convergence of the single record analysis. The most suitable model was determined as described in Chapter 3.

The genetic, environmental and phenotypic correlations among the reproduction traits were estimated using two-trait models with ASREML (Gilmour et al., 2009). The (co)variance component values obtained with the single-trait models were used as starting values for the two-trait models. Correlations were also estimated of the reproduction traits with body weight and fleece traits as described in Chapter 3. Animal solutions derived from single traits repeatability analyses were averaged within birth years and used to obtain genetic trends for number of lambs weaned and total weight of lamb weaned. Average annual estimated breeding values were regressed on the year of birth to get an indication of the annual gain that was achieved. Three separate linear regressions were fitted, viz. from 1988 to 1995, 1996 to 2003 and from 2004 to 2010, to describe the three distinct periods during which different selection objectives were applied (Chapter 2).

RESULTS AND DISCUSSION

The significance (P<0.01) level of different non-genetic effects for NLB, NLW and TWW are summarised in Table 4.1. The non-genetic effects tested for significance was year of birth (1988 to 2010) and age at lambing (2 to 6+ year). It is evident from Table 4.1 that year of lambing and age at lambing had a significant (P<0.01) effect on NLB, NLW and TWW. Year of birth had a significant influence on NLB3, NLW3, TWW3 and TWW-L.

Table 4.1 The significance level of the different non-genetic effects for the respective reproduction traits

Trait	Repeat records animal model		Single record animal model
	Year of lambing	**Age at lambing**	**Year of birth**
NLB	*	*	-
NLW	*	*	-
TWW	*	*	-
TWW-L	-	-	*
NLB3	-	-	*
NLW3	-	-	*
TWW3	-	-	*

* P < 0.05; "-" – effect not fitted; NLB - number of lambs born per lambing opportunity; NLW -number of lambs weaned per lambing opportunity; TWW - total weight of lamb weaned per lambing opportunity; NLB3 - number of lambs born over three lambing opportunities; NLW3 - number of lambs weaned over three lambing opportunities; TWW3 - the total weight of lamb weaned over three lambing opportunities and total weight of lamb weaned per ewe per lambing opportunity (TWW-L).

Descriptive statistics for reproduction traits are summarised in Table 4.2. It is clear that the coefficient of variation (CV) of the reproduction traits measured over the lifetime of a ewe (NLB, NLW, TWW and TWW-

L) were very high compared to other production traits, as well as reproduction traits measured over a specific number of lambing opportunities. This is the result of the very wide range that exists in these traits, as the number of lambs born ranged from 0 to 16 (multiple lambs per lambing opportunity). This is further influenced by the number of lambing opportunities that each ewe had over her lifetime. For this stud it ranged from 1 to 6 with an average of 2.8.

The CV of NLB3, NLW3 and TWW3 obtained in this study were within the range (35% to 58%) of the corresponding values for South African woolled sheep for reproduction traits over specific lambing opportunities (Snyman et al., 1997; Olivier et al., 2001; Van Wyk et al., 2003).

Table 4.2 The number of records, mean and coefficient of variation (CV) of the different reproduction traits

Trait	Nr of records	Nr of sires	Nr of dams	Mean	CV(%)
NLB (n)	5968	148	1030	1.4	58.8
NLW (n)	5968	148	1030	1.1	71.2
TWW (kg)	5968	148	1030	28.4	68.7
TWW-L (kg)	1775	148	1030	23.8	61.5
NLB3 (n)	1090	148	519	4.6	27.0
NLW3 (n)	1090	148	519	3.7	36.2
TWW3 (kg)	1090	148	519	93.4	35.2

NLB - number of lambs born per lambing opportunity; NLW - number of lambs weaned per lambing opportunity; TWW - total weight of lamb weaned per lambing opportunity; NLB3 - number of lambs born over three lambing opportunities; NLW3 - number of lambs weaned over three lambing opportunities; TWW3 - the total weight of lamb weaned over three lambing opportunities and total weight of lamb weaned per ewe per lambing opportunity (TWW-L)

The Log likelihood values for reproduction traits are presented as a deviation from the most suitable model in Tables 4.3 and 4.4. The most suitable model for NLB, NLW and TWW for the repeatability analysis included the direct additive and the ewe permanent environmental effect. For NLB3, NLW3, TWW3 and TWW-L the most suitable model included only the direct additive effect (σ^2_a).

Estimates of the direct heritability (h^2_a) and ewe permanent environmental effect (c^2_{pe}) for the reproduction traits are summarised in Table 4.5. The h^2_a of 0.04 estimated for NLB in this study was at the lower end of the range (0.05 to 0.23) reported in the literature for Merinos (Woolaston et al., 1995; Olivier et al., 2001; Swan et al. 2001; Cloete et al., 2004). These estimates reported in the literature for Merino sheep were comparable with the estimates for all sheep breeds that ranged from 0.00 to 0.27 (Brash et al., 1994c; Snyman et al., 1998a; Van Wyk et al., 2003; Safari et al., 2005; Safari et al. 2007a; Vatankhah & Talebi, 2008; Zishiri et al., 2013).

Table 4.3 Log likelihoods as a deviation from the most suitable models (in bold) for multiple records reproduction traits (Repeatability analysis)

Model	NLB	NLW	TWW
σ^2_a	7.12	13.74	19.346
$\sigma^2_a + \sigma^2_{pe}$	**0.00**	**0.00**	**0.00**
$\sigma^2_a + \sigma^2_{pe} + \sigma^2_{mpe}$	0.00	-1.14	-0.002
$\sigma^2_a + \sigma^2_{pe} + \sigma^2_m$	-1.38	0.00	-0.10
$\sigma^2_a + \sigma^2_{pe} + \sigma^2_m + \sigma_{am}$	-1.78	-0.44	-3.672
$\sigma^2_a + \sigma^2_{pe} + \sigma^2_m + \sigma^2_{mpe}$	-1.38	-0.08	-0.10
$\sigma^2_a + \sigma^2_{pe} + \sigma^2_m + \sigma^2_{mpe} + \sigma_{am}$	-1.78	0.00	-3.672

NLB - number of lambs born per lambing opportunity; NLW -number of lambs weaned per lambing opportunity; TWW - total weight of lamb weaned per lambing opportunity; σ^2_a - direct additive variance; σ^2_m - maternal additive variance; σ^2_{pe} – ewe permanent environmental variance; σ^2_{mpe} - maternal permanent environmental variance; σ_{am} – covariance between the direct and maternal additive variance

Table 4.4 Log likelihoods as a deviation from the most suitable models (in bold) for single record reproduction traits

Model	NLB3	NLW3	TWW-L	TWW 3
σ^2_a	**0.00**	**0.00**	**0.00**	**0.00**
$\sigma^2_a + \sigma^2_{mpe}$	0.00	0.00	-0.10	0.00
$\sigma^2_a + \sigma^2_m$	-0.10	0.00	0.00	0.00
$\sigma^2_a + \sigma^2_m + \sigma_{am}$	-0.16	0.62	-1.74	-0.72
$\sigma^2_a + \sigma^2_m + \sigma^2_{mpe}$	-0.10	0.00	-0.10	0.00
$\sigma^2_a + \sigma^2_m + \sigma^2_{mpe} + \sigma_{am}$	-0.16	0.62	-1.74	-0.72

NLB3 - number of lambs born over three lambing opportunities; NLW3 - number of lambs weaned over three lambing opportunities; TWW3 - the total weight of lamb weaned over three lambing opportunities and total weight of lamb weaned per ewe per lambing opportunity (TWW-L); σ^2_a - direct additive variance; σ^2_m - maternal additive variance; σ^2_{mpe} - maternal permanent environmental variance; σ_{am} – covariance between the direct and maternal additive variance

The h^2_a estimate for NLB was also at the lower end of the range of estimates reported for repeatability model analyses. The c^2_{pe} estimated in the current study for NLB was within the range (0.02 to 0.14) of values reported in the literature (Brash et al. 1994a; Woolaston et al., 1995; Swan et al., 2001; Van Wyk et al., 2003; Cloete et al., 2004; Safari et al., 2005; Safari et al., 2007a; Vatankhah & Talebi, 2008). The ewe permanent environmental variance stems from common ewe effects across seasons not associated with pedigree information when analysing repeated reproduction records.

Table 4.5 Estimates of heritability (h^2_a) and ewe permanent environmental effect (c^2_{pe}) for the reproduction traits ($\pm$ s.e.)

Trait	h^2_a	c^2_{pe}
NLB	0.04 ± 0.02	0.05 ± 0.02
NLW	0.02 ± 0.01	0.07 ± 0.02
TWW	0.02 ± 0.01	0.09 ± 0.01

NLB - number of lambs born per lambing opportunity; NLW -number of lambs weaned per lambing opportunity; TWW - total weight of lamb weaned per lambing opportunity

Heritability estimates (0.04 to 0.17; Swan et al., 2001; Olivier et al., 2001; Cloete et al., 2004) reported in the literature for NLW of Merino sheep were higher than the 0.02 estimated in this study. However, the c^2_{pe} estimated in the current study was comparable with the permanent environmental effect of 0.09 and 0.11 reported by Swan et al. (2001) and Cloete et al. (2004) respectively. These reported h^2_a estimates for Merino sheep were in the same order as the range (0.01 to 0.19) reported in the literature for all sheep breeds (Van Wyk et al., 2003; Safari et al., 2007a; Notter, 2008; Vatankhah & Talebi, 2008; Lee et al., 2009; Zishiri et al., 2013). The corresponding estimates for c^2_{pe} ranged from 0.03 to 0.12 (Brash et al., 1994d; Fogarty et al., 1994; Van Wyk et al., 2003; Safari et al., 2005; Safari et al., 2007a; Vatankhah & Talebi, 2008).

The h^2_a estimate of the current study for TWW were within the range of estimates (0.02 to 0.29) reported in the literature (Shelton & Menzies, 1970; Fogarty et al., 1985; Bunge et al., 1990; Fogarty et al., 1994; Hall et al., 1994; Snyman et al., 1997; Okut et al., 1999; Bromley et al., 2001; Rosati et al., 2002; Van Wyk et al., 2003; Safari et al., 2005; Safari et al., 2007a; Notter, 2008; Vatankhah & Talebi, 2008; Lee et al., 2009; Zishiri et al., 2013) for total weight of lamb weaned per ewe joined in all sheep breeds. The estimates of the current study for TWW-L and TWW were similar to the lower end of the range (0.04 to 0.26) reported in the literature for South African Merinos (Snyman et al., 1997; Olivier et al., 2001; Cloete et al. 2002b; Cloete et al., 2004). Okut et al. (1999), Bromley et al. (2001), Cloete et al. (2002b), Rosati et al. (2002) and Cloete et al. (2004) indicated that TWW was also influenced by a permanent environmental effect and the c^2_{pe} ranged from 0.00 to 0.13. These c^2_{pe} estimates concur with the value obtained in this study for $c^2_{pe.}$

The genetic (r_g), phenotypic (r_p) and environmental (r_e) correlations among the reproduction traits are presented in Table 4.6. All the correlations among the reproduction traits are very high and significant and range from 0.701 (r_e between NLW and TWW-L) to 0.999 (r_g between NLB and NLW). The r_g between NLB and NLW reported in the literature ranged from 0.71 to 1.00 (Brash et al., 1994d; Fogarty et al., 1994; Snyman et al., 1998a; Olivier et al., 2001; Hanford et al., 2002; Van Wyk et al., 2003; Cloete et al., 2004; Vatankhah & Talebi, 2008; Zishiri et al., 2013). The current r_g estimate between these two traits was equal to the upper boundary of this range.

The r_g between the number of lambs born or weaned and the weight of lamb weaned were within the ranges reported in the literature between these traits. The published estimates between NLB and TWW ranged from 0.41 to 0.91 and the corresponding range between NLW and TWW was 0.60 to 0.98

(Fogarty et al., 1994; Snyman et al., 1998a; Olivier et al., 2001; Van Wyk et al., 2003; Cloete et al., 2004; Zishiri et al., 2013)

Table 4.6 Genetic, environmental and phenotypic correlations among the reproduction traits (± s.e.)

Trait	NLW	TWW
Additive genetic correlations		
NLB	0.999 ± 0.043	0.868 ± 0.105
NLW		0.908 ± 0.057
Ewe permanent environmental correlations		
NLB	0.783 ± 0.061	0.874 ± 0.068
NLW		0.985 ± 0.008
Environmental correlations		
NLB	0.757 ± 0.07	0.702 ± 0.008
NLW		0.961 ± 0.001
Phenotypic correlations		
NLB	0.760 ± 0.006	0.716 ± 0.007
NLW		0.961 ± 0.001

NLB - number of lambs born over the ewe's lifetime; NLW - number of lambs weaned over the ewe's lifetime; TWW - total weight of lamb weaned over the ewe's lifetime

The genetic, environmental and phenotypic correlations of the reproduction traits measured over three lambing opportunities and TWW-L with BirthC and the body weights at different ages are summarised in Table 4.7. It is clear from this Table that the r_e and r_p were very low and most correlations were zero and non-significant. The r_g between the reproduction traits and BirthC was low positive and mostly non-significant, suggesting that selection for reproduction would not affect BirthC appreciably. This accorded with findings from Ponzoni et al. (1996), indicating that changes in birth coat score would not adversely affect reproduction.

The r_g between the number of lambs born or weaned and body weights early in life (6 months and younger) were low to highly negative. However, high estimates for PWW were associated with large standard errors and on the border of not being significant. These estimates from the current study were in agreement with the values reported by other studies in the literature that ranged from 0.08 to 0.65 and 0.06 to 0.57 for NLB and NLW with early body weights respectively (Olivier et al., 2001; Swan et al., 2001; Van Wyk et al., 2003; Safari et al., 2007b; Huisman & Brown, 2008; Vatankhah & Talebi, 2008; Zishiri et al., 2013). For body weights 12 months and older the r_g with NLB or NLW was close to zero and were within the range of -0.28 to 0.58 reported in the literature for similar ages (Snyman et al., 1998a; Hansen & Shrestha 1999, 2002; Safari et al., 2007b)

The favourable r_g between TWW3 and body weights were in contrast to the r_g between NLB and NLW and the body weights. The r_g between the weaning and post weaning body weights and reproduction traits were higher than the corresponding r_g with BirthW and PWW. The estimate between BirthW and TWW3 were higher than the values published in the literature that ranged from 0.10 to 0.28 (Bromley et al. 2001; Safari et al., 2007b), but lower than the 0.74 reported by Vatankhah & Talebi (2008).

The r_g between WW and TWW3 were in the same order as the lower end of the range (0.65 to 0.97) reported in literature (Olivier et al., 2001; Van Wyk et al., 2003; Vatankhah & Talebi, 2008; Zishiri et al., 2013). The estimates obtained in the current study between body weights 6 months and older were within the range of estimates (0.51 to 0.97) published in the literature (Fogarty et al. 1994; Snyman et al., 1998a, 1998c; Cloete et al., 2001a, 2002b; Vatankhah & Talebi, 2008; Zishiri et al., 2013).

Table 4.7 Genetic, environmental and phenotypic correlations between the reproduction traits and BirthC and body weights at different ages (± s.e.)

Trait	BirthW	BirthC	PWW	WW	BW6	BW12	BW15
Additive genetic correlations							
NLB3	-0.44 ± 0.21	0.18 ± 0.26	-0.67 ± 0.32	-0.20 ± 0.40	-0.31 ± 0.31	0.20 ± 0.29	0.16 ± 0.30
NLW 3	-0.42 ± 0.21	0.13 ± 0.20	-0.65 ± 0.31	-0.08 ± 0.30	-0.32 ± 0.25	0.27 ± 0.22	0.31 ± 0.22
TWW3	0.40 ± 0.17	0.25 ± 0.19	0.41 ± 0.20	0.79 ± 0.12	0.86 ± 0.11	0.80 ± 0.13	0.78 ± 0.13
TWW-L	0.29 ± 0.12	0.21 ± 0.02	0.23 ± 0.12	0.58 ± 0.12	0.55 ± 0.12	0.57 ± 0.11	0.56 ± 0.11
Environmental correlations							
NLB3	0.02 ± 0.04	-0.08 ± 0.04	0.06 ± 0.03	0.08 ± 0.03	0.12 ± 0.04	0.14 ± 0.04	0.13 ± 0.04
NLW3	0.01 ± 0.04	-0.06 ± 0.04	0.05 ± 0.03	0.04 ± 0.03	0.07 ± 0.04	0.07 ± 0.04	0.07 ± 0.04
TWW3	-0.02 ± 0.04	-0.05 ± 0.04	0.00 ± 0.03	-0.03 ± 0.04	-0.04 ± 0.04	-0.05 ± 0.04	-0.05 ± 0.04
TWW-L	-0.04 ± 0.04	-0.06 ± 0.04	-0.01 ± 0.03	-0.04 ± 0.03	-0.02 ± 0.04	-0.03 ± 0.04	-0.01 ± 0.04
Phenotypic correlations							
NLB3	-0.04 ± 0.02	-0.03 ± 0.03	-0.01 ± 0.03	0.01 ± 0.03	0.04 ± 0.03	0.09 ± 0.03	0.09 ± 0.03
NLW3	-0.03 ± 0.02	-0.02 ± 0.03	-0.03 ± 0.03	0.00 ± 0.03	0.01 ± 0.03	0.03 ± 0.03	0.05 ± 0.03
TWW3	0.02 ± 0.02	0.02 ± 0.03	0.04 ± 0.03	0.08 ± 0.03	0.11 ± 0.03	0.15 ± 0.03	0.13 ± 0.03
TWW-L	0.02 ± 0.02	-0.01 ± 0.03	0.01 ± 0.03	0.04 ± 0.03	0.07 ± 0.03	0.11 ± 0.03	0.12 ± 0.03

NLB3 - number of lambs born over three lambing opportunities; NLW3 - number of lambs weaned over three lambing opportunities; TWW3 - the total weight of lamb weaned over three lambing opportunities and total weight of lamb weaned per ewe per lambing opportunity (TWW-L); BirthC – birth coat score; Body weight: BirhtW – birth; PWW – pre-weaning (42 days of age); WW – weaning; BW6 – 6 months of age; BW12 – 12 months of age; BW15 – 15 months of age

The genetic, environmental and phenotypic correlations between the reproduction and wool traits are summarised in Tables 4.8 and 4.9. It is evident from these two tables that only the r_g of FD and Wrinkle with the reproduction traits were significant. Furthermore, the r_p and r_e between the reproduction and wool traits were low and almost zero. The r_g between FD at different ages and reproduction were moderate unfavourable (positive), except between FD6 and NLB and NLW where the correlation was low. The estimates reported in the literature between FD and the reproduction traits ranged from -0.11 to 0.26 (Snyman et al., 1998a, 1998c; Cloete et al., 2002c; Safari et al., 2007b), which were lower than the estimates of the current study.

The same unfavourable relationship between fleece weight and number of lambs were reported in the literature as what was found in this study. These reported estimates ranged from -0.05 to -0.41 (Snyman et al., 1998a, 1998c; Hanford et al., 2002; Ingham & Ponzoni, 2002; Cloete et al., 2004; Safari et al., 2007b). The r_g between fleece weight and TWW3 were moderate positive and were similar to estimates (0.06 to 0.41) obtained by Fogarty et al. (1994); Snyman et al. (1998a) and Cloete et al. (2002c). However, both Snyman et al. (1998c) and Cloete et al. (2004) found negative r_g between these traits. The correlations of both SL and CY with the reproduction traits were low, which were similar to the estimates reported in the literature (Bromley et al., 2001; Cloete et al., 2002c; Hanford et al., 2002; Safari et al., 2007a).

Table 4.8 Genetic, environmental and phenotypic correlations between the reproduction traits and FD6, FD12, GFW, CFW, FD, SL and CY (± s.e.)

Trait	FD6	FD12	GFW	CFW	FD	SL	CY
Additive genetic correlations							
NLB	-0.11 ± 0.30	0.35 ± 0.27	-0.33 ± 0.40	-0.56 ± 0.51	0.38 ± 0.16	-0.07 ± 0.27	-0.27 ± 0.30
NLW	0.16 ± 0.21	0.50 ± 0.19	-0.14 ± 0.23	-0.23 ± 0.24	0.56 ± 0.18	0.16 ± 0.22	-0.23 ± 0.21
TWW3	0.47 ± 0.18	0.58 ± 0.18	-0.28 ± 0.18	-0.21 ± 0.18	0.59 ± 0.18	0.21 ± 0.19	-0.04 ± 0.17
TWW-L	0.37 ± 0.15	0.35 ± 0.14	-0.09 ± 0.15	-0.04 ± 0.15	0.38 ± 0.15	-0.09 ± 0.15	-0.15 ± 0.14
Environmental correlations							
NLB	0.07 ± 0.03	0.06 ± 0.04	0.07 ± 0.04	0.05 ± 0.04	0.02 ± 0.04	-0.03 ± 0.04	0.00 ± 0.04
NLW	0.04 ± 0.03	0.03 ± 0.04	0.01 ± 0.04	-0.01 ± 0.04	0.04 ± 0.04	-0.03 ± 0.04	-0.01 ± 0.04
TWW3	-0.06 ± 0.04	0.00 ± 0.05	-0.11 ± 0.04	-0.11 ± 0.04	0.00 ± 0.04	-0.08 ± 0.04	-0.04 ± 0.04
TWW-L	0.00 ± 0.03	0.05 ± 0.04	-0.06 ± 0.04	-0.07 ± 0.04	0.04 ± 0.04	-0.04 ± 0.03	-0.01 ± 0.04
Phenotypic correlations							
NLB	0.06 ± 0.03	0.10 ± 0.03	-0.03 ± 0.03	-0.05 ± 0.03	0.08 ± 0.03	-0.03 ± 0.03	-0.05 ± 0.03
NLW	0.04 ± 0.03	0.08 ± 0.03	-0.04 ± 0.03	-0.06 ± 0.03	0.05 ± 0.03	-0.04 ± 0.03	-0.05 ± 0.03
TWW3	0.04 ± 0.03	0.05 ± 0.03	0.01 ± 0.03	0.00 ± 0.03	0.06 ± 0.03	-0.08 ± 0.03	-0.05 ± 0.03
TWW-L	0.07 ± 0.03	0.12 ± 0.03	-0.02 ± 0.03	-0.03 ± 0.03	0.12 ± 0.03	-0.05 ± 0.03	-0.04 ± 0.03

NLB3 - number of lambs born over three lambing opportunities; NLW3 - number of lambs weaned over three lambing opportunities; TWW3 - the total weight of lamb weaned over three lambing opportunities and total weight of lamb weaned per ewe per lambing opportunity (TWW-L); Fibre diameter: FD6 – 6 months of age; FD12 – 12 months of age; FD – 15 months of age; GFW – greasy fleece weight; CFW – clean fleece weight; SL – staple length

The genetic relationships of Wrinkle with the reproduction traits were favourable. The reproduction traits were low negatively correlated with SDFD and CVFD, which were similar to the values obtained by Safari et al. (2007b). The r_g between SS and the reproduction traits were low positive. No other r_g was found in the literature between any of the reproduction traits and SS.

Table 4.9 Genetic, environmental and phenotypic correlations between the reproduction traits and Crimp, Duer, SDFD, CVFD, Wrinkle, CF and SS (± s.e.)

Trait	Crimp	Duer	SDFD	CVFD	Wrinkle	CF	SS
Additive genetic correlations							
NLB	0.00 ± 0.25	0.19 ± 0.24	-0.05 ± 0.25	-0.11 ± 0.21	-0.62 ± 0.29	-0.02 ± 0.25	0.30 ± 0.27
NLW	-0.14 ± 0.22	0.27 ± 0.19	-0.02 ± 0.27	-0.15 ± 0.22	-0.49 ± 0.24	-0.15 ± 0.21	0.19 ± 0.23
TWW3	-0.18 ± 0.20	0.22 ± 0.17	-0.09 ± 0.24	-0.11 ± 0.19	-0.37 ± 0.17	0.10 ± 0.21	0.15 ± 0.25
TWW-L	-0.07 ± 0.15	0.23 ± 0.14	-0.05 ± 0.21	-0.07 ± 0.16	-0.36 ± 0.16	-0.03 ± 0.17	0.24 ± 0.21
Environmental correlations							
NLB	0.00 ± 0.04	0.02 ± 0.04	0.04 ± 0.04	-0.02 ± 0.04	0.10 ± 0.04	-0.01 ± 0.05	0.04 ± 0.05
NLW	-0.03 ± 0.03	0.00 ± 0.04	0.03 ± 0.04	-0.03 ± 0.04	0.05 ± 0.04	0.01 ± 0.05	0.03 ± 0.05
TWW3	0.01 ± 0.04	0.01 ± 0.04	-0.03 ± 0.04	-0.03 ± 0.04	0.07 ± 0.04	-0.02 ± 0.05	-0.04 ± 0.05
TWW-L	-0.02 ± 0.03	0.01 ± 0.04	-0.01 ± 0.04	-0.05 ± 0.04	0.01 ± 0.04	-0.04 ± 0.05	0.03 ± 0.05
Phenotypic correlations							
NLB	0.01 ± 0.03	0.08 ± 0.03	-0.05 ± 0.03	-0.05 ± 0.03	0.02 ± 0.03	-0.06 ± 0.03	0.09 ± 0.04
NLW	-0.03 ± 0.03	0.05 ± 0.03	-0.01 ± 0.03	-0.04 ± 0.03	-0.01 ± 0.03	-0.05 ± 0.03	0.07 ± 0.04
TWW3	0.01 ± 0.03	0.05 ± 0.03	-0.04 ± 0.03	-0.06 ± 0.03	0.00 ± 0.03	0.00 ± 0.03	0.01 ± 0.03
TWW-L	-0.03 ± 0.03	0.05 ± 0.03	-0.02 ± 0.03	-0.05 ± 0.03	-0.03 ± 0.03	-0.03 ± 0.03	0.06 ± 0.04

NLB3 - number of lambs born over three lambing opportunities; NLW3 - number of lambs weaned over three lambing opportunities; TWW3 - the total weight of lamb weaned over three lambing opportunities and total weight of lamb weaned per ewe per lambing opportunity (TWW-L); Crimp – number of crimps per 25 mm; Duer – Duerden; SDFD – standard deviation of fibre diameter; CVFD - coefficient of variation of fibre diameter; Wrinkle – wrinkle score; CF – comfort factor; SS – staple strength

The reproduction potential of any sheep enterprise is of the utmost importance for economic survival (Olivier, 1999; Olivier, 2002). It is therefore important that reproduction forms an integral part of any selection program. In order to include reproduction, an important decision is pending for animal breeders, namely, will selection be based on the composite trait TWW or on one of its component traits. The answer to this question is dependent on the environment and production system. For flocks with poor reproduction potential, NLB or NLW can be the quickest and easiest route followed to improve reproduction. Despite the low h^2_a for both of these traits, the selection gain will be faster than anticipated due to the large variation in these traits (Notter, 2008). An experiment done by Echternkamp et al. (2002) is a very good example for achieving changes in litter size in cattle, within six years the twining percentage was increased with 45%. Cloete et al. (2004) reported substantial increases of between 1.3% and 1.8% per annum in NLB, NLW and TWW in a line selected for increased reproduction.

In contrast to selection to increase the number of lambs, flocks with a high reproductive rate should not follow this route. This is even more applicable to sheep farmers in South Africa that farm in arid and harsh environments (Cloete & Olivier, 2010). In these instances, selection should rather be based on the

composite trait TWW. This combination may improve not only the quantity of the lambs but also the quality, which can benefit profitability.

However, reproduction is not the only trait that is important to wool farmers. There are several wool and conformation traits that are also important and their underlying relationship with one another must be taken into consideration. This is especially true if the correlation between the traits is unfavourable. Fibre diameter is the second most important trait after reproduction with regard to its influence on the income of a farm. It is evident from the results of this study, as well as the literature that reproduction and FD is unfavourably correlated. This implies reducing FD or increasing reproduction will lead to an unwanted change in the other trait. The r_g of the reproduction traits with Wrinkle were favourable which implies that plainer animals tend to be better reproducers. The changes in TWW and NLW were achieved in a flock where FD was one of the main selection criteria for a large part of the duration of the project. Therefore, reproduction can be improved in conjunction with selection for reduced fibre diameter

The unfavourable correlations that exist between number of lambs born/weaned and body weights early in life, suggest that blindly increasing NLB will lead to smaller lambs at birth and pre-weaning. This could have a detrimental effect on the viability of these lambs and subsequently on the survival rate of the lambs, as lambs that are too small will not survive in harsh environments (Chapter 5).

The positive correlation between TWW and body weight, might not always be a favourable correlation. This is because if TWW is increased, BirthW will also increase and if the lambs get too large dystocia will become a problem and this will negatively affect the survival rate of lambs. Furthermore, the increase in body weight as an indirect response to selection for TWW will lead to larger animals with higher nutritional requirements (Herselman & Olivier, 2010), which are not desirable.

It is therefore evident from the results of this study, as well as the literature, that selection of replacement animals is not something that can be done blindly. All the traits that are economically important must be included in a selection program, either as a selection criterion or as a monitoring criterion. This implies that traits that are not a main selection objective must be monitored to ensure that there is no unwanted change in these traits.

The genetic trends in number of lambs weaned per lambing opportunity (NLW), total weight of lamb weaned per lambing opportunity (TWW), and fibre diameter (FD) are summarised in Table 4.10 and illustrated in Figure 4.1. The genetic trend for fibre diameter was also depicted in Chapter 3, and is included here only for the sake of comparing it with the other traits. The regression coefficients for NLW and TWW were obtained for the three different selection objective stages (Chapter 2), as was described for the objective traits in Chapter 3. During the first stage selection emphasis for BW15 resulted in increases of 0.2% per annum for TWW and 0.06% per annum for NLW. During stage 2 emphasis on the reduction of FD led to lower, but still positive changes per annum in TWW, while the trend in NLW were similar to Stage 1. Genetic change for TWW during Stage 3 was higher than in Stages 1 and 2. These trends corresponded to the changes in BW reported in Chapter 3. No evidence of an improvement in NLW was seen during Stage 3.

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Table 4.10 The genetic trends in number of lambs weaned (NLW) and total weight of lamb weaned (TWW)

Stage	Trend line information	NLW (%)	TWW (kg)
	Mean	114.0[1]	28.41
Stage 1	Regression coefficient	0.065 ± 0.025	0.063 ± 0.025
	Change per annum (%)	0.057	0.220
Stage 2	Regression coefficient	0.068 ± 0.037	0.017 ± 0.050
	Change per annum (%)	0.060	0.060
Stage 3	Regression coefficient	-0.018 ± 0.000	0.119 ± 0.022
	Change per annum (%)	-0.016	0.418

[1] Expressed as per 100 ewes joined
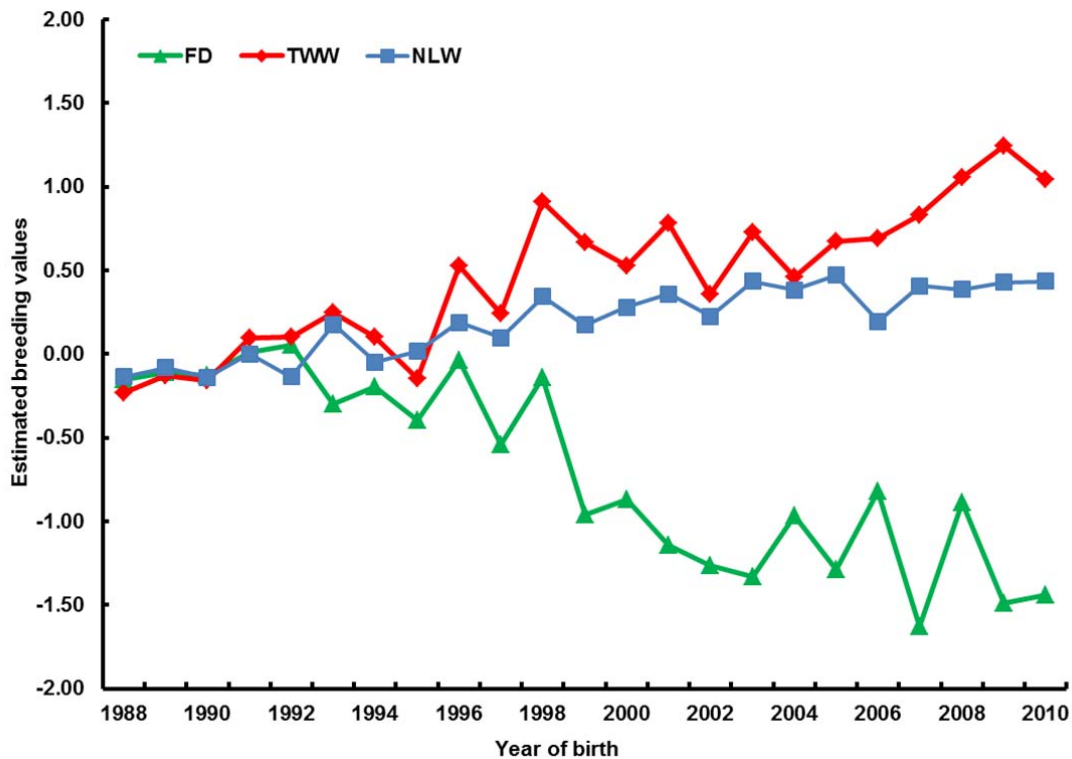
Figure 4.1 Genetic trends in number of lambs weaned (NLW), total weight of lamb weaned (TWW) and fibre diameter (FD) expressed relative to the standard deviation of each trait to allow comparison on an equitable basis

Cloete et al. (2004) reported genetic change per annum of 0.372± 0.017 for TWW in a Merino flock selected for improved reproduction. The corresponding changes in NLB and NLW were 0.0185±0.0004 and 0.0158±0.0006 respectively. The genetic change per annum for TWW in the current study was lower compared to that of Cloete et al. (2004). However, reproduction was improved indirectly through selection for BW during Stages 1 and 2, while TWW was one of the selection criteria since 1999. The outcome of the present study is thus in contrast with that of Cloete et al. (2004). It needs to be stated that the latter authors only included selection for reproduction in the selection objective.

CONCLUSION

It can therefore be concluded that selection for increased reproduction is a viable option and it would ensure that a sheep farm remains profitable. This can either be achieved through selection for TWW or one of the component traits. It is however of paramount importance that the reproduction potential of the flock is taken into consideration, as a further increase in the number of lambs born in an already high reproducing flock, can be detrimental. The unfavourable correlation of BirthW with NLB and NLW may have an adverse effect on the survival rate of lambs in harsh environments, where lambs need to survive with the minimum assistance from the stockman.

Furthermore, it is important that selection be done appropriately to ensure that the unfavourable correlations do not lead to unwanted change in traits of economic importance. The selection for reproduction without monitoring the other economically important traits will have a detrimental effect on the sustainability of sheep production.

CHAPTER 5.GENETIC RELATIONSHIPS AMONG LAMB SURVIVAL, BIRTH COAT SCORE, BIRTH, PRE-WEANING AND WEANING WEIGHT IN A GENETIC FINE WOOL MERINO STUD

INTRODUCTION

The production of meat is the most important source of income for South African Merino farmers. An increase in meat production can be achieved through selection for increased growth rate and lamb weight or an increase in the number of lambs that survived until weaning, as well as a reduction in slaughter age. Increasing the number of lambs that survive until weaning can have an immediate effect on the efficiency of the enterprise. The importance of lamb survival was emphasised in studies by Amer et al. (1999), Lopez-Villalobos & Garrick (1999), Conington et al. (2004) and Herselman & Van Heerden (2013), indicating that it is an important economic trait that influence overall productivity.

Superfine wool Merinos in Australia was reputed to have low lambing percentages and these ewes were also regard as poor mothers by Australian breeders (Kuchel & Lindsay, 1999). This view was also superted by South African producers which was of opion that fine wool animals could not be reared succesfully in arid and extensive farming conditions. Kuchel & Lindsay (1999) suggested that two of the reasons for this might firstly be because these superfine wool animals are kept in more harsher environments than the broader wool sheep. Secondly, the superfine wool lambs are smaller and less viable, which can lead to inadequate stimulation to the ewes to promote good mothers (Lindsay et al., 1990; Nowak, 1990; Murphy & Lindsay, 1996).

These views and assumptions were supported by the results obtained by Kuchel & Lindsay (1999) that indicated that superfine wool ewes were poorer mothers than Peppin Merinos and their lambs were also 1.5kg lighter at birth. This contributed to the fact that the survival rate of the superfine wool lambs was 20% poorer than the Peppin Merinos.

Survival rate of lambs is a trait that varies considerably between production environments, farms, breeds and flocks and it is also influenced by various genetic, environmental and management factors (Bahri Binabaja et al., 2013). Non-genetic factors such as weight and litter size at birth, year and season of birth and the age of the dam can also influence the survival rate of lambs (Morris et al., 2000; Mandal et al., 2007; Dwyer, 2008). Several studies have reported that birth weight is the single largest contributor to lamb survival (Malik & Acharya, 1972; Smith, 1977; Meyer & Clarke, 1978; Dalton et al., 1980; Hinch et al., 1983; Yapi et al., 1990; Gama et al., 1991; Fogarty et al., 2000; Morris et al., 2000; Dwyer, 2008), and it has an inverted U-shape relationship with lamb survival. This means that lambs with a low birth weight tends to die due to exposure or starvation, and too heavy lambs are more likely to die due to dystocia (Smith, 1977; Meyer & Clarke, 1978; Dalton et al., 1980; Scales et al., 1986; Dwyer & Morgan, 2006; Dwyer, 2008).

Lamb death rate before weaning can range from as low as 3% to as high as 42% (Hight & Jury, 1970; Dalton et al., 1980; Eales et al., 1983; Yapi et al., 1990; Green & Morgan, 1993; Nash et al., 1996; Herselman & Van Heerden, 2013). Excessively high mortality rates will greatly reduce the efficiency and profitability of a lamb production enterprise. Moreover, Dwyer (2008) stated that survival rate is also a good indicater of the state of animal welfare, which has become an emotional issue (Cloete et al., 2009) and is subsequently an indication of the environmental conditions and management practices under which animals are kept.

Reproduction and survival rate are undoubtedly the most important traits in all systems of sheep production and in all environments (Fogarty et al., 1985; Matika et al., 2003), despite optimal management practices (Alexander, 1984; Haughey, 1991). It can therefore not be emphasised enough that at least one of these should be incorporated in the breeding objectives of sheep breeds in South Africa. The number of lambs weaned per ewe per lambing season, is the most important measure of a flock's overall reproductive performance. This is the sum of the proportion of ewes lambing (fertility), litter size at birth (prolificacy) and the survival of lambs from birth to weaning (Lee & Atkins, 1994).

The survival of Merino lambs is linked directly to its genetic makeup and management factors. Management problems can be rectified with immediate effect, however, the genetic makeup of the lambs is also of utmost importance. Changing the genetic makeup of the lambs will lead to more viable lambs being born.

Improving lamb survival through genetic selection is challenging because of the large number of environmental factors influencing the trait (Lopez-Villalobos & Garrick, 1999; Dwyer, 2007; Maxa et al., 2009), as well as the challenge of properly evaluating a binomially expressed trait. Heritability estimates for lamb survival are typically low (0.00 to 0.11; Safari et al., 2005), often prompting analysts to suggest that genetic improvement is unlikely and that managerial interventions have a better probability of success. However, genetic progress is also impacted upon by other factors such as the variability in the trait, selection intensity or relationships with other traits included in the selection objectives in addition to heritability. Therefore, selection can be effective under certain circumstances, even for traits with a low heritability (Vostrý &Milerski, 2013).

Limited genetic variation were found in studies researching the genetic improvement of survival rate (Olivier et al., 1998; Snyman et al., 1998b; Lopez-Villalobos & Garrick, 1999) and it led to recommendations that selection should rather be based on related traits and the improvement of the environment to increase lamb survival (Olivier et al., 1998; Morris et al., 2000; Everett-Hincks et al., 2005). Contrary to these findings, Haughey (1983) and Knight et al. (1988) reported that selective breeding can bring about differences between lines within breeds. These results are further supported by variation in lamb survival between the progeny of different sires (Gudex et al., 2005). Similar results were also reported by Cloete & Scholtz (1998), while Cloete et al. (2009) reported differences in the mortality of Merino lambs in two lines selected divergently for the ability of ewes to rear multiples.

Four traits could possibly be linked to the postnatal survival of Merino lambs and could therefore be included in selection programs, namely birth coat score (Alexander, 1964), birth weight (Morris et al. 2000; Gudex et al., 2005), as well as pre-weaning weight and weaning weight (as possible indicators of maternal milk production; Brand & Franck, 2000). So far, only birth coat score and birth weight have been studied as possible indirect criteria for lamb survival.

Against this background, the genetic relationships among these traits and lamb survival must be quantified before they can be included in selection programs. The aim of this study was therefore to estimate the genetic relationships among lamb survival, birth coat score, birth weight, pre-weaning weight and weaning weight in a South African fine wool Merino stud.

MATERIALS AND METHODS

The Cradock Fine Wool Merino Stud was established in 1988 as described by Olivier et al. (2006a). Ewes were bought from 30 Merino farmers with the finest clips throughout South Africa and four fine wool rams were imported from Australia as sires. Since then, another eight rams were introduced into the stud to be used as sires. The stud is kept at the Cradock Experimental Station (32º 13' S, 25º 41' E, elevation 847 m) near Cradock in the Eastern Cape Province of South Africa. The flock is run on irrigated pastures throughout the year. The ewes are mated during April each year. Data collected on 9 010 lambs that were born alive within this stud from 1988 to 2010, were used for the analyses. Unfortunately, anti-natal deaths and parturient deaths were not recorded.

The traits included in the analyses were birth weight, birth coat score, pre-weaning live weight, weaning weight and lamb survival. Birth weight and birth coat score were recorded within 24 h after the lambs were born. Birth coat scores were recorded since 1992 and were assessed on a scale from 1 to 4 with 1 being woolly and 4 being hairy (Figure 5.1). The pre-weaning weight was recorded at an average age of 49 ± 7 days and weaning weight was recorded at an average age of 109 ± 10 days.

Lamb survival was defined as the number of lambs born alive that survived until weaning. This trait was coded as a binary trait with two categories, namely lambs born alive that died before weaning (coded as 1) and lambs that survived until weaning (coded as 2).

The means, standard deviations, coefficients of variation, minima and maxima for the respective traits were obtained with the PROC MEANS-procedure of SAS, and significance levels for the fixed effects were obtained with the PDIFF-option under the PROC GLM-procedure of SAS (SAS, 2009). The fixed effects tested for inclusion in the final model were year of birth (1988 - 2010), sex (male or female), age of the dam in years (2 to 7+) and birth status (single or multiple), as well as the two-way interactions between these effects. The actual age of the animals when the pre-weaning and weaning weights were recorded was also tested for significance as linear regressions. Only effects that had a significant (P<0.01) effect in these preliminary analyses were included in the final model for each trait.
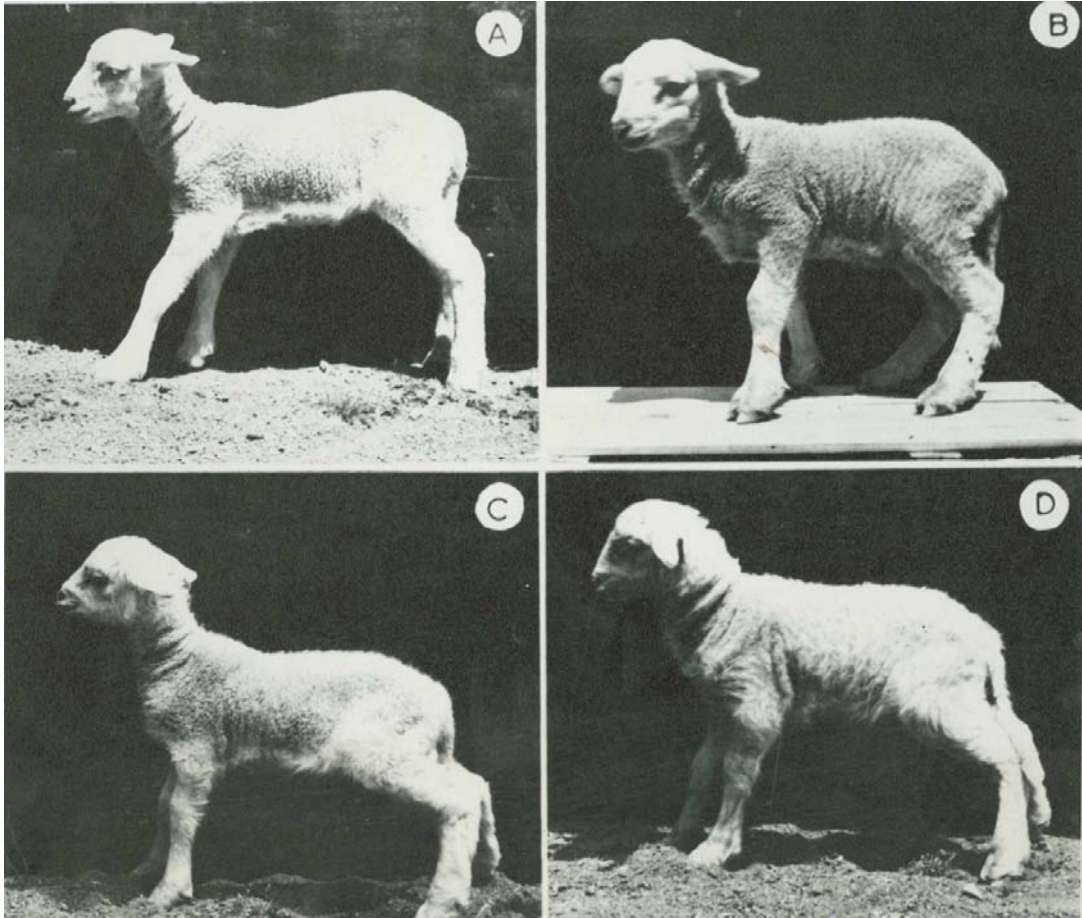
Figure 5.1 Classification of birth coat scores with 1 being woolly and 4 being hairy

A five trait analysis was then fitted to the traits mentioned above. The direct additive genetic variance, maternal additive genetic variance, the maternal permanent environmental variance (DamPE) and the covariance between the direct and maternal genetic effects were tested for significance and only random effects that had a significant effect were included in the final model. Based on these preliminary runs, the covariances between the direct and maternal genetic effects were excluded from the final model for all five traits. The equation for the final five-trait model was as follows:

$$y_{ijklm} = f_{ij} + a_{ik} + m_{ik} + c_{il} + e_{ijklm}$$

Where y is the vector of observations for lamb birth weight, pre-weaning weight, weaning weight and underlying values for birth coat score and lamb survival; i was indicative of the respective traits (I = 1,2,3,4,5), f_{ij} was the jth fixed effect for the ith trait, a_{ik} was the additive genetic effect of the kth animal for the ith trait, m_{ik} was the maternal genetic effect of the kth animal for the ith trait, c_{il} was the maternal permanent environmental effect of the lth dam for the ith trait and e_{ijklm} was the randomly distributed residual effects.

Variance components and genetic parameters were estimated with THRGIBBS1F90 (Misztal et al., 2002). This software can be used to derive variance components and genetic parameters in linear-threshold mixed animal models for any combination of categorical and continuous traits (Lee et al., 2002b). POSTGIBBSF90 was used for Post Gibbs analysis to obtain posterior means for the random effects (Misztal et al., 2002).

A single chain of 300 000 cycles were run and the first 100 000 cycles were used as the burn-in period (Donoghue et al., 2004). Every 10th sample after the burn-in period was stored, giving a total of 20 000 samples for the computation of posterior means and posterior standard deviations (SD), as well as 95% highest posterior density (HPD) confidence intervals. Point estimates were calculated as the posterior means of the specific variance component, using the results of the final 20 000 samples. Direct genetic, maternal genetic, maternal permanent environmental and environmental (residual) correlations were obtained from this analysis. The environmental correlation between lamb survival and weaning weight was set to zero because all lambs that survived until weaning had a weaning weight.

RESULTS AND DISCUSSION

Descriptive statistics for the respective traits analysed in this study are summarised in Table 5.1. The lamb survival rate score can be translated to almost 90% (7 903 lambs) of the lambs that were born alive survived until weaning age. It is evident from Table 5.1 that all the traits were variable, as the coefficients of variation for all traits were above 10%.

Table 5.1 Descriptive statistics for birth weight, birth coat score, pre-weaning weight and lamb survival

	Birth weight (kg)	Birth coat score	Pre-weaning weight (kg)	Weaning weight (kg)	Lamb survival
Number of records	9010	7190	8085	7903	9010
Mean	4.55	1.77	16.69	27.27	1.88
Standard deviation	0.84	0.81	3.71	5.12	0.33
Coefficient of variation	18.55	45.50	22.20	18.78	17.50
Minimum	1.10	1	4.40	8.20	1
Maximum	8.40	4	30.20	46.00	2

The posterior density distributions for the genetic variance components (direct additive genetic variance – Direct; maternal additive genetic variance – maternal; maternal permanent environmental variance – (DamPE) of birth weight (panel a), birth coat score (panel b), survival rate (panel c), pre-weaning weight (panel d) and weaning weight (panel e) are depicted in Figure 5.2. It is evident from this figure that the distributions for the body weights, which are continuous traits, as well as for birth coat score are largely symmetric. In contrast to this, the distributions of survival rate are more skewed than symmetric.

The direct-maternal covariance for all five traits went to zero after approximately 80 000 rounds when all five traits were included in a multivariate analysis. Similar tendencies were observed when the direct-maternal covariance for only one trait was included per analysis. It was therefore decided to exclude the direct-maternal covariance components of all five traits in the final model as it was observed not to be significant.

Lamb survival is one of the most important factors that influence the profitability and viability of a sheep enterprise and it was therefore the main focus area of this study. The effectiveness of the inclusion of lamb survival in selection objectives either through direct or indirect criteria are dependent on the heritability of the trait and the relationships with other traits that may have higher heritability estimates than lamb survival.

The mean (co)variance components, posterior SD (PSD), 95% highest posterior density (HPD) confidence intervals and the variance ratios ($\pm$ s.e.; h^2_a = direct heritability, h^2_m = maternal heritability, c^2_{mpe} = maternal permanent environment) for the five traits are presented in Table 5.2.

The 95% HPD confidence intervals of the variance components involving lamb survival excluded zero in all cases and ranged from 0.01 to 0.26. The h^2_a, h^2_m and c^2_{mpe} estimates for lamb survival were all significant ($P<0.05$) as the values were greater than double the corresponding standard error.

The direct heritability of lamb survival estimated in this study (0.11) falls within the range of literature estimates (0.00 to 0.17) fitting threshold models (Safari et al., 2005; Welsh et al., 2006). The h^2 estimated for lamb survival with linear models ranged from 0.03 to 0.16 (Matos et al., 2000; Ceyhan et al., 2009; Plush et al., 2011; Zishiri et al., 2013). Matos et al. (2000) found that higher h^2_a estimates can be obtained on the same data set when the data was analysed with threshold models rather than with linear models. In a study on the lamb survival of Ripollesa sheep, Casellas et al. (2007) obtained a heritability estimate of 0.14 with Gibbs sampling, which is in the same order as the h^2 obtained in this study. However, Cloete et al. (2009) reported a higher h^2_a of 0.28 for overall lamb survival, from before birth until weaning obtained with THRGIBBSF90 (Misztal et al., 2002). Cloete et al. (2009) also reported h^2_a estimates of 0.12 and 0.39 for lamb survival respectively from before birth to tail docking (4weeks) and tail docking to weaning.

It needs to be stated that Cloete et al. (2009) derived fairly large genetic correlations between the direct and maternal effects of -0.61 and -0.60 for overall lambs survival and lamb survival from tail docking to weaning respectively. Therefore, the selection response would be considerably lower than expected for these two traits, as a result of the large negative genetic correlation between the direct and maternal effects compared to when these correlations are closer to zero (Baker, 1980; Eler et al., 1995).
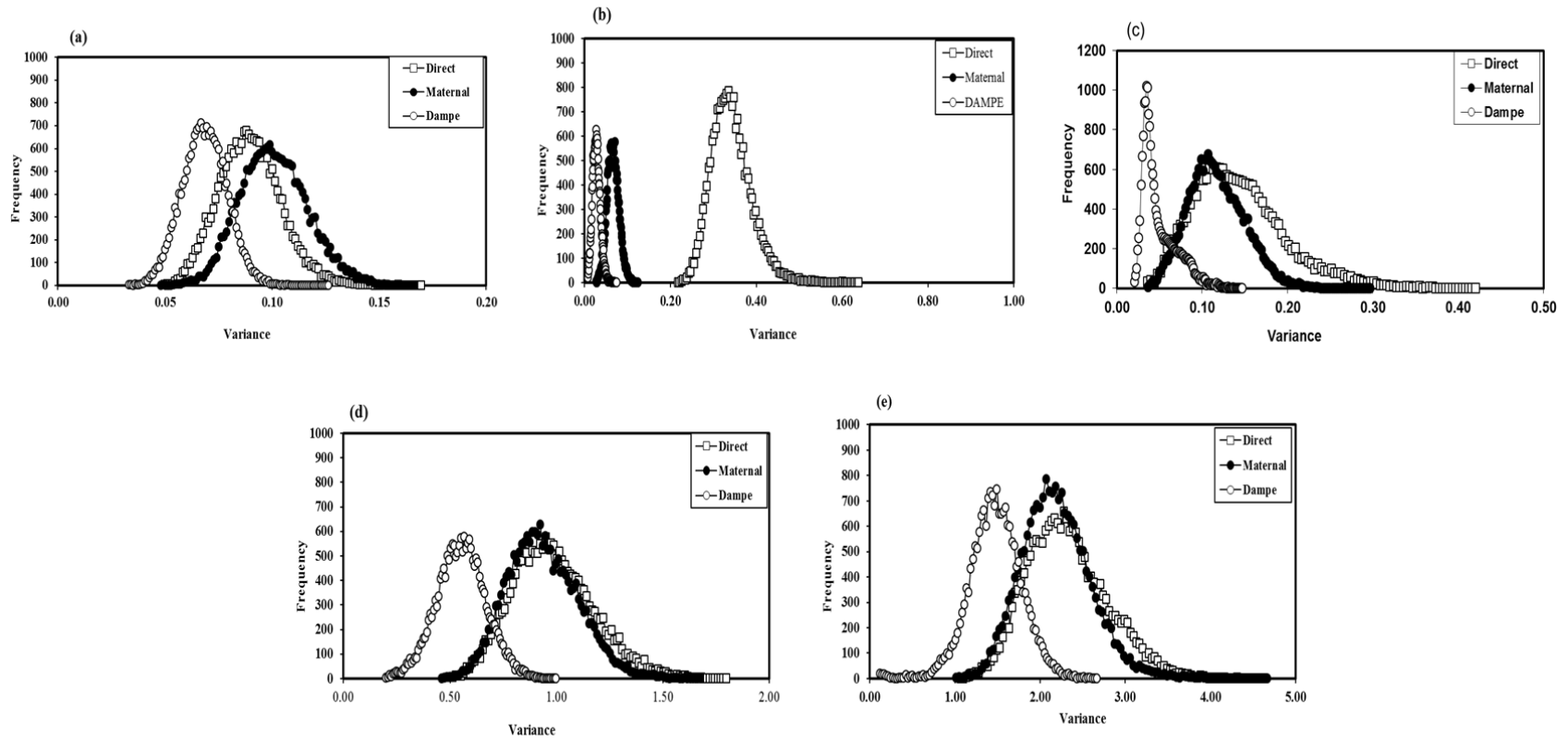
Figure 5.2 Posterior density distributions for the genetic variance components of birth weight (panel a), birth coat score (panel b), survival rate (panel c), pre-weaning weight (panel d) and weaning weight (panel e)

Table 5.2 The mean (co)variance components, posterior SD (PSD), 95% highest posterior density (HPD) confidence intervals and the variance ratios ($\pm$ s.e.) lamb survival, birth coat score, birth weight, pre-weaning weight and weaning weight

Trait and item[1]	Variance		95% HPD confidence interval		Ratio	Ratio $\pm$ s.e.
	Component	PSD	Lower	Upper		
Birth weight						
σ^2_a	0.09	0.02	0.06	0.12	h^2_a	0.15 ± 0.03
σ^2_m	0.10	0.02	0.07	0.13	h^2_m	0.17 ± 0.03
σ^2_{mpe}	0.07	0.01	0.05	0.09	c^2_{mpe}	0.12 ± 0.02
σ^2_e	0.32	0.01	0.30	0.34		
Birth coat score						
σ^2_a	0.34	0.05	0.25	0.44	h^2_a	0.54 ± 0.07
σ^2_m	0.07	0.01	0.04	0.10	h^2_m	0.11 ± 0.02
σ^2_{mpe}	0.03	0.01	0.01	0.04	c^2_{mpe}	0.04 ± 0.01
σ^2_e	0.20	0.03	0.14	0.25		
Lamb survival						
σ^2_a	0.15	0.05	0.04	0.26	h^2_a	0.11 ± 0.04
σ^2_m	0.12	0.03	0.05	0.18	h^2_m	0.09 ± 0.02
σ^2_{mpe}	0.05	0.02	0.01	0.10	c^2_{mpe}	0.04 ± 0.02
σ^2_e	1.00	0.02	0.96	1.04		
Pre-weaning weight						
σ^2_a	0.99	0.19	0.62	1.36	h^2_a	0.12 ± 0.02
σ^2_m	0.94	0.17	0.62	1.27	h^2_m	0.12 ± 0.02
σ^2_{mpe}	0.56	0.12	0.33	0.79	c^2_{mpe}	0.07 ± 0.01
σ^2_e	5.50	0.15	5.20	5.79		
Weaning weight						
σ^2_a	2.33	0.47	1.40	3.26	h^2_a	0.13 ± 0.03
σ^2_m	2.21	0.41	1.40	3.01	h^2_m	0.12 ± 0.02
σ^2_{mpe}	1.48	0.31	0.88	2.09	c^2_{mpe}	0.08 ± 0.02
σ^2_e	11.83	0.35	11.14	12.51		

[1] σ^2_a = direct additive genetic variance, σ^2_m = maternal genetic variance, σ^2_{mpe} = maternal permanent environment variance, σ^2_e = environmental (residual) variance, h^2 = direct heritability, m^2 = maternal heritability, c^2 = maternal permanent environment effect

The h^2_m (0.09) estimated in this study falls within the range of 0.04 to 0.26 reported in the literature for lamb survival from birth to weaning (Matos et al., 2000; Safari et al., 2005; Welsh et al., 2006). Cloete el al. (2009) reported h^2_m estimates of 0.14, 0.16 and 0.14 for lamb survival from before birth to tail docking, tail docking to weaning and overall survival rate (before birth to weaning) respectively.

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Several authors have reported direct-maternal correlations (r_{am}) for lamb survival that ranged from -0.75 to 0.62 fitting either linear or threshold models (Lopez-Villalobos & Garrick, 1999; Matos et al., 2000; Morris et al., 2000; Everett-Hincks et al., 2005; Safari et al., 2005; Welsh et al., 2006; Cloete et al., 2009). However, none of the reported r_{am} was significant, as the correlations were consistently smaller than the value of double the standard errors.

The c^2_{mpe} of 0.04 obtained in this study for lamb survival is lower than the values reported in the literature (Barwick et al., 1990; Welsh et al., 2006; Cassellas et al., 2007; Ceyhan et al., 2009) that ranged from 0.07 to 0.10. Similar estimates of 0.09, 0.05 and 0.09 for lamb survival from before birth to tail docking, tail docking to weaning and overall survival rate (before birth to weaning) were reported by Cloete et al. (2009), respectively. The total heritability (h^2_T) for lamb survival can be calculated as $h_T^2 = (\sigma_a^2 + 0.5\sigma_m^2)/\sigma_p^2$ when the r_{am} was excluded from the analysis (Willham, 1972). A h^2_T of 0.16 ± 0.05 was estimated for lamb survival in this study and this value is similar to the value of 0.17 estimated by Riggio et al. (2008).

The zero to very low heritability estimates reported in the literature for lamb survival suggested that there is a lack of genetic variation that might limit the genetic improvement of lamb survival (Olivier et al., 1998; Snyman et al. 1998b; Lopez-Villalobos & Garrick, 1999; Morris et al., 2000; Everett-Hincks et al., 2005). This has led to recommendations that the management and environment of sheep should rather be adapted to improve survival rate.

However, contrary to this, it is evident from literature that there was an underestimation of genetic variation in some earlier studies, as there is an increase in evidence that threshold animal models is better equipped to partition variance components and to detect higher genetic variance levels (Matos et al., 2000; Welsh et al., 2006; Ceyhan et al., 2009; Cloete et al., 2009; Plush et al., 2011; Zishiri et al., 2013). This is further supported by findings from Haughey (1983), Knight et al. (1988) and Cloete et al. (2009) that differences in lamb survival between lines within breeds were the result of selection progress. It is therefore evident from this study, as well as several other studies that it would be feasible to improve lamb survival genetically as this trait is variable and heritable.

The 95% HPD confidence intervals of the variance components for birth weight, pre-weaning weight and weaning weight excluded zero in all cases and ranged from 0.05 to 0.13, 0.31 to 1.37 and 0.82 to 3.27 respectively. It is evident from Table 5.2 that the h^2_a, h^2_m and c^2_{mpe} estimates for the three body weights were significant (P<0.05) as the values were greater than double the corresponding standard error (s.e.).

The h^2_a estimated in this study for birth weight falls within the range of values reported in literature for all wool types of sheep breeds that range from 0.04 to 0.41 (Safari et al., 2005; Safari et al., 2007a; Ceyhan et al., 2009; Cloete et al. 2009). However, most of these studies were done on dual-purpose breeds. The corresponding values estimated 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., 2003b; Safari et al., 2007a). Cloete et al. (2009)

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estimated a h^2 of 0.16 to 0.17 for Merino sheep with Gibbs sampling, which is similar to the estimate obtained in this study.

Mortimer & Atkins (1998), Vaez Torshizi et al. (1996), Analla & Serradilla (1998), Wuliji et al. (2001), Duguma et al. (2002b), Cloete et al. (2003) and Safari et al. (2007) reported h^2_m linear animal model estimates for birth weight in Merino sheep that ranged from 0.14 to 0.29. The value estimated in this study compares favourably with values in this range, but is slightly lower than the range (0.28 to 0.37) reported by Cloete et al. (2009) for Merino sheep, obtained with a threshold-linear model employing Gibbs sampling.

The c^2_{mpe} estimated for birth weight (0.12) was within the range 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). However, it is slightly higher than the estimates of 0.04 to 0.08 reported by Cloete et al. (2009). Olivier et al. (2013) estimated h^2_a, h^2_m and c^2_{mpe} of 0.24, 0.29 and 0.12 respectively with a linear animal model on this same dataset with a r_{am} of -0.47.

The h^2_a estimates reported in the literature for Merino pre-weaning weights (2 to 5 months of age) 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 value of 0.12 estimated in this study falls within the lower part of this range. The corresponding h^2_m of 0.12 estimated in this study also falls within the lower part of the range (0.11 to 0.38) reported in the literature (Swan & Hickson, 1994; Mortimer & Atkins, 1995; Vaez Torshizi et al., 1996; Analla & Serradilla, 1998).

The c^2_{mpe} estimate of 0.07 for pre-weaning weight in this study is similar to the values reported in the literature for pre-weaning weight (2 to 5 months of age). These values ranged from 0.01 to 0.07 (Swan & Hickson, 1994; Mortimer & Atkins, 1995; Vaez Torshizi et al., 1996; Analla & Serradilla, 1998). For pre-weaning weight Olivier et al. (2013) estimated h^2_a, h^2_m and c^2_{mpe} of 0.16, 0.21 and 0.07 respectively with a linear animal model on the same dataset with a r_{am} of -0.39.

Heritability estimates reported in the literature for weaning weight (± 110 days of age) for Merino sheep ranged from 0.06 to 0.34 (Snyman et al., 1996; Analla & Serradilla, 1998; Cloete et al., 2001b; Wuliji et al., 2001; Duguma et al., 2002b; Cloete et al., 2003b; Safari et al., 2007a). The h^2_a for weaning weight estimated in this study falls within this range. The h^2_m estimated in this study are similar to 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., 2001b; Wuliji et al., 2001; Duguma et al., 2002b; Cloete et al., 2003b; Safari et al., 2007a).

The range of c^2_{mpe} estimates for weaning weight reported in the literature of 0.05 to 0.08 (Snyman et al., 1996; Duguma et al., 2002b; Cloete et al., 2003b; Safari et al., 2007a) is in the same order as the value estimated in this study. The respective h^2_a, h^2_m and c^2_{mpe} for weaning weight reported by (Chapter 3) on the same dataset estimated with a uni-variate linear animal model were 0.10, 0.17 and 0.07 respectively.

The 95% HPD confidence intervals ranged from 0.01 to 0.44 and excluded zero in all cases for the variance components of birth coat score. It is evident from Table 5.2 that the h^2_a, h^2_m and c^2_{mpe} estimates for birth coat score were greater than double the corresponding s.e. and were therefor significant (P<0.05).

The h^2_a values reported in the literature for birth coat score ranged from 0.55 to 0.70 (Morley, 1955a; Gregory, 1982; Davis, 1987; Ponzoni et al., 1996; Cloete et al., 2003b; Kemper at al., 2003) and is somewhat higher than the present estimate of 0.54. The c^2_{mpe} estimated in this study (0.04) is in the same order as the value reported by Cloete et al. (2003). Estimated h^2_a, h^2_m and c^2_{mpe} of 0.36, 0.04 and 0.04 respectively were derived with a linear animal model on the same dataset (Chapter 3). No other literature with regard to h^2_m of birth coat score was found.

The mean (co)variance components, posterior SD (PSD), 95% highest posterior density (HPD) confidence intervals and the correlations among lamb survival, birth coat score, birth weight, pre-weaning weight and weaning weight are summarised in Tables 5.3 and 5.4.

It is evident from these tables that all the correlations were low to moderate among the respective traits. The genetic, maternal, maternal permanent environment and environmental correlations among the body weights reached levels of double their corresponding standard errors and were therefore significant (P<0.05). Other correlations that were considered significant were the r_m between BCS and birth weight; r_c between lamb survival and birth weight and r_e between lamb survival and birth weight and pre-weaning weight and between BCS and the body weights.

The correlations between lamb survival and BCS and body weights were generally low and non-significant. The genetic correlation between lamb survival and birth coat score in this study support findings in the literature that lamb survival is not highly related to the birth coat score of Merino lambs (Ponzoni et al. 1996; Cloete et al. 2003). Cloete et al. (2009) also reported genetic, maternal, maternal permanent environment and environmental correlations of 0.04, 0.13, 0.08 and 0.16 between overall lamb survival (before birth to weaning) and birth weight respectively. Sawalha et al. (2007) reported an unfavourable genetic correlation between lamb viability (coded as 0 for survivors and 1 for animals that had died) and birth weight of 0.21 and a favourable environmental correlation of -0.25. Zishiri et al. (2013) reported moderate favourable genetic and environmental correlations between survival and weaning weight.

The correlations estimated in this study among the body weights falls within the range reported by Safari et al. (2005). The correlations estimated with ASREML (Gilmour et al., 2009) are similar to values estimated with Gibbs sampling (Chapter 3). The correlations between BCS and body weights were generally low and non-significant; this is similar to the values reported by Cloete et al. (2003) between BCS and birth and weaning weight. No other comparable correlations were found in the literature.

Table 5.3 The mean covariance components, posterior SD (PSD), 95% highest posterior density (HPD) confidence intervals and the correlations ($\pm$ s.e.) between lamb survival and birth coat score, birth weight, pre-weaning weight and weaning weight

Trait and item[1]	Covariance		95% HPD confidence interval		Correlation	Correlation ± s.e.
	Component	PSD	Lower	Upper		
Covariance components and correlations between lamb survival and birth coat score						
σ_a	-0.02	0.04	-0.09	0.05	r_g	-0.10 ± 0.16
σ_m	0.01	0.02	-0.02	0.04	r_m	0.15 ± 0.18
σ_{mpe}	0.02	0.02	-0.01	0.04	r_c	0.43 ± 0.31
σ_e	0.04	0.03	-0.01	0.09	r_e	0.09 ± 0.06
Covariance components and correlations between lamb survival and birth weight						
σ_a	-0.03	0.02	-0.07	0.01	r_g	-0.27 ± 0.18
σ_m	-0.01	0.02	-0.04	0.02	r_m	-0.05 ± 0.16
σ_{mpe}	0.04	0.01	0.02	0.05	r_c	0.59 ± 0.15
σ_e	0.15	0.02	0.12	0.18	r_e	0.26 ± 0.03
Covariance components and correlations between lamb survival and pre-weaning weight						
σ_a	-0.04	0.07	-0.18	0.10	r_g	-0.12 ± 0.19
σ_m	0.02	0.05	-0.07	0.11	r_m	0.06 ± 0.14
σ_{mpe}	-0.03	0.03	-0.08	0.02	r_c	-0.20 ± 0.15
σ_e	1.08	0.09	0.90	1.25	r_e	0.46 ± 0.04
Covariance components and correlations between lamb survival and weaning weight						
σ_a	-0.10	0.12	-0.32	0.13	r_g	-0.17 ± 0.20
σ_m	0.01	0.08	-0.14	0.16	r_m	0.02 ± 0.15
σ_{mpe}	-0.08	0.04	-0.16	0.00	r_c	-0.29 ± 0.16

[1]σ_a = additive covariance, σ_m = maternal covariance, σ_{mpe} = maternal permanent environment covariance, σ_e = environmental (residual) covariance, r_g = genetic correlation, r_m = maternal correlation, r_c = maternal permanent environment correlation, r_e = environmental correlation

Table 5.4 The mean covariance components, posterior SD (PSD), 95% highest posterior density (HPD) confidence intervals and the correlations ($\pm$ s.e.) among birth coat score, birth weight, pre-weaning weight and weaning weight

Trait and item[1]	Covariance		95% HPD confidence interval		Correlations	Correlations $\pm$ s.e.
	Component	PSD	Lower	Upper		
Covariance components and correlations between birth coat score and birth weight						
σ_a	0.00	0.02	-0.03	0.03	r_g	0.01 $\pm$ 0.09
σ_m	0.03	0.01	0.01	0.05	r_m	0.35 $\pm$ 0.14
σ_{mpe}	0.00	0.01	-0.01	0.02	r_c	0.06 $\pm$ 0.17
σ_e	0.03	0.01	0.01	0.05	r_e	0.12 $\pm$ 0.04
Covariance components and correlations between birth coat score and pre-weaning weight						
σ_a	-0.00	0.06	-0.13	0.12	r_g	-0.01 $\pm$ 0.11
σ_m	0.03	0.04	-0.04	0.10	r_m	0.11 $\pm$ 0.14
σ_{mpe}	-0.00	0.02	-0.04	0.04	r_c	-0.01 $\pm$ 0.18
σ_e	0.11	0.04	0.03	0.18	r_e	0.10 $\pm$ 0.04
Covariance components and correlations between birth coat score and weaning weight						
σ_a	0.01	0.10	-0.19	0.20	r_g	0.01 $\pm$ 0.11
σ_m	0.04	0.06	-0.07	0.14	r_m	0.09 $\pm$ 0.14
σ_{mpe}	-0.04	0.04	-0.11	0.03	r_c	-0.21 $\pm$ 0.18
σ_e	0.13	0.06	0.01	0.25	r_e	0.08 $\pm$ 0.04
Covariance components and correlations between birth weight and pre-weaning weight						
σ_a	0.18	0.04	0.09	0.26	r_g	0.58 $\pm$ 0.14
σ_m	0.15	0.04	0.07	0.23	r_m	0.49 $\pm$ 0.13
σ_{mpe}	0.10	0.03	0.04	0.15	r_c	0.50 $\pm$ 0.14
σ_e	0.61	0.03	0.55	0.67	r_e	0.46 $\pm$ 0.02
Covariance components and correlations between birth weight and weaning weight						
σ_a	0.22	0.04	0.10	0.35	r_g	0.48 $\pm$ 0.14
σ_m	0.17	0.07	0.05	0.29	r_m	0.36 $\pm$ 0.14
σ_{mpe}	0.10	0.05	0.02	0.19	r_c	0.31 $\pm$ 0.14
σ_e	0.67	0.05	0.58	0.76	r_e	0.34 $\pm$ 0.02
Covariance components and correlations between pre-weaning weight and weaning weight						
σ_a	1.22	0.27	0.68	1.75	r_g	0.80 $\pm$ 0.18
σ_m	1.29	0.25	0.81	1.77	r_m	0.89 $\pm$ 0.17
σ_{mpe}	0.79	0.18	0.45	1.13	r_c	0.87 $\pm$ 0.20
σ_e	5.97	0.35	5.55	6.39	r_e	0.74 $\pm$ 0.03

[1]σ_a = additive covariance, σ_m = maternal covariance, σ_{mpe} = maternal permanent environment covariance, σ_e = environmental (residual) covariance, r_g = genetic correlation, r_m = maternal correlation, r_c = maternal permanent environment correlation, r_e = environmental correlation

The relationship between lamb survival and birth weight is complicated by the non-linear relationship that exists between these two traits (Sawalha et al., 2007; Barazandeh et al., 2012). This relationship suggest that it would be better to produce lambs with intermediate birth weights, compared to the extremes to both sides, i.e. both too light or too heavy birth weights will reduce lamb survival. Small and ill thrifty lambs will most probably die due to starvation and hypothermia, whereas dystocia is considered as the largest problem in lambs that are too large and heavy (Sawalha et al., 2007; Barazandeh et al., 2012). Hatcher et al. (2010) also reported a genetic correlation of approximately zero between lamb survival and birth weight.

The generally low and non-significant genetic correlations between pre-weaning weight, weaning weight and lamb survival suggest the improvement in the growth rate of lambs would not have a marked effect on the number of lambs that survived until weaning in the current study. However, Zishiri et al. (2013) has suggested that for Dorpers it would be possible to improve lamb survival indirectly through selection for weaning weight because of the low, but significant genetic correlation between these two traits.

It is evident from the results of this study and literature cited that lamb survival is a complex trait that is influenced by the mothering ability of the dam as well as the ability of the lamb to survive (Cundiff et al., 1982; Piper et al., 1982; Riggio et al., 2008; Brien et al., 2010). The effect of the ewe is superior to the lamb's own performance at this stage of its life. It might be a more viable option to select ewes with better mothering ability at this stage, because lambs depend on the milk production and behaviour conducive to facilitate suckling of ewes prior to weaning.

CONCLUSIONS

It can be concluded from the results of this study, as well as several other cited studies that it would be feasible to improve lamb survival genetically. Genetic progress can be achieved by selecting directly for lamb survival to eliminate the progeny of sires and dams that have a tendency to produce lambs that do not survive until weaning and also to cull these sires and dams. This selection can be augmented by selection for traits directly related to lamb survival in ewes (i.e. rearing ability or multiple rearing ability) by culling of unproductive ewes that failed to rear lambs. Based on the present results, the scope for indirectly selecting for lamb survival by considering birth weight, birth coat score, pre-weaning weight and weaning weight appears to be limited.

CHAPTER 6. GENETIC PARAMETERS FOR SUBJECTIVE TRAITS OF A GENETIC FINE WOOL MERINO STUD AND CORRELATIONS BETWEEN PRODUCTION AND REPRODUCTION TRAITS

INTRODUCTION

An integral part of selecting replacement animals in the small stock industry is the use of subjectively assessed wool and conformation traits. This hand and eye subjective appraisal system was especially important in years gone by, before objective selection for economically important traits were put into practice. The importance of subjective conformation traits was based on the assumption that they are of economic importance or that these traits are closely related to production traits of economic importance (Morley, 1955a; Young et al., 1963; Cloete et al., 1992; Lewer et al., 1994; Matebesi et al., 2009c).

Subjective traits are still regularly used by Merino breeders to select the sires and dams of the next generation (Lewer & McLeod, 1990; Groenewald et al., 1999; Snyman & Olivier, 2002; Naidoo et al., 2004; Olivier et al., 2006b; Matebesi et al., 2009c). According to Olivier et al. (2006b) it is sometimes the only selection criteria used by both meat and wool producers. Furthermore, lambs are also culled on these traits (Snyman & Olivier, 2002), sometimes even before evaluation on the economically important traits are practised. This happens although most of these traits cannot strictly be classified as economically important traits. However, traits such as wool quality and body conformation can either be directly or indirectly linked to the viability and economic survival of a sheep farming enterprise. Furthermore, the indiscriminate culling of animals on these traits might have a negative and detrimental effect on the traits of economic importance.

According to Olivier et al. (1987) type classification systems was developed by breeders' societies as possible genetic or phenotypic indicators of the production potential of animals. The major advantages of the linear scoring of type traits is firstly that the traits are evaluated more accurately because only a specific aspect is assessed at a time, rather than just looking at overall wool or conformation. Secondly, as these traits are assessed on a wide linear scale, the distributions tend to be more normal. The current system used in the Merino industry in South Africa was developed by Olivier et al. (1987).

Although subjective conformation scores are widely used in the industry for selection purposes, an understanding of the interactions among subjective and objectively measured traits is important (Gregory, 1982). This knowledge will aid producers in effectively incorporate these traits together with economically important traits in their breeding programs. The aim of this study was therefore to estimate variance components for the subjective traits and to quantify the relationships among the subjectively assessed traits and objective production and reproduction traits.

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MATERIALS AND METHODS

In 1988, on request from the South African Wool industry, the Cradock fine wool Merino stud was established. Ewes were purchased from Merino breeders with the finest clips throughout South Africa and mated to four Australian fine wool Merino rams (Olivier et al., 1989; Olivier et al., 2006a). The stud is kept on irrigated pastures and the ewes were artificially inseminated annually during March to April (Chapter 2). The selection objectives were initially to increase body weight, maintain fleece weight and maintain or decrease fibre diameter. This was changed in 1996 to increase body weight, maintain fleece weight and to reduce fibre diameter (Chapter 2).

Data collected on 7 363 ram and ewe progeny born in this stud from 1988 to 2010, were used for the analysis of the subjectively measure wool and conformation traits. The traits included in the analysis, as well as the scale of assessment are summarised in Table 6.1. Wool quality (WQ) is assessed on the regularity and definition of the crimp and the handle of the fleece, as well as the presence or absence of deviant fibres. The ideal (excellent) are therefore a fleece with well, clearly defined and regular crimps, soft handling and the absence of deviant fibres. Evenness of the fleece (EF) assesses the variation, definition and regularity of the crimps and the ideal is a fleece with no variation. The ideal wool yolk (WY) has an intermediate score and is indicative of a fleece with the correct amount and flow of yolk. The ideal yolk is a white to light cream in colour, spread through the fleece. Excessive yolk and yolk flow will be scored higher than the ideal, while fleeces with an inadequate amount and flow of yolk will be score lower than the ideal. A score of 25 is given for the ideal amount of wool yolk (WY) with drier wool scoring lower and excessive yolk is scored higher (Olivier et al., 1987; Steyn, 1996).

Staple formation (SF) is used to assess the bulkiness of the fleece through the length and thickness of the staples. The ideal is staples of good length that is thick and block shaped. Short, thin or ropy staples are unacceptable and are discriminated against. Belly and points (BP) assess the length and quality of the wool on the belly of a sheep and must have good quality, length, staple formation and colour. Animals with a creeping belly or very short and watery fleeces are culled. Problems with regard to wool quality and staple formation are normally first observed in the belly wool of wool sheep (Olivier et al., 1987; Steyn, 1996).

The ideal Merino head is a strong looking head with good depth, breadth and length. It must also be without the following culling faults: Overshot jaw, undershot jaw, loose teeth, inverted eyelids (entropion) and woolly face and jowls. Pigmentation score is used to assess the presence or absence of brown or black pigmentation around the eyes, ears, lips and tongue and brown or black fibres on horn buds, legs or fleece. The colour of the hoofs is also taken into consideration and must be amber colour (Olivier et al., 1987; Steyn, 1996).

The mobility and stance of an animal in the extensive farming condition of South Africa is of the utmost importance as it can have a detrimental effect on production and reproduction. Three subjective conformation traits are used to assess different indicators of mobility and stance. Hocks are used to assess the stance of the hind legs and an intermediate score is the ideal. Hocks that are turning in and

are therefore narrow are scored lower than the intermediate score. Bowleggedness, in contrast, i.e. hocks turning out are scored higher than the intermediate. Pastern score is an indication if an animal has strong front and hind pasterns, angled between 50 ° and 60 °. The mobility of an animal with poor and weak pasterns, angled below 50 ° will be hampered, while rams might also struggle to mount ewes during mating. Front quarters (FQ) assess the stance of the front legs and conformation of the front quarters. The ideal is a front quarter with good width and depth and straight front legs that are the same width as the front quarter. Legs that are to narrow or bend inwards (knock knees) are discriminated against (Oliver et al., 1987; Steyn, 1996).

The overall body conformation score includes the neck, middle and hind quarters. The length and depth of the body are an integral part of this score and the different parts must be joined symmetrically. The following cull faults must be taken into consideration, U-neck, narrow chest or flat sides, devil's grip, hollow back, sharp or loose shoulders, drooping rump and flat hind quarters (Olivier et al., 1987; Steyn, 1996).

Table 6.1 The subjectively assessed wool and conformation traits included in the analysis, as well as the scale of assessment

Trait	Scale of assessment[1]		
	1	25	50
Wool quality (WQ)	Poor	Average	Ideal
Evenness of the fleece (EF)	Uneven	Average	No variation
Wool yolk (WY)	None	Ideal	Excessive
Staple formation (SF)	Ropy	Average	Thick, blocky
Belly and points (BP)	Watery	Average	Thick
Conformation of the head (Head)	Weak	Average	Strong
Pigmentation (Pigm)	Excessive	Ideal	None
Hocks (Hock)	Narrow	Ideal	Wide
Pasterns (Pas)	Weak	Average	Strong
Front quarter (FQ)	Narrow	Average	Wide
Overall body conformation (BC)	Weak	Average	Strong

[1](With the exception of wool yolk, pigmentation and hocks): 1 - 10 = Poor; 11 - 20 = Below average; 21 - 30 = Average; 31 - 40 = Above average; 41 - 50 = Excellent; Intermediate optimum for the excluded traits

The Proc MEANS-procedure of SAS (SAS, 2009) was used to obtain the descriptive statistics of the data set. The significance levels for the non-genetic effects were obtained with the Proc GLM-procedure of SAS (SAS, 2009). Only effects and interactions which had a significant influence (P<0.01) on a specific trait were included in the final operational model.

The estimation of the genetic parameters was done with ASREML (Gilmour et al., 2009) by fitting single-trait animal models. These models included different combinations of the direct additive, maternal additive and maternal permanent environment effects, as well as the covariation between the direct and maternal additive effects. These different combinations led to the following six models:

$$\mathbf{y} = X\mathbf{b} + Z_1\mathbf{a} + \mathbf{e} \tag{1}$$

$$\mathbf{y} = X\mathbf{b} + Z_1\mathbf{a} + Z_2\mathbf{mpe} + \mathbf{e} \tag{2}$$

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

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

$$\mathbf{y} = X\mathbf{b} + Z_1\mathbf{a} + Z_2\mathbf{m} + Z_3\mathbf{mpe} + \mathbf{e}; \text{with cov}(a,m) = 0 \tag{5}$$

$$\mathbf{y} = X\mathbf{b} + Z_1\mathbf{a} + Z_2\mathbf{m} + Z_3\mathbf{mpe} + \mathbf{e}; \text{with cov}(a,m) = A\sigma_{am} \tag{6}$$

where $\mathbf{y}$ is a vector of observed traits of animals; $\mathbf{b}$, $\mathbf{a}$, $\mathbf{m}$ and $\mathbf{mpe}$ are 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 are incidence matrices respectively relating fixed effects, direct additive genetic effects, maternal additive genetic effects and maternal permanent environmental effects to $\mathbf{y}$; $\mathbf{e}$ is the vector of residuals; A is the numerator relationship matrix, and σ_{am} is 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 is an identity matrix, σ^2_a, σ^2_m, σ^2_{mpe} and σ^2_e are 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, $\sigma_{am}, \sigma^2_{mpe}$, and σ^2_e, were derived at convergence of the log likelihood. The most suitable model was determined as described in Chapter 3.

The genetic, environmental and phenotypic correlations among the subjectively assessed wool and conformation traits were estimated using two-trait models with ASREML (Gilmour et al., 2009). The (co)variance component values obtained with the single-trait models was used as starting values for the two-trait models. Correlations were also estimated of the subjective traits with body weight, fleece and reproduction traits as described in Chapters 3 and 4.

RESULTS AND DISCUSSION

The significance (P<0.01) level of different non-genetic effects for the different traits are summarised in Table 6.2. The non-genetic effects tested for significance were year of birth (1988 to 2010), sex (male/female), rearing status (single/multiple) and age of dam in years (2 – 6+). Several two-factor interactions between the non-genetic effects, as well as age of the animal for a specific trait as a linear regression were also tested.

It is evident from Table 6.2 that year of birth had a highly significant influence (P<0.01) on all the traits, while sex did not affect EF, WY, BP, Head and Hock significantly. Only the two-way interaction between year of birth and sex are included in Table 6.2 as none off the other interactions tested had a significant effect on any of the traits.

Table 6.2 The significance level of the different non-genetic effects, two-way interactions and age of the animal for the respective traits

Trait	Year of birth	Sex	RS	Dam age	Year x Sex	Animal Age
WQ	*	*	ns	*	*	*
EF	*	ns	*	*	*	*
WY	*	ns	*	*	ns	*
SF	*	*	*	*	ns	*
BP	*	ns	*	*	ns	*
Head	*	ns	*	*	ns	*
Pigm	*	*	*	ns	ns	*
Hock	*	ns	*	ns	*	ns
Pas	*	*	ns	*	ns	*
FQ	*	*	ns	*	*	*
BC	*	*	*	*	ns	*

* $P < 0.05$; ns - non significant; RS - rearing status; WQ - Wool quality; EF - Evenness of the fleece; WY - Wool yolk; SF - Staple formation; BP - Belly and points; Head - Conformation of the head; Pigm - Pigmentation; Hock - Hocks; Pas - Pasterns; FQ - Front quarters; BC - Overall body conformation

Descriptive statistics for subjectively assessed wool and conformation traits are summarised in Table 6.3. WY had the lowest coefficient of variation, which is in accordance with the literature (Groenewald et al., 1999; Naidoo et el., 2004; Matebesi et al., 2009b). In contrast, BP and Pigm had the most variation. The coefficient of variation of WQ, which is the most important subjective wool trait, was similar to the values reported by Groenewald et al. (1999), Naidoo et al. (2004) and Matebesi et al. (2009b) for South African Merinos. The variation in BC and FQ, which is the most important conformation traits were in the same range as the reported CV (Groenewald et al., 1999; Matebesi et al., 2009b).

Table 6.3 The number of records, number of sires, number of dams, mean, coefficient of variation (CV), skewness (SK) and Kurtosis (Kurt) of the different subjective wool and conformation traits

Trait	Nr of records	Nr of sires	Nr of dams	Mean	CV (%)	SK	Kurt
WQ	7362	150	1600	31.1	24.7	0.3	-0.5
EF	7362	150	1600	36.4	18.5	0.9	-0.8
WY	7362	150	1600	24.3	12.4	6.2	0.1
SF	7362	150	1600	28.5	21.7	0.6	-0.5
BP	7362	150	1600	25.6	31.2	0.3	-0.6
Head	7362	150	1600	28.6	24.6	0.9	-0.5
Pigm	7362	150	1600	34.1	28.3	1.0	-1.0
Hock	7362	150	1600	23.8	29.2	0.9	-0.2
Pas	7362	150	1600	33.4	26.4	-0.1	-0.8
FQ	7362	150	1600	25.4	27.8	-0.2	-0.3
BC	7362	150	1600	27.8	25.2	-0.1	-0.4

WQ - Wool quality; EF - Evenness of the fleece; WY - Wool yolk; SF - Staple formation; BP - Belly and points; Head - Conformation of the head; Pigm - Pigmentation; Hock - Hocks; Pas - Pasterns; FQ - Front quarters; BC - Overall body conformation

The Log Likelihood values for the subjectively assessed wool and conformation traits are presented in Table 6.4 as a deviation from the most suitable model. The most suitable model for WQ, EF, Pigm and Hock included only the direct additive effect (σ^2_a). For WY, SF, BP, Head, Pas, FQ and BC the inclusion

of the maternal additive effect (σ^2_m) also contributed significantly (P<0.05) to the variation in the respective traits.

Table 6.4 Log Likelihood deviations from the most suitable model (in bold) for the subjectively assessed wool and conformation traits

Trait	σ^2_a	$\sigma^2_a + \sigma^2_{pe}$	$\sigma^2_a + \sigma^2_m$	$\sigma^2_a + \sigma^2_m + \sigma_{am}$	$\sigma^2_a + \sigma^2_m + \sigma^2_{mpe}$	$\sigma^2_a + \sigma^2_m + \sigma^2_{mpe} + \sigma_{am}$
WQ	**0.00**	-0.56	-0.84	-0.86	-0.92	-0.92
EF	**0.00**	-2.76	-3.58	-3.66	-3.70	-3.70
WY	7.00	3.60	**0.00**	-0.80	0.00	-0.80
SF	10.06	2.28	**0.00**	-0.82	-0.80	-2.14
BP	12.38	-3.74	**0.00**	-0.80	-3.36	-3.42
Head	33.42	16.52	**0.00**	-0.52	-0.46	-0.84
Pigm	**0.00**	-0.10	-0.58	-2.22	-0.58	-2.42
Hock	**0.00**	0.00	-3.46	-3.60	-3.46	-3.68
Pas	**4.94**	3.40	0.00	1.14	0.00	1.14
FQ	**5.98**	5.90	0.00	-0.12	0.00	-0.12
BC	25.16	17.74	**0.00**	-2.46	0.00	-2.46

WQ - Wool quality; EF - Evenness of the fleece; WY - Wool yolk; SF - Staple formation; BP - Belly and points; Head - Conformation of the head; Pigm - Pigmentation; Hock - Hocks; Pas - Pasterns; FQ - Front quarters; BC - Overall body conformation

The direct heritability (h^2_a) and maternal heritability (h^2_m) for the subjectively assessed wool and conformation traits are summarised in Table 6.5. It is evident from this table that all the h^2_a estimates of the subjective traits, except Pas (0.11) were moderate to high (0.28 to 0.54). The h^2_m estimates of the subjective traits were all low (<0.10). The h^2_a estimated in the current study for WQ was similar to the estimate obtained by Matebesi et al. (2009b), but higher than the estimates of Groenewald et al. (1999) and Naidoo et al. (2004). It should be noted that the former estimate was obtained with a sire model. Matebesi et al. (2009b) estimated a maternal effect of 0.06 for WQ with a negative correlation between the direct and maternal effects. The two main characteristics of WQ are seen as two separate traits in the Australian Wool industry, namely wool handle (1 being soft and 5 harsh) and wool character (1 being well defined crimps). Mortimer et al. (2010) reported heritabilities of 0.33 and 0.34 for wool handle and wool character respectively, which are lower than the estimate for WQ in the current study. In contrast, Brown et al. (2002b) estimated higher heritabilities of 0.40 and 0.44 for wool handle and character respectively.

Evenness of the fleece and SF are also two important subjective wool traits on which animals are being selected or culled. The h^2_a estimates of these two traits are higher than the values reported by Groenewald et al. (1999), Naidoo et al. (2004) and Matebesi et al. (2009b) that ranged from 0.19 to 0.29 and 0.09 to 0.21 for regularly of crimp and SF respectively. The corresponding values of the two most important body conformation traits, namely FQ and BC were higher than the values reported in the literature (Groenewald et al., 1999; Matebesi et al., 2009b).

Table 6.5 Direct heritability (h^2_a) and maternal heritability (h^2_m) estimates for subjectively assessed wool and conformation traits (± s.e.)

Trait	h^2_a	h^2_m
Wool quality (WQ)	0.54 ± 0.03	-
Evenness of the fleece (EF)	0.38 ± 0.03	-
Wool yolk (WY)	0.29 ± 0.04	0.03 ± 0.02
Staple formation (SF)	0.39 ± 0.04	0.04 ± 0.02
Belly and points (BP)	0.37 ± 0.04	0.05 ± 0.02
Conformation of the head (Head)	0.39 ± 0.04	0.08 ± 0.02
Pigmentation (Pigm)	0.39 ± 0.03	-
Hocks (Hock)	0.61 ± 0.04	-
Pasterns (Pas)	0.11 ± 0.02	0.02 ± 0.01
Front quarters (FQ)	0.45 ± 0.03	0.02 ± 0.01
Overall body conformation (BC)	0.48 ± 0.04	0.05 ± 0.02

The genetic (r_g), maternal (r_m), environmental (r_e) and phenotypic (r_p) correlations among the subjectively assessed wool and conformation traits are summarised in Tables 6.6 to 6.8. The r_e and r_p among the subjectively wool and conformation traits were lowly positive or negative to zero and comparable in sign to the corresponding r_g. In contrast to this, the r_m estimated between the relevant traits are moderate to highly positive. Wool quality was positively correlated with EF and WY, while SF was unfavourably (negatively) correlated with WQ and EF (Table 6.6).

Table 6.6 The genetic (r_g), maternal (r_m), environmental (r_e) and phenotypic (r_p) correlations among the subjectively assessed wool traits (± s.e.)

Trait	EF	WY	SF	BP
	Additive genetic correlations			
WQ	0.44 ± 0.06	0.55 ± 0.06	-0.54 ± 0.06	-0.13 ± 0.07
EF		0.34 ± 0.08	-0.60 ± 0.06	-0.38 ± 0.07
WY			-0.10 ± 0.10	0.17 ± 0.10
SF				0.70 ± 0.05
	Maternal genetic correlation			
WY			0.70 ± 0.27	0.41 ± 0.26
SF				0.72 ± 0.14
	Environmental correlations			
WQ	0.36 ± 0.02	0.04 ± 0.02	-0.04 ± 0.03	0.01 ± 0.03
EF		0.09 ± 0.02	-0.01 ± 0.02	0.01 ± 0.02
WY			0.01 ± 0.01	0.06 ± 0.01
SF				0.39 ± 0.02
	Phenotypic correlations			
WQ	0.39 ± 0.01	0.20 ± 0.01	-0.23 ± 0.01	-0.04 ± 0.02
EF		0.15 ± 0.01	-0.19 ± 0.01	-0.11 ± 0.02
WY			0.02 ± 0.02	0.01 ± 0.02
SF				0.50 ± 0.01

WQ - Wool quality; EF - Evenness of the fleece; WY - Wool yolk; SF - Staple formation; BP - Belly and points

An unfavourable genetic correlation was also estimated between EF and BP, while SF was favourable correlated with BP. The correlation between SF and WQ is in accordance with the findings of Matebesi et al. (2009b). The r_g correlation estimates between WQ, SF and the conformation traits were all non-

significant and ranged from -0.11 to 0.18 (Table 6.7) and were similar to the estimates reported by Matebesi et al.(2009b) on SA Merinos. Evenness of the fleece and WY were unfavourably (negatively) correlated to all the subjectively assessed conformation traits that are an indication of size. Snyman & Olivier (2002) reported similar findings between EF and conformation traits. The genetic correlations among BP and Head, FQ and BC were unfavourable (negative), which is in contrast to the estimates obtained by Matebesi et al. (2009b). Snyman & Olivier (2002) reported similar unfavourable correlations between creeping belly, which is a trait closely related to BP and subjective conformation traits than the estimates between BP and conformations traits in the current study.

Table 6.7 The genetic (r_g), maternal (r_m), environmental (r_e) and phenotypic (r_p) correlations among the subjectively assessed wool and conformation traits (± s.e.)

Trait	Head	Pigm	Hock	Pas	FQ	BC
	Additive genetic correlations					
WQ	-0.03 ± 0.07	-0.01 ± 0.06	-0.04 ± 0.06	0.12 ± 0.09	-0.11 ± 0.06	0.02 ± 0.06
EF	-0.31 ± 0.08	0.02 ± 0.07	-0.28 ± 0.07	0.11 ± 0.10	-0.24 ± 0.07	-0.37 ± 0.07
WY	-0.34 ± 0.09	-0.09 ± 0.08	-0.09 ± 0.09	-0.09 ± 0.12	-0.34 ± 0.08	-0.46 ± 0.08
SF	0.18 ± 0.09	-0.02 ± 0.07	-0.01 ± 0.08	0.02 ± 0.10	0.02 ± 0.07	0.06 ± 0.08
BP	-0.23 ± 0.09	0.12 ± 0.07	-0.22 ± 0.07	0.11 ± 0.10	-0.24 ± 0.06	-0.30 ± 0.07
	Maternal genetic correlation					
OLIE	0.28 ± 0.26	-	-	-	0.34 ± 0.27	0.36 ± 0.28
STAP	0.86 ± 0.18	-	-	-	0.54 ± 0.23	0.52 ± 0.20
PENP	0.75 ± 0.17	-	-	-	0.72 ± 0.22	0.71 ± 0.20
	Environmental correlations					
WQ	0.09 ± 0.03	0.02 ± 0.03	0.07 ± 0.03	0.03 ± 0.02	0.08 ± 0.03	0.12 ± 0.03
EF	0.06 ± 0.02	0.01 ± 0.02	0.08 ± 0.03	0.00 ± 0.02	0.02 ± 0.03	0.08 ± 0.03
WY	0.01 ± 0.02	0.01 ± 0.02	0.00 ± 0.02	0.03 ± 0.02	0.05 ± 0.03	0.03 ± 0.03
SF	0.25 ± 0.02	0.03 ± 0.03	0.05 ± 0.03	-0.04 ± 0.02	0.20 ± 0.03	0.30 ± 0.03
BP	0.23 ± 0.02	0.00 ± 0.03	0.10 ± 0.03	-0.05 ± 0.02	0.17 ± 0.03	0.29 ± 0.03
	Phenotypic correlations					
WQ	0.05 ± 0.02	0.01 ± 0.02	0.02 ± 0.02	0.05 ± 0.01	-0.01 ± 0.02	0.07 ± 0.02
EF	-0.05 ± 0.01	0.01 ± 0.02	-0.03 ± 0.02	0.02 ± 0.01	-0.07 ± 0.02	-0.08 ± 0.02
WY	-0.06 ± 0.01	-0.02 ± 0.01	-0.03 ± 0.02	0.01 ± 0.01	-0.07 ± 0.02	-0.10 ± 0.02
SF	0.22 ± 0.01	0.01 ± 0.02	0.02 ± 0.02	-0.03 ± 0.01	0.13 ± 0.02	0.22 ± 0.02
BP	0.11 ± 0.02	0.04 ± 0.02	-0.02 ± 0.02	-0.01 ± 0.01	0.00 ± 0.02	0.08 ± 0.02

WQ- Wool quality; EF - Evenness of the fleece; WY - Wool yolk; SF - Staple formation; BP - Belly and points; Head - Conformation of the head; Pigm - Pigmentation; Hock - Hocks; Pas - Pasterns; FQ - Front quarters; BC - Overall body conformation

High positive (favourable) r_g were estimated among Head, FQ and BC (Table 6.8). The r_g between Head and FQ is higher than the reported value for Merinos (Matebesi et al., 2009b) but similar to estimates for Afrino sheep (Snyman & Olivier, 2002). Positive r_g among BC, Pas and Hock were estimated in the current study, as well as between FQ and Hock. The latter estimate was lower than corresponding estimates reported by Snyman & Olivier (2002) and Matebesi et al. (2009b).

Table 6.8 The genetic (r_g), maternal (r_m), environmental (r_e) and phenotypic (r_p) correlations among the subjectively assessed conformation traits (± s.e.)

Trait	Pigm	Hock	Pas	FQ	BC
	Additive genetic correlations				
Head	-0.15 ± 0.07	0.23 ± 0.07	0.11 ± 0.10	0.79 ± 0.04	0.87 ± 0.03
Pigm		-0.03 ± 0.07	0.13 ± 0.09	-0.16 ± 0.06	-0.20 ± 0.07
Hock			0.43 ± 0.08	0.56 ± 0.05	0.53 ± 0.05
Pas				0.16 ± 0.09	0.34 ± 0.09
FQ					0.93 ± 0.02
	Maternal genetic correlation				
Head			0.83 ± 0.09	0.87 ± 0.07	0.86 ± 0.08
Pas				0.75 ± 0.10	0.78 ± 0.09
FQ					0.89 ± 0.06
	Environmental correlations				
Head	0.07 ± 0.03	0.08 ± 0.03	-0.02 ± 0.02	0.25 ± 0.02	0.44 ± 0.02
Pigm		0.00 ± 0.03	0.00 ± 0.02	0.07 ± 0.03	0.12 ± 0.03
Hock			-0.05 ± 0.02	0.12 ± 0.03	0.21 ± 0.03
Pas				0.14 ± 0.02	0.05 ± 0.02
FQ					0.55 ± 0.02
	Phenotypic correlations				
Head	0.00 ± 0.02	0.13 ± 0.02	0.00 ± 0.01	0.45 ± 0.01	0.61 ± 0.01
Pigm		-0.01 ± 0.02	0.03 ± 0.01	-0.03 ± 0.02	-0.01 ± 0.02
Hock			0.07 ± 0.01	0.32 ± 0.01	0.33 ± 0.01
Pas				0.14 ± 0.01	0.12 ± 0.01
FQ					0.72 ± 0.01

Head - Conformation of the head; Pigm - Pigmentation; Hock - Hocks; Pas - Pasterns; FQ - Front quarters; BC - Overall body conformation

The genetic (r_g), maternal (r_m), environmental (r_e) and phenotypic (r_p) correlations among the subjectively assessed wool traits and body weights at different ages are presented in Table 9. The r_e and r_p among the subjectively assessed wool traits and body weights at different ages, ranged from lowly positive to zero and the r_m from approximately 0.04 to 0.69. Almost all r_m were non-significant, with the only exceptions between BP and BirthW and body weights at 6 and 12 months of age, as well as WQ and BirthW.

The r_g among WQ, EF and SF and the different body weights were all non-significant and ranged from -0.17 to 0.18 (Table 6.9). These correlations are consistent with findings by Snyman & Olivier (2002) and Matebesi et al. (2009c) for the major subjective wool traits and body weights at different ages. The only significant r_g (unfavourable) were estimated between WY and body weights older than weaning and BP and body weights older than 12 months of age. These estimates are in contrast to the r_g of approximately zero between these traits as reported by Matebesi et al. (2009c). However, Snyman & Olivier (2002) reported similar findings to the current study between body weight at different ages and creeping belly, which is a trait closely related to BP.

Table 6.9 The genetic (r_g), maternal (r_m), environmental (r_e) and phenotypic (r_p) correlations among the subjectively assessed wool traits and body weights at different ages (± s.e.)

Trait	BirthW	PWW	WW	BW6	BW12	BW15
	Additive genetic correlations					
WQ	0.07 ± 0.08	0.03 ± 0.10	-0.06 ± 0.10	-0.15 ± 0.08	-0.05 ± 0.06	-0.01 ± 0.06
EF	-0.04 ± 0.09	0.06 ± 0.11	-0.13 ± 0.11	-0.17 ± 0.09	-0.11 ± 0.07	-0.11 ± 0.07
WY	0.08 ± 0.11	0.06 ± 0.13	-0.30 ± 0.12	-0.39 ± 0.10	-0.27 ± 0.09	-0.35 ± 0.08
SF	0.18 ± 0.09	0.23 ± 0.12	0.15 ± 0.12	0.14 ± 0.09	0.05 ± 0.07	0.03 ± 0.07
BP	0.11 ± 0.09	-0.03 ± 0.11	-0.16 ± 0.11	-0.13 ± 0.09	-0.26 ± 0.07	-0.27 ± 0.07
	Maternal genetic correlation					
WY	0.39 ± 0.16	0.31 ± 0.20	0.42 ± 0.24	0.12 ± 0.18	0.22 ± 0.27	0.28 ± 0.26
SF	0.17 ± 0.13	0.04 ± 0.17	0.09 ± 0.18	0.12 ± 0.15	0.39 ± 0.21	0.18 ± 0.21
BP	0.34 ± 0.13	0.32 ± 0.16	0.38 ± 0.18	0.40 ± 0.15	0.69 ± 0.22	0.37 ± 0.21
	Environmental correlations					
WQ	0.08 ± 0.03	0.07 ± 0.03	0.08 ± 0.03	0.09 ± 0.03	0.08 ± 0.03	0.06 ± 0.03
EF	0.07 ± 0.02	0.03 ± 0.02	0.03 ± 0.02	0.05 ± 0.02	0.03 ± 0.03	0.04 ± 0.03
WY	0.06 ± 0.02	0.07 ± 0.02	0.08 ± 0.02	0.07 ± 0.02	0.03 ± 0.03	0.03 ± 0.03
SF	0.10 ± 0.02	0.15 ± 0.02	0.20 ± 0.02	0.23 ± 0.02	0.30 ± 0.03	0.24 ± 0.03
BP	0.11 ± 0.03	0.14 ± 0.02	0.17 ± 0.02	0.18 ± 0.03	0.27 ± 0.03	0.21 ± 0.03
	Phenotypic correlations					
WQ	0.06 ± 0.02	0.05 ± 0.02	0.03 ± 0.02	0.00 ± 0.02	0.02 ± 0.02	0.03 ± 0.02
EF	0.03 ± 0.01	0.03 ± 0.01	0.00 ± 0.01	-0.01 ± 0.02	-0.02 ± 0.02	-0.01 ± 0.02
WY	0.08 ± 0.01	0.08 ± 0.01	0.03 ± 0.01	-0.03 ± 0.02	-0.06 ± 0.02	-0.08 ± 0.02
SF	0.12 ± 0.01	0.15 ± 0.01	0.17 ± 0.01	0.19 ± 0.02	0.20 ± 0.02	0.15 ± 0.02
BP	0.13 ± 0.02	0.10 ± 0.02	0.10 ± 0.02	0.10 ± 0.02	0.07 ± 0.02	0.02 ± 0.02

WQ - Wool quality; EF - Evenness of the fleece; WY - Wool yolk; SF - Staple formation; BP - Belly and points; Body weights: BirthW - birth; PWW - pre-weaning; WW - weaning; BW6 - 6 months of age; BW12 - 12 months of age; BW - 15 months of age

The genetic (r_g), maternal (r_m), environmental (r_e) and phenotypic (r_p) correlations among the subjectively assessed conformation traits and body weight at different ages are summarised in Table 6.10. Almost all of the r_p and r_e among the subjectively assessed conformation traits and the body weights at different ages were significant and ranged from -0.06 to 0.61. The r_m between Head, Pas, FQ and BC and the different body weights were all significant and ranged from 0.35 to unity.

The genetic relationship between BirthW and all of the subjective conformation traits were low to moderate positive or negative. Only the r_g between BirthW and the conformation traits linked to size were significant. The r_g between Pigm and the body weights older than weaning were moderate unfavourable (negative). Hock and BW 12 months and older were moderate positive correlated. The r_g between Head, FQ, BC and the different body weights were all significant and ranged from 0.40 to 0.82, furthermore it also increased with age from PWW. Matebesi et al. (2009b) reported similar r_g of FQ, Hock and Head with live weight in Merinos, while the estimates reported by Snyman & Olivier (2002) among these traits in Afrinos were generally higher.

Table 6.10 The genetic (r_g), maternal (r_m), environmental (r_e) and phenotypic (r_p) correlations among the subjectively assessed conformation traits and body weights at different ages (± s.e.)

Trait	BirthW	PPW	WW	BW6	BW12	BW15
Additive genetic correlations						
Head	0.23 ± 0.09	0.57 ± 0.08	0.59 ± 0.08	0.60 ± 0.06	0.72 ± 0.04	0.71 ± 0.04
Pigm	-0.07 ± 0.08	-0.11 ± 0.10	-0.22 ± 0.10	-0.27 ± 0.08	-0.23 ± 0.06	-0.24 ± 0.06
Hock	-0.14 ± 0.08	0.08 ± 0.10	0.17 ± 0.11	0.20 ± 0.09	0.28 ± 0.07	0.23 ± 0.06
Pas	-0.04 ± 0.11	0.14 ± 0.13	0.23 ± 0.13	0.19 ± 0.11	0.03 ± 0.09	0.05 ± 0.09
FQ	0.09 ± 0.07	0.40 ± 0.08	0.59 ± 0.07	0.62 ± 0.05	0.68 ± 0.04	0.66 ± 0.04
BC	0.22 ± 0.08	0.54 ± 0.08	0.63 ± 0.07	0.69 ± 0.05	0.80 ± 0.03	0.82 ± 0.04
Maternal genetic correlation						
Head	0.56 ± 0.10	0.79 ± 0.10	0.88 ± 0.08	0.72 ± 0.08	0.96 ± 0.07	0.87 ± 0.08
Pas	0.49 ± 0.09	0.72 ± 0.11	0.83 ± 0.09	0.78 ± 0.09	0.93 ± 0.08	0.85 ± 0.07
FQ	0.35 ± 0.12	0.82 ± 0.12	0.98 ± 0.09	0.81± 0.10	0.87 ± 0.08	1.00 ± 0.07
BC	0.37 ± 0.12	0.81 ± 0.12	0.98 ± 0.09	0.79 ± 0.09	0.89 ± 0.09	1.00 ± 0.06
Environmental correlations						
Head	0.18 ± 0.02	0.21 ± 0.02	0.28 ± 0.02	0.32 ± 0.02	0.43 ± 0.02	0.38 ± 0.02
Pigm	0.01 ± 0.03	0.03 ± 0.02	0.06 ± 0.02	0.09 ± 0.03	0.10 ± 0.03	0.12 ± 0.03
Hock	0.07 ± 0.03	0.06 ± 0.02	0.08 ± 0.02	0.05 ± 0.03	0.05 ± 0.03	0.06 ± 0.03
Pas	-0.01 ± 0.02	-0.04 ± 0.02	-0.05 ± 0.02	-0.04 ± 0.02	-0.01 ± 0.02	-0.03 ± 0.03
FQ	0.14 ± 0.03	0.18 ± 0.02	0.20 ± 0.02	0.19 ± 0.03	0.29 ± 0.03	0.27 ± 0.03
BC	0.19 ± 0.03	0.23 ± 0.02	0.29 ± 0.02	0.30 ± 0.02	0.44 ± 0.02	0.42 ± 0.03
Phenotypic correlations						
Head	0.22 ± 0.01	0.32 ± 0.01	0.38 ± 0.01	0.43 ± 0.01	0.57 ± 0.01	0.52 ± 0.01
Pigm	-0.01 ± 0.01	0.00 ± 0.01	-0.01 ± 0.01	-0.03 ± 0.02	-0.04 ± 0.02	-0.04 ± 0.02
Hock	0.00 ± 0.02	0.06 ± 0.02	0.09 ± 0.02	0.09 ± 0.02	0.14 ± 0.02	0.13 ± 0.02
Pas	-0.01 ± 0.01	-0.01 ± 0.01	-0.01 ± 0.01	0.01 ± 0.01	-0.02 ± 0.02	-0.01 ± 0.01
FQ	0.10 ± 0.01	0.21 ± 0.01	0.29 ± 0.01	0.34 ± 0.01	0.48 ± 0.01	0.46 ± 0.01
BC	0.20 ± 0.02	0.32 ± 0.01	0.39 ± 0.01	0.46 ± 0.01	0.61 ± 0.01	0.59 ± 0.01

Head - Conformation of the head; Pigm – Pigmentation; Hock – Hocks; Pas – Pasterns; FQ - Front quarters; BC - Overall body conformation; Body weights: BirthW – birth; PWW – pre-weaning; WW – weaning ; BW6 –6 months of age; BW12 –12 months of age; BW15 – at 15 months of age

The genetic (r_g), maternal (r_m), environmental (r_e) and phenotypic (r_p) correlations among the subjectively assessed wool traits, BirthC and objectively measured wool traits are summarised in Tables 6.11 to 6.13. It is evident from these tables that most of the r_e and r_p among the subjectively assessed wool, objectively measured wool traits and BirthC ranged from moderately negative to moderately positive. These correlations were also comparable in sign to the corresponding r_g.

Fibre diameter at different ages was moderately to highly negatively (favourably) correlated with WQ and EF and positively (unfavourably) correlated with SF (Table 6.11). The r_g estimates of SDFD and CVFD with WQ and EF (Table 6.13) were in the same order as the correlations between FD and these traits. These findings were consistent with the estimates obtained by Snyman & Olivier (2002) and Matebesi et al. (2009c). Staple formation and BP were positively (thus unfavourably) correlated to FD (Table 6.11) and the FD related traits of SDFD and CVFD, which were in accordance with the literature (Snyman & Olivier, 2002; Matebesi et al., 2009c).

Wool quality (Table 6.11) is favourably (moderate positive) correlated (r_g) with fleece weights, while EF are unfavourably correlated to GFW and CFW. Favourable r_g estimates were obtained in the current study between GFW and CFW with SF and BP. The high positive r_g between the fleece weights and WY were unfavourable. Matebesi et al. (2009b) reported similar estimates that were lower in magnitude compared to the current study, while Naidoo et al. (2004) also reported positive r_g estimates between CFW and WQ, SF and BP. The estimates for the r_g between creeping belly and fleece weight in Afrino sheep (Snyman & Olivier, 2002) is in agreement with the correlations between BP and fleece weight in the current study. The r_g between BirthC and EF was favourable (negative), while the relationship with SF was unfavourable. This implies that the more woolly lambs (BirthC) will have less variation over the fleece with thinner staples.

Table 6.11 The genetic (r_g), maternal (r_m), environmental (r_e) and phenotypic (r_p) correlations among the subjectively assessed wool traits, BirthC, FD6, FD12, GFW, CFW and FD (± s.e.)

Trait	BirthC	FD6	FD12	GFW	CFW	FD
	Additive genetic correlations					
WQ	-0.11 ± 0.07	-0.42 ± 0.06	-0.42 ± 0.04	0.15 ± 0.06	0.28 ± 0.05	-0.45 ± 0.05
EF	-0.29 ± 0.08	-0.61 ± 0.06	-0.58 ± 0.05	-0.14 ± 0.07	-0.23 ± 0.06	-0.60 ± 0.05
WY	-0.10 ± 0.09	-0.27 ± 0.09	-0.33 ± 0.07	0.57 ± 0.06	0.45 ± 0.07	-0.29 ± 0.08
SF	0.22 ± 0.08	0.51 ± 0.06	0.61 ± 0.04	0.53 ± 0.06	0.52 ± 0.06	0.68 ± 0.04
BP	0.12 ± 0.08	0.13 ± 0.08	0.21 ± 0.06	0.71 ± 0.04	0.78 ± 0.04	0.26 ± 0.06
	Maternal genetic correlation					
WY	0.03 ± 0.28	0.02 ± 0.27	0.38 ± 0.41	0.34 ± 0.24	0.35 ± 0.24	-0.23 ± 0.33
SF	0.02 ± 0.24	0.03 ± 0.22	0.54 ± 0.26	0.50 ± 0.16	0.69 ± 0.15	0.59 ± 0.21
BP	0.26 ± 0.22	0.08 ± 0.21	0.23 ± 0.29	0.31 ± 0.16	0.28 ± 0.16	0.11 ± 0.28
	Environmental correlations					
WQ	-0.06 ± 0.03	-0.23 ± 0.02	-0.23 ± 0.04	0.00 ± 0.03	0.06 ± 0.03	-0.19 ± 0.03
EF	-0.03 ± 0.03	-0.04 ± 0.02	-0.08 ± 0.03	-0.03 ± 0.03	-0.01 ± 0.03	-0.09 ± 0.03
WY	0.03 ± 0.02	-0.04 ± 0.02	-0.02 ± 0.03	0.07 ± 0.03	0.05 ± 0.03	-0.03 ± 0.03
SF	0.03 ± 0.03	0.12 ± 0.03	0.22 ± 0.03	0.26 ± 0.03	0.28 ± 0.03	0.13 ± 0.03
BP	0.02 ± 0.03	0.12 ± 0.03	0.18 ± 0.04	0.27 ± 0.03	0.26 ± 0.03	0.12 ± 0.03
	Phenotypic correlations					
WQ	-0.07 ± 0.02	-0.11 ± 0.03	-0.33 ± 0.02	0.08 ± 0.02	0.17 ± 0.02	-0.32 ± 0.02
EF	-0.11 ± 0.02	-0.23 ± 0.01	-0.29 ± 0.01	-0.07 ± 0.02	-0.10 ± 0.02	-0.30 ± 0.02
WY	-0.01 ± 0.02	-0.10 ± 0.01	-0.12 ± 0.02	0.24 ± 0.01	0.19 ± 0.02	-0.11 ± 0.02
SF	0.09 ± 0.02	0.25 ± 0.01	0.39 ± 0.01	0.37 ± 0.01	0.38 ± 0.01	0.38 ± 0.01
BP	0.07 ± 0.02	0.12 ± 0.02	0.18 ± 0.02	0.45 ± 0.01	0.47 ± 0.01	0.18 ± 0.02

WQ- Wool quality; EF - Evenness of the fleece; WY - Wool yolk; SF - Staple formation; BP - Belly and points; BirthC – birth coat score; FD6 fibre diameter at 6 months of age; FD12 – fibre diameter at 12 months of age; GFW - greasy fleece weight; CFW – clean fleece weight; FD – fibre diameter

Crimp are negatively correlated with WQ, WY, SF and BP and positively correlated with EF (Table 6.12). This implies that more crimps/25 mm (i.e. finer wool) was associated with lower scores for WQ, WY, SF and BP, while it would result in higher scores for EF. Wool quality and BP were positively correlated (favourable) with SL and CY, while CY was also positively correlated with SF. These estimates were in accordance to the values reported by Matebesi et al. (2009b) for South African Merino sheep. In contrast to this were the r_g among EF, SL and CY moderate negative and thus unfavourable.

The r_g estimates of SS with SF and BP were lowly positive, while WY was lowly negatively related to SS (Table 6.13). These estimates from the current study were higher than the values obtained by Matebesi et al. (2009c). The r_g estimate obtained between Wrinkle and WQ were moderate but favourable. In contrast to this was Wrinkle (Table 6.13) unfavourable correlated to WY, SF and BP. Comfort factor was favourable correlated to WQ and EF, while the r_g among SF and BP are unfavourable.

Table 6.12 The genetic (r_g), maternal (r_m), environmental (r_e) and phenotypic (r_p) correlations among the subjectively assessed conformation and SL, CY, Crimp and Duer (± s.e.)

Trait	SL	CY	Crimp	Duer
	Additive genetic correlations			
WQ	0.30 ± 0.06	0.35 ± 0.05	-0.34 ± 0.06	-0.57 ± 0.04
EF	-0.43 ± 0.06	-0.18 ± 0.06	0.51 ± 0.06	-0.02 ± 0.07
WY	-0.11 ± 0.08	-0.28 ± 0.07	-0.23 ± 0.09	-0.45 ± 0.07
SF	0.04 ± 0.07	0.26 ± 0.06	-0.27 ± 0.07	0.27 ± 0.06
BP	0.45 ± 0.06	0.43 ± 0.05	-0.39 ± 0.06	-0.18 ± 0.06
	Maternal genetic correlations			
WY			-0.45 ± 0.32	
SF			-0.57 ± 0.25	
BP			-0.57 ± 0.22	
	Environmental correlations			
WQ	0.07 ± 0.03	0.16 ± 0.03	-0.04 ± 0.03	-0.14 ± 0.03
EF	0.03 ± 0.03	0.07 ± 0.03	-0.03 ± 0.03	-0.10 ± 0.03
WY	-0.06 ± 0.02	-0.07 ± 0.03	0.00 ± 0.02	0.00 ± 0.03
SF	0.08 ± 0.03	0.08 ± 0.03	0.06 ± 0.03	0.16 ± 0.03
BP	0.06 ± 0.03	0.03 ± 0.03	0.03 ± 0.03	0.13 ± 0.03
	Phenotypic correlations			
WQ	0.17 ± 0.02	0.26 ± 0.02	-0.17 ± 0.02	-0.34 ± 0.01
EF	-0.13 ± 0.02	-0.04 ± 0.02	0.16 ± 0.01	-0.07 ± 0.02
WY	-0.07 ± 0.02	-0.14 ± 0.02	-0.08 ± 0.02	-0.13 ± 0.02
SF	0.07 ± 0.02	0.15 ± 0.02	-0.08 ± 0.02	0.19 ± 0.02
BP	0.21 ± 0.02	0.21 ± 0.02	-0.15 ± 0.02	0.00 ± 0.02

WQ- Wool quality; EF - Evenness of the fleece; WY - Wool yolk; SF - Staple formation; BP - Belly and points; SL – staple length; CY – clean yield; Crimp – number of crimps/25 mm; Duer – Duerden

The genetic (r_g), maternal (r_m), environmental (r_e) and phenotypic (r_p) correlations among the subjectively assessed conformation, objectively measured wool traits and BirthC are summarised in Tables 6.14 to 6.16. The phenotypic and environmental relationship between the subjectively assessed conformation and objectively measured wool traits ranged from zero to 0.36 and most of these correlations were not significant.

Table 6.13 The genetic (r_g), maternal (r_m), environmental (r_e) and phenotypic (r_p) correlations among the subjectively assessed wool traits and SDFD, CVFD, Wrinkle, CF and SS (± s.e.)

Trait	SDFD	CVFD	Wrinkle	CF	SS
	Additive genetic correlations				
WQ	-0.60 ± 0.06	-0.28 ± 0.06	-0.23 ± 0.05	0.54 ± 0.06	0.13 ± 0.10
EF	-0.70 ± 0.06	-0.33 ± 0.07	0.14 ± 0.07	0.63 ± 0.07	0.07 ± 0.11
WY	-0.01 ± 0.11	0.16 ± 0.09	0.43 ± 0.08	0.08 ± 0.09	-0.25 ± 0.11
SF	0.68 ± 0.06	0.31 ± 0.07	0.54 ± 0.06	-0.76 ± 0.05	0.28 ± 0.10
BP	0.39 ± 0.09	0.21 ± 0.07	0.51 ± 0.06	-0.31 ± 0.07	0.23 ± 0.10
	Maternal genetic correlation				
WY	-	-	0.64 ± 0.28	-	-
SF	-	-	0.36 ± 0.23	-	-
BP	-	-	0.19 ± 0.23	-	-
	Environmental correlations				
WQ	-0.22 ± 0.03	-0.18 ± 0.03	-0.08 ± 0.03	0.11 ± 0.04	0.03 ± 0.04
EF	-0.19 ± 0.03	-0.14 ± 0.03	-0.06 ± 0.03	0.07 ± 0.03	0.01 ± 0.03
WY	-0.03 ± 0.03	0.00 ± 0.03	0.07 ± 0.03	-0.01 ± 0.04	-0.04 ± 0.03
SF	0.06 ± 0.03	-0.04 ± 0.03	0.10 ± 0.03	0.05 ± 0.04	0.10 ± 0.03
BP	0.05 ± 0.03	-0.01 ± 0.03	0.12 ± 0.03	0.00 ± 0.04	0.11 ± 0.03
	Phenotpic correlations				
WQ	-0.39 ± 0.02	-0.22 ± 0.02	-0.15 ± 0.02	0.34 ± 0.02	0.06 ± 0.02
EF	-0.37 ± 0.02	-0.21 ± 0.02	0.02 ± 0.02	0.28 ± 0.02	0.03 ± 0.02
WY	-0.02 ± 0.02	0.05 ± 0.02	0.20 ± 0.02	0.02 ± 0.02	-0.09 ± 0.02
SF	0.29 ± 0.02	0.10 ± 0.02	0.29 ± 0.02	-0.30 ± 0.02	0.15 ± 0.02
BP	0.18 ± 0.02	0.08 ± 0.02	0.29 ± 0.02	-0.14 ± 0.02	0.15 ± 0.02

WQ- Wool quality; EF - Evenness of the fleece; WY - Wool yolk; SF - Staple formation; BP - Belly and points; SDFD – standard deviation of fibre diameter; CVFD – coefficient of variation of fibre diameter; Wrinkle – wrinkle score; CF – comfort factor; SS- staple strength

A large number of the r_g estimates (Table 6.14) that were also not significant ranged between -0.10 to 0.10. The r_g estimates of FD with FQ and BC were moderately positive (i.e. unfavourable), while SDFD and CVFD were negatively correlated with FQ and BC (Table 6.16). Overall body conformation was also positively correlated with SL and CY and the r_g of FQ with SL were also positive and favourable (Table 6.15). Estimates obtained by Matebesi et al. (2009c) were comparable to the values of the current study.

Table 6.14 The genetic (r$_g$), maternal (r$_m$), environmental (r$_e$) and phenotypic (r$_p$) correlations among the subjectively assessed conformation traits, BirthC, FD6, FD12, GFW, CFW, FD (± s.e.)

Trait	BirthC	FD6	FD12	GFW	CFW	FD
Additive genetic correlations						
Head	0.04 ± 0.08	0.15 ± 0.08	0.28 ± 0.06	0.06 ± 0.07	0.11 ± 0.07	0.29 ± 0.06
Pigm	-0.03 ± 0.07	-0.04 ± 0.07	-0.09 ± 0.05	-0.05 ± 0.06	-0.01 ± 0.06	-0.10 ± 0.06
Hock	-0.11 ± 0.07	0.12 ± 0.07	0.07 ± 0.05	-0.16 ± 0.06	-0.10 ± 0.06	0.04 ± 0.06
Pas	-0.12 ± 0.1	0.06 ± 0.09	0.09 ± 0.08	0.00 ± 0.09	0.14 ± 0.09	0.08 ± 0.09
FQ	0.01 ± 0.07	0.12 ± 0.06	0.18 ± 0.05	-0.11 ± 0.06	-0.08 ± 0.05	0.16 ± 0.05
BC	0.15 ± 0.08	0.13 ± 0.07	0.21 ± 0.05	-0.05 ± 0.06	0.06 ± 0.06	0.27 ± 0.06
Maternal genetic correlations						
Head	0.41 ± 0.20	0.14 ± 0.17	0.05 ± 0.26	0.82 ± 0.11	1.00 ± 0.09	0.06 ± 0.24
Pas	0.21 ± 0.22	0.18 ± 0.15	0.12 ± 0.23	0.78 ± 0.12	0.84 ± 0.11	0.07 ± 0.23
FQ	0.11 ± 0.19	0.27 ± 0.16	0.24 ± 0.22	0.84 ± 0.12	0.80 ± 0.14	-0.08 ± 0.22
BC	0.15 ± 0.22	0.24 ± 0.18	0.29 ± 0.27	0.81 ± 0.13	0.81 ± 0.13	-0.05 ± 0.27
Environmental correlations						
Head	0.02 ± 0.03	0.10 ± 0.03	0.14 ± 0.04	0.29 ± 0.03	0.30 ± 0.03	0.08 ± 0.03
Pigm	0.01 ± 0.03	0.01 ± 0.03	0.07 ± 0.04	0.06 ± 0.03	0.03 ± 0.03	0.06 ± 0.03
Hock	0.02 ± 0.03	-0.04 ± 0.03	-0.03 ± 0.04	0.06 ± 0.03	0.08 ± 0.03	-0.02 ± 0.04
Pas	0.00 ± 0.02	-0.05 ± 0.02	-0.08 ± 0.03	-0.06 ± 0.03	-0.04 ± 0.03	-0.06 ± 0.03
FQ	-0.04 ± 0.03	0.08 ± 0.03	0.13 ± 0.04	0.22 ± 0.03	0.24 ± 0.03	0.09 ± 0.04
BC	-0.04 ± 0.03	0.11 ± 0.03	0.15 ± 0.04	0.34 ± 0.03	0.36 ± 0.03	0.08 ± 0.04
Phenotypic correlations						
Head	0.05 ± 0.02	0.12 ± 0.02	0.19 ± 0.02	0.23 ± 0.02	0.26 ± 0.02	0.16 ± 0.02
Pigm	0.00 ± 0.02	-0.01 ± 0.02	-0.02 ± 0.02	0.01 ± 0.02	0.01 ± 0.02	-0.02 ± 0.02
Hock	-0.03 ± 0.02	0.03 ± 0.02	0.03 ± 0.02	-0.04 ± 0.02	-0.01 ± 0.02	0.01 ± 0.02
Pas	-0.02 ± 0.02	-0.02 ± 0.01	-0.01 ± 0.02	-0.04 ± 0.02	0.01 ± 0.02	-0.01 ± 0.02
FQ	-0.01 ± 0.02	0.09 ± 0.02	0.15 ± 0.02	0.04 ± 0.02	0.07 ± 0.02	0.13 ± 0.02
BC	0.04 ± 0.02	0.12 ± 0.02	0.18 ± 0.02	0.18 ± 0.02	0.24 ± 0.02	0.17 ± 0.02

Head - Conformation of the head; Pigm – Pigmentation; Hock – Hocks; Pas – Pasterns; FQ - Front quarters; BC - Overall body conformation; BirthC – birth coat score; FD6 fibre diameter at 6 months of age; FD12 – fibre diameter at 12 months of age; GFW - greasy fleece weight; CFW – clean fleece weight; FD – fibre diameter

Table 6.15 The genetic (r_g), maternal (r_m), environmental (r_e) and phenotypic (r_p) correlations among the subjectively assessed conformation traits and SL, CY, Crimp and Duer (± s.e.)

Trait	SL	CY	Crimp	Duer
Additive genetic correlations				
Head	0.34 ± 0.06	0.24 ± 0.06	-0.12 ± 0.08	0.05 ± 0.07
Pigm	-0.10 ± 0.06	0.04 ± 0.05	0.04 ± 0.06	-0.03 ± 0.06
Hock	0.15 ± 0.06	0.10 ± 0.05	-0.19 ± 0.06	-0.12 ± 0.06
Pas	0.10 ± 0.09	0.32 ± 0.08	-0.11 ± 0.09	0.02 ± 0.09
FQ	0.23 ± 0.06	0.02 ± 0.05	-0.11 ± 0.06	0.05 ± 0.05
BC	0.45 ± 0.05	0.26 ± 0.05	-0.20 ± 0.07	0.00 ± 0.06
Maternal genetic correlations				
Head	-	-	-0.73 ± 0.18	-
Pas	-	-	-0.53 ± 0.21	-
FQ	-	-	-0.62 ± 0.21	-
BC	-	-	-0.59 ± 0.21	-
Environmental correlations				
Head	0.09 ± 0.03	0.08 ± 0.03	0.03 ± 0.03	0.09 ± 0.03
Pigm	0.06 ± 0.03	-0.01 ± 0.03	-0.02 ± 0.03	0.01 ± 0.03
Hock	0.03 ± 0.03	0.03 ± 0.03	0.05 ± 0.03	0.04 ± 0.03
Pas	0.00 ± 0.02	-0.03 ± 0.03	0.00 ± 0.02	-0.04 ± 0.02
FQ	0.10 ± 0.03	0.12 ± 0.03	0.06 ± 0.03	0.10 ± 0.03
BC	0.13 ± 0.03	0.11 ± 0.03	-0.08 ± 0.02	0.11 ± 0.03
Phenotypic correlations				
Head	0.18 ± 0.02	0.14 ± 0.02	-0.05 ± 0.02	0.07 ± 0.02
Pigm	0.00 ± 0.02	0.02 ± 0.02	0.01 ± 0.02	-0.01 ± 0.02
Hock	0.08 ± 0.02	0.06 ± 0.02	-0.05 ± 0.02	-0.03 ± 0.02
Pas	0.03 ± 0.01	0.07 ± 0.01	-0.02 ± 0.01	-0.02 ± 0.01
FQ	0.16 ± 0.02	0.07 ± 0.02	-0.02 ± 0.02	0.08 ± 0.02
BC	0.26 ± 0.02	0.18 ± 0.02	0.05 ± 0.03	0.06 ± 0.02

Head - Conformation of the head; Pigm – Pigmentation; Hock – Hocks; Pas – Pasterns; FQ - Front quarters; BC - Overall body conformation; SL – staple length; CY – clean yield; Crimp – number of crimps/25 mm; Duer – Duerden

Favourable r_g estimates between SS and the subjectively assessed conformation traits linked to size were estimated in this study, Wrinkle score was moderately negatively (favourably) correlated (r_g) with Head, FQ and BC. These values are in agreement with the values reported by Matebesi et al. (2009c)

Table 6.16 The genetic (r_g), maternal (r_m), environmental (r_e) and phenotypic (r_p) correlations among the subjectively assessed conformation traits and SDFD, CVFD, Wrinkle, CF and SS (± s.e.)

Trait	SDFD	CVFD	Wrinkle	CF	SS
Additive genetic correlations					
Head	-0.25 ± 0.09	-0.36 ± 0.07	-0.26 ± 0.07	-0.10 ± 0.08	0.31 ± 0.09
Pigm	-0.04 ± 0.09	0.05 ± 0.07	0.06 ± 0.06	-0.14 ± 0.07	0.00 ± 0.11
Hock	-0.10 ± 0.10	-0.09 ± 0.07	-0.40 ± 0.06	-0.14 ± 0.07	0.07 ± 0.11
Pas	-0.34 ± 0.11	-0.28 ± 0.09	-0.25 ± 0.09	0.00 ± 0.10	-0.07 ± 0.14
FQ	-0.33 ± 0.08	-0.36 ± 0.06	-0.32 ± 0.05	-0.07 ± 0.07	0.31 ± 0.10
BC	-0.21 ± 0.09	-0.35 ± 0.06	-0.55 ± 0.06	-0.18 ± 0.07	0.35 ± 0.09
Maternal genetic correlations					
Head	-	-	0.20 ± 0.22	-	-
Pas	-	-	0.18 ± 0.19	-	-
FQ	-	-	0.23 ± 0.21	-	-
BC	-	-	0.22 ± 0.23	-	-
Environmental correlations					
Head	0.03 ± 0.03	-0.04 ± 0.03	0.11 ± 0.03	0.01 ± 0.04	0.09 ± 0.03
Pigm	-0.01 ± 0.03	-0.04 ± 0.03	-0.01 ± 0.03	0.10 ± 0.05	0.00 ± 0.03
Hock	0.00 ± 0.04	-0.01 ± 0.03	0.10 ± 0.03	0.12 ± 0.05	0.00 ± 0.04
Pas	0.05 ± 0.03	0.06 ± 0.03	0.00 ± 0.03	0.01 ± 0.04	0.02 ± 0.03
FQ	0.08 ± 0.04	-0.05 ± 0.04	0.09 ± 0.03	0.02 ± 0.05	0.14 ± 0.04
BC	0.01 ± 0.04	-0.11 ± 0.04	0.18 ± 0.03	0.07 ± 0.05	0.16 ± 0.04
Phenotypic correlations					
Head	-0.07 ± 0.02	-0.17 ± 0.02	-0.03 ± 0.02	-0.04 ± 0.02	0.16 ± 0.02
Pigm	-0.02 ± 0.02	0.00 ± 0.02	0.02 ± 0.02	-0.03 ± 0.02	0.00 ± 0.02
Hock	-0.04 ± 0.02	-0.04 ± 0.02	-0.14 ± 0.02	-0.02 ± 0.02	0.03 ± 0.02
Pas	-0.04 ± 0.02	-0.03 ± 0.02	-0.07 ± 0.02	0.00 ± 0.02	0.01 ± 0.02
FQ	-0.11 ± 0.02	-0.2 ± 0.02	-0.12 ± 0.02	-0.03 ± 0.02	0.19 ± 0.02
BC	-0.08 ± 0.02	-0.21 ± 0.02	-0.16 ± 0.02	-0.07 ± 0.02	0.22 ± 0.02

Head - Conformation of the head; Pigm – Pigmentation; Hock – Hocks; Pas – Pasterns; FQ - Front quarters; BC - Overall body conformation; SDFD – standard deviation of fibre diameter; CVFD – coefficient of variation of fibre diameter; Wrinkle – wrinkle score; CF – comfort factor; SS- staple strength

The genetic (r_g), environmental (r_e) and phenotypic (r_p) correlations among the subjectively assessed wool and reproduction traits are summarised in Table 6.17. It is evident that all of the genetic correlations, except those of BP with NLB3 and NLW3 were non-significant. The negative r_g between BP and number of lambs born and weaned are unfavourable. These estimates are in accordance with estimates reported by Snyman & Olivier (2002) of creeping belly (defined as wool with a belly-like appearance occurring in the fleece, and creeping up against the sides from the belly) with number of lambs born or weaned. The r_e and r_p among subjective wool and reproduction traits were all close to zero and not significant.

Table 6.17 The genetic (r_g), environmental (r_e) and phenotypic (r_p) correlations among the subjectively assessed wool and reproduction traits (± s.e.)

Trait	NLB3	NLW3	TWW3	TOTSPM
	Additive genetic correlations			
WQ	-0.36 ± 0.27	-0.21 ± 0.21	-0.05 ± 0.19	-0.05 ± 0.15
EF	-0.49 ± 0.32	-0.33 ± 0.24	-0.26 ± 0.20	-0.20 ± 0.17
WY	-0.05 ± 0.28	0.05 ± 0.23	0.05 ± 0.23	0.12 ± 0.19
SF	-0.22 ± 0.36	-0.13 ± 0.25	0.09 ± 0.20	-0.04 ± 0.17
BP	-0.37 ± 0.16	-0.38 ± 0.16	-0.02 ± 0.21	-0.27 ± 0.16
	Environmental correlations			
WQ	-0.04 ± 0.04	-0.05 ± 0.04	-0.09 ± 0.04	-0.05 ± 0.04
EF	0.02 ± 0.03	-0.05 ± 0.03	0.02 ± 0.03	-0.02 ± 0.03
WY	0.06 ± 0.03	0.05 ± 0.03	0.00 ± 0.03	0.05 ± 0.03
SF	0.03 ± 0.03	0.05 ± 0.03	0.01 ± 0.04	0.03 ± 0.03
BP	0.02 ± 0.04	0.04 ± 0.04	0.03 ± 0.04	0.00 ± 0.03
	Phenotypic correlations			
WQ	-0.07 ± 0.03	-0.05 ± 0.03	-0.06 ± 0.03	-0.04 ± 0.03
EF	-0.04 ± 0.03	-0.03 ± 0.03	-0.01 ± 0.03	-0.05 ± 0.03
WY	0.03 ± 0.03	0.05 ± 0.03	0.00 ± 0.03	0.05 ± 0.03
SF	0.00 ± 0.03	0.01 ± 0.03	0.05 ± 0.03	0.02 ± 0.03
BP	-0.05 ± 0.03	-0.03 ± 0.03	-0.02 ± 0.03	-0.04 ± 0.03

WQ - Wool quality; EF - Evenness of the fleece; WY - Wool yolk; SF - Staple formation; BP - Belly and points; NLB3 – number of lambs born over three lambing opportunities; NLW3 – number of lambs weaned over three lambing opportunities;TWW3 – total weight of lamb weaned over three lambing opportunities; TOTSPM – total weight of lamb weaned

The genetic (r_g), environmental (r_e) and phenotypic (r_p) correlations among the subjectively assessed conformation and reproduction traits are summarised in Table 6.18. The r_g and r_p among the subjective conformation traits related to size were all favourably (positively) related to TWW3 and TOTSPM. These estimates between reproduction and the subjective conformation traits are lower in magnitude but similar in sign to the values reported for Afrino sheep by Snyman & Olivier (2002). None of the other r_g and r_p estimates, as well as r_e estimates were significant.

Table 6.18 The genetic (r_g), environmental (r_e) and phenotypic (r_p) correlations among the subjectively assessed conformation and reproduction traits ($\pm$ s.e.)

Trait	NLB3	NLW3	TWW3	TOTSPM
	Additive genetic correlations			
Head	-0.08 ± 0.32	0.20 ± 0.25	0.61 ± 0.19	0.34 ± 0.16
Pigm	-0.52 ± 0.35	-0.39 ± 0.23	-0.36 ± 0.19	-0.21 ± 0.15
Hock	-0.03 ± 0.26	-0.09 ± 0.22	0.15 ± 0.19	0.12 ± 0.16
Pas	0.23 ± 0.31	0.39 ± 0.23	0.49 ± 0.20	0.33 ± 0.20
FQ	0.18 ± 0.29	0.31 ± 0.23	0.75 ± 0.19	0.52 ± 0.14
BC	0.31 ± 0.30	0.35 ± 0.23	0.77 ± 0.15	0.43 ± 0.15
	Environmental correlations			
Head	0.05 ± 0.04	0.02 ± 0.03	0.00 ± 0.04	0.00 ± 0.03
Pigm	0.04 ± 0.04	0.00 ± 0.04	0.02 ± 0.04	-0.01 ± 0.04
Hock	0.02 ± 0.04	0.05 ± 0.04	0.06 ± 0.04	0.05 ± 0.04
Pas	-0.02 ± 0.03	-0.06 ± 0.03	-0.03 ± 0.03	-0.08 ± 0.03
FQ	0.00 ± 0.04	0.03 ± 0.04	-0.01 ± 0.04	0.02 ± 0.04
BC	0.09 ± 0.04	0.10 ± 0.04	0.06 ± 0.04	0.07 ± 0.04
	Phenotypic correlations			
Head	0.03 ± 0.03	0.01 ± 0.03	0.08 ± 0.03	0.05 ± 0.03
Pigm	-0.03 ± 0.03	-0.04 ± 0.03	0.00 ± 0.03	-0.04 ± 0.03
Hock	0.02 ± 0.03	0.03 ± 0.03	0.04 ± 0.03	0.06 ± 0.03
Pas	0.00 ± 0.03	-0.03 ± 0.03	0.01 ± 0.03	-0.04 ± 0.03
FQ	0.04 ± 0.03	0.06 ± 0.03	0.13 ± 0.03	0.13 ± 0.03
BC	0.06 ± 0.03	0.07 ± 0.03	0.14 ± 0.03	0.14 ± 0.03

Head - Conformation of the head; Pigm – Pigmentation; Hock – Hocks; Pas – Pasterns; FQ - Front quarters; BC - Overall body conformation; NLB3 – number of lambs born over three lambing opportunities; NLW3 – number of lambs weaned over three lambing opportunities;TWW3 – total weight of lamb weaned over three lambing opportunities; TOTSPM – total weight of lamb weaned

It is imperative that the effects and relationships of subjectively assessed wool and conformation traits with other wool, conformation and reproduction traits are understood, as these subjective traits are extensively used for selection purposes. It was evident from the results of this study that there were both favourable and unfavourable genetic correlations between the subjective traits and the economically important traits that are objectively measured.

The favourable r_g between WQ and EF indicate that selection on either of the traits will lead to an improvement of the other trait. This is an important result because WQ and EF are the most important subjective wool traits and an unfavourable correlation would have been detrimental to the production of good quality wool that are demanded by wool buyers. This finding is in agreement with the high favourable correlation reported by Snyman & Olivier (2002) for Afrino sheep and Matebesi et al. (2009b) for Merino sheep.

The results from these South African studies on subjective wool quality concur with results obtained in Australia on related traits. Mortimer et al. (2009) reported favourable genetic correlations between wool and handle characteristics that implied that the wool quality traits will improve if selection are aimed to lower the scores (assessment scale reversed to the South African scale) in one of the wool quality traits.

These results concur with estimates reported by Morley (1955b), Mullaney et al. (1970), James et al. (1990), Lewer et al. (1995), Swan et al. (1997) and Brown et al. (2002b).

The unfavourable relationship SF with WQ and EF, which is in agreement with Matebesi et al. (2009b), implies that the fleece with the better WQ and high EF will tend to have thinner and ropier staples. It is therefore important that this unfavourable relationship is taken into consideration to ensure that SF is not adversely affected by selection for WQ or EF. The unfavourable correlation between EF and BP implies that the more even fleeces will have a poorer belly and points. Snyman & Olivier (2002) reported similar findings between creeping belly and evenness of the fleece, as well as with crimp definition.

The unfavourable correlation between subjective conformation traits linked to size (Head, FQ and BC) with EF, WY and BP implies that larger animals will tend to have more variation over the fleece, an excessive amount and flow of yolk and also poorer belly and points. It is therefore important that, when selection for improved conformation is practised, these subjective wool traits are monitored or included in the selection criteria. These correlations are in contrast to corresponding values, which were close to zero, reported by Matebesi et al. (2009b) for Merino sheep and Snyman & Olivier (2002) for Afrino sheep.

The relationships between FQ and BC, which are the most important subjective conformation traits, as well as with Head were highly favourable. This implies that improvement in one of these traits will lead to an improvement of the other traits as well. These findings are in agreement with the studies done by Snyman & Olivier (2002) and Matebesi et al. (2009b). The correlations of Hock with FQ and BC must be taken into consideration, because it implies that larger animals will tend to have wider hocks and smaller animals will have narrower hocks. Selection for BC (i.e. an increased size) can therefore lead to problems with Hock and great care must be taken to ensure that wider or narrower hocks do not become a problem in flocks as a result of this trait not being monitored.

It is important to note that selection for body weight will not have any effect on the WQ, EF or SF. However, body weights at different ages are unfavourable correlated with WY and BP. With regard to WY these correlations indicate that there are a tendency for larger animals to have drier wool with little yolk flow, whereas smaller animals will tend to have an excessive amount and flow of yolk.

An important concern is the unfavourable r_g estimates of BP with FQ, BC and body weight at different ages because of the impact that animals with lower BP scores are likely to have on the monetary value of the wool clip. This implies that the larger animals are more likely to have poorer BP. The poorer BP is in most cases linked to an increase in the incidence of creeping belly, which is one of the criteria of BP in Merino sheep and animals are subsequently culled on this trait (BP score of 5 and below). This problem is further accentuated by the positive (unfavourable) genetic correlations of BP, FQ and BC with FD. BP scores are also negatively correlated with number of lambs born and weaned on the genetic level. These findings are supported by results of Snyman & Olivier (2002) that suggested that a strong discrimination against creeping belly will lead to an increase in fibre diameter and a reduced reproduction rate.

The favourable correlations between WQ and FD, fleece weight and SL suggest that animals that have fleeces with the better WQ will tend to produce more and finer wool with longer staples. The FD related trait CVFD is also favourable correlated with WQ indicating that better wool quality scores will result in more uniform staples. The results from the current study with regard to FD and CVFD are supported by the favourable correlations estimated between wool quality and FD and CVFD for Afrino (Snyman & Olivier, 2002) and Merino sheep (Matebesi et al., 2009c).

Furthermore, Mortimer et al. (2009) also estimated favourable correlations between wool quality traits and FD and CVFD, indicating that FD and CVFD will be reduced if animals with softer wool and better crimp definition are selected. The results obtained by Mortimer et al. (2009) concurs with estimates between wool quality traits and FD reported by Morley (1955b), Mullaney et al. (1970), Gregory (1982), James et al. (1990), Raadsma & Wilkinson (1990), Lewer et al. (1995), Swan et al. (1997) and Taylor et al. (1999).

Wrinkle was favourable correlated with WQ, meaning an increase in WQ will lead to a reduction in Wrinkle. However, the relationships of SF and BP with Wrinkle are unfavourable, which implies that an improvement in one of these two traits will lead to an increase in wrinkle score. The correlation between SF and Wrinkle are in contrast to the estimate reported by Matebesi et al. (2009c) of approximately zero. However, the correlations between BP and Wrinkle, as well as between WY and Wrinkle concur well with the values reported by Matebesi et al. (2009c).

CONCLUSION

It can be concluded from the results of this study that the selection to improve WQ will lead to an indirect decrease of fibre diameter and decrease the variation in the fleece. Furthermore, the improvement of WQ will not be adversely affected when selection for increased body weight or conformation is practised. However, the biggest concern is unfavourable relationships of BP, especially with creeping belly in mind, with indicators of wool price (FD and CVFD) and reproduction traits. The relationship of BP and reproduction needs to be investigated further, as reproduction is the most important trait for small stock farmers in South Africa and the rest of the world. A possible option might be more lenient to especially ewes exhibiting creeping belly and to cull only animals that has a severe creeping belly.

Therefore, the use of subjectively assessed wool and conformation traits as selection or culling criteria should be done with great care. The indiscriminate culling of animals might hamper the progress that is made in the economically important traits as a result of unfavourable correlations. Selection should therefore rather be aimed firstly at improving the economically important traits and secondly, to use the subjective traits as individual culling levels.

CHAPTER 7. GENETIC RELATIONSHIPS AMONG PRODUCTION TRAITS MEASURED AT DIFFERENT AGES IN A GENETIC FINE WOOL MERINO STUD

INTRODUCTION

Selection is the tool used by progressive small stock breeders to improve the profitability of their sheep enterprise by increasing the value of lamb production and by decreasing production cost (Borg et al., 2009). Thus, the aim of any selection program is to improve future generations of the breeding flock. The economically important production traits which are normally included in a selection program for Merino sheep are body weight, fleece weight, fibre diameter and staple length. The combination and importance of the different traits vary between breeders and production systems.

Selection for these economically important traits at selection age has an indirect effect on the trait measured in the adult ewes at different ages because traits measured at selection age are correlated with the traits measured at different ages in the adult ewe flock (Safari et al., 2005; Borg et al., 2009). The breeding ewe flock is the biggest asset of any small stock farmer and it is therefore important that the flock is constantly genetically improved.

However, the selection of replacement animals in the Merino industry is mainly exercised at performance testing age and little or no attention is given to the subsequent performance of adult breeding ewes. This selection procedure is practised despite the large contribution that the wool from the adult ewes make to the total wool clip of a farm and the large effect the maintenance costs of these ewes has on the profitability of the farm.

It is furthermore important to consider that certain phenotypes change with age (Huisman et al., 2002) and that there is evidence that these changes in the performance of an animal are influenced by genetic factors (Mrode & Kennedy, 1993; Atchley et al., 1997; Atchley, 1998). The estimation of genetic parameters that describe these changes over time is important as it will give an indication to the extent that selection can change the performance over time (Huisman et al., 2002).

The potential to increase the economic value of livestock through changing their growth curves through selection is of the utmost importance for animal breeders (Fitzhugh, 1976; Kirkpatrick et al., 1990). Biologists' interest in the growth curves, on the other hand, can be related to the possible impact that these curves have on the morphology, size mediated ecological interactions, and life-history characters of species (Ebenman & Persson, 1988).

The aim of recording repeated measures for a specific trait is to quantify the change in performance with age and subsequently to determine what effect does an increase in age has on the production traits of a flock or breed. These phenotypic changes that occur over time could therefore be expressed as a function of time (Kirkpatrick et al., 1990).

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Multi-trait analyses were for many years the preferred method of analysing traits measured over time, including measures at different ages as different traits. In recent years, there was a shift towards the use of longitudinal models to express the changes over time that use all the available records (Van der Werf, 2005).Since Kirkpatrick et al. (1990) first proposed the use of random regression models (RR) it has become the preferred method of analyses for growth traits (Schaeffer & Jamrozik, 2008) and it has been used extensively in the dairy industry for the analysis of milk traits (Huisman et al., 2002; Meyer, 2004; Nephawe, 2004; Schaeffer, 2004; Misztal, 2006).

The major advantage of using RR models over multivariate models is the possibility to estimate (co)variances between or at every time point. The RR (co)variance estimates are also smoother and less bias than values estimated with multivariate models (Kirkpatrick et al., 1990). The fact that fewer parameters are needed to describe the same data set as a multivariate model (Huisman et al., 2002) has the computational advantage that less memory and time is needed for analysis compared to some multivariate analyses (Nobre et al., 2002).

The correlation between measurements of production traits recorded at different ages is defined as the repeatability of a trait (Lush, 1937; Roman et al., 2000). Repeatability is an indication of the variance within an animal for a specific trait and its main uses are to explain gains to be obtained through repetition of measurements and to predict future performance from past records (Falconer, 1989).

Thus, repeatability can be defined as the average proportion of differences likely to be repeated in later records (Dohm, 2002). This value can therefore only be calculated for traits that are expressed multiple times in an animal's life, such as body weight and fleece traits. Repeatability models can also be used to analyse repeated measures of production by treating each measurement as a repeated record of the same trait of a specific animal. This model has been implemented in the past in various populations for traits such as milk traits and body weights in successive lactations in dairy cattle (Jamrozik et al., 1997; Interbull, 2000; Dohm, 2002).

The performance of the adult ewe flock with regard to the economically important production traits is a major contributor to the income generated from wool production on the farm. The size of adult ewes on the other hand has a big influence on the maintenance cost of a sheep farming enterprise, because larger animals needs more feed. The income generated from wool production are to a large extent influenced by fibre diameter, as it is one of the major factors influencing the wool price (Erasmus & Delport, 1987; Olivier, 2009).

This fact and the subsequent price premium for fibre diameter since the 1990s have led to the emphasis being shifted to selection for decreased fibre diameter in the wool industry of South Africa. In some flocks, it is the only selection objective regardless of the impact on the other traits.

It is therefore important to quantify the effect that selection for economically important production traits will have on the expression of traits later in life and the subsequent effect on profitability. Subsequently, the

aim of this study was to quantify the genetic relationship among body weight, fleece weight, fibre diameter, staple length and staple strength measured at different ages in a fine wool Merino stud in South Africa with repeatability and random regression models.

MATERIALS AND METHODS

Data description

The Cradock Fine Wool Merino Stud was established in 1988 as described by Olivier et al. (2006). Ewes (fine wool line) were bought from Merino farmers with the finest clips throughout South Africa and four fine wool rams were imported from Australia. A second group of ewes (strong x fine wool line), originating from the strong wool Merino flock at Cradock, was run together with the fine wool line and were also mated to the same sires (Olivier, 2009). Data collected on 1954 adult ewes from the Cradock Fine wool Merino stud from 1988 to 2010, were used for this analysis. A detailed description of the history, management and selection of this stud are presented in Chapter 2.

Statistical analyses

The means and standard deviationsfor the traits were obtained as described in Chapter 3. The traits included body weight (4 to 94 months of age), fibre diameter (6 to 94 months of age) and fleece weight, staple length and staple strength (15 to 94 months of age). Staple strength was only recorded from 2000 onwards. Only data from ewes which have records at 22 months of age (first adult measurement) were included in the analysis. Several fixed effects (year of birth, line (fine or strong x fine), rearing status, age of the dam in years and age at measurement in months as a linear regression) were tested and only effects which had a significant effect (P<0.01) were included in the final operational model.

The estimation of the genetic parameters with the repeatability models was done with ASREML (Gilmour et al., 2009). 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. In terms of random regression analysis a simple repeatability model fits the intercept for random factors included therein. The matrix representation of the repeatability model used is:

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

where X, Z and W are incidence matrices relating the repeated observations in $\mathbf{y}$ to fixed (vector $\mathbf{b}$), additive animal genetic (vector $\mathbf{a}$), additive maternal genetic (vector $\mathbf{m}$), the animal permanent environmental (vector $\mathbf{pe}$) and the maternal permanent environmental (vector $\mathbf{mpe}$) effects, with $\mathbf{e}$ defining a vector of random residual errors.

The log-likelihood ratio test (LogL) was used to determine the most suitable model. LogL is an asymptotic test statistic that is used to determine whether the inclusion of a random parameter have a significant

effect in the analysis of a trait (Morrell, 1998). The statistic –2 x log (likelihood ratio) has a χ^2 distribution with degrees of freedom that is linked to the difference in the number of parameters of the two models that is evaluated. A significance level of P<0.05 was used to determine whether the inclusion of an effect resulted in a significant increase in the log-likelihood.

The estimation of the genetic parameters with the random regression models was done with ASREML (Gilmour et al., 2009). The population curves for the traits were modelled by treating the random deviations from the linear regression of the respective traits on age as splines (Marx & Eiler, 1998) with between 8 to 10 knot points depending on the trait. Direct and maternal genetic effects, as well as animal and maternal permanent environmental effects were included and modelled with Legendre polynomials of different orders (k) (Boligon et al., 2010, 2012). Residual variances were modelled considering two age classes (4 to 15 months and 22 to 94 months) for body weight. The matrix representation of the model was:

$$\mathbf{y} = X\boldsymbol{\beta} + Z_1\mathbf{a} + Z_2\mathbf{m} + W_3\mathbf{pe} + W_4\mathbf{mpe} + \mathbf{e}$$

where $\mathbf{y}$ is the vector of observations, X is an incidence matrix relating records to the fixed effects and random spline components ($\boldsymbol{\beta}$); Z_1, Z_2, W_3 and W_4 were incidence matrices relating records to the additive genetic effects, additive maternal effects, animal permanent environmental effects and the maternal permanent environmental effects and $\mathbf{a}$, $\mathbf{m}$, $\mathbf{pe}$, $\mathbf{mpe}$ and $\mathbf{e}$ were vectors of additive genetic, maternal genetic, animal permanent environmental, maternal permanent environmental and residual effects, respectively.

Different methods were used to determine the most suitable model for analysis. The different models were compared with the LogL test; however, according to Meyer (2004) this test only allows for the comparison of nested models and favours the model with the most parameters. Results from the analyses were therefore also compared with Akaike's Information Criterion (AIC) and Schwartz Bayesian Information Criterion (BIC) (Huisman et al., 2002). AIC is -2 x Log L + 2 x k, where L is the likelihood and k is the number of parameters. The most suitable model is the model with the lowest AIC value. BIC is -2 x log L + k x log n where L is the likelihood, k is the number of parameters and n is the number of observations. The model with the lowest BIC value is the most suitable model. The different models were evaluated by adding an additional random effect or fitting of single higher order effect, such as adding a quadratic effect to a linear effect.

Genetic parameters were calculated from the results of the random regression analysis for the different traits. The (co)variance components were calculated at 4, 6, 15, 22, 34, 46, 58, 70, 82 and 94 months of age depending on the respective traits.

RESULTS AND DISCUSSION

Data description

The number of records, mean, coefficients of variation, minima and maxima of the different body weight (BW), greasy fleece weight (GFW), clean fleece weight (CFW), fibre diameter (FD), staple length (SL) and staple strength (SS) measures are presented in Tables 7.1 to 7.6. It is evident from Table 7.1 that the body weight of the ewes increased to 67.7 kg in the 34th month, after which it remained constant at approximately 70 kg. The coefficient of variation also decreased with age from 16.4% at BW4 to approximately 12% at 15 months of age.

Table 7.1 The number of records (n), mean, coefficient of variation (CV), minimum and maximum of the different body weight measures

Traits	Number of records	Mean (kg)	CV(%)	Minimum (kg)	Maximum (kg)
BW4[1]	1954	27.3	16.4	13.8	41.0
BW6	1954	35.5	16.0	19.8	59.5
BW15	1954	55.6	12.3	33.7	86.1
BW22	1954	63.1	11.3	43.9	96.2
BW34	1541	67.7	11.6	45.6	94.6
BW46	1220	71.8	11.8	49.2	100.4
BW58	872	72.5	12.0	38.1	99.4
BW70	613	72.4	12.1	38.1	98.2
BW82	404	72.2	12.0	48.5	93.2
BW94	147	68.5	12.2	41.9	94.2

[1] BW4 = Body weight at 4 months of age, etc.

It is evident from Tables 7.2 and 7.3 that there was a slight decrease in the amount of wool produced with age from 22 months to 94 months of age. The same tendency was observed in the coefficient of variation of the fleece weights and body weight. It is well-known that wool production changes with age (Corbett, 1979) and that wool production increases to about 3 years of age (Brown et al., 1966; Brown et al., 1968; Swan & Purvis; 2000). This is supported by the wool production and staple length measured on the animals used in this study.

Table 7.2 The number of records (n), mean, coefficient of variation (CV), minimum and maximum of the different greasy fleece weight measures

Traits	Number of records	Mean (kg)	CV(%)	Minimum (kg)	Maximum (kg)
GFW15[1]	1954	5.4	25.7	2.0	16.0
GFW22	1954	6.5	23.5	2.6	13.4
GFW34	1541	5.9	22.6	2.9	12.3
GFW46	1220	5.9	21.6	2.4	10.2
GFW58	872	5.8	19.9	2.3	13.0
GFW70	613	5.7	19.0	2.6	10.2
GFW82	404	5.5	17.2	3.4	9.4
GFW94	147	5.2	16.0	3.7	8.5

[1] GFW15 = Greasy fleece weight at 15 months of age, etc.

Table 7.3 The number of records (n), mean, coefficient of variation (CV), minimum and maximum of the different clean fleece weight measures

Traits	Number of records	Mean (kg)	CV (%)	Minimum (kg)	Maximum (kg)
CFW15[1]	1954	4.5	25.0	2.0	11.6
CFW22	1954	4.8	25.2	1.8	10.7
CFW34	1541	4.4	20.2	2.1	9.9
CFW46	1220	4.4	21.9	1.7	7.9
CFW58	872	4.3	21.4	1.8	10.4
CFW70	613	4.2	20.7	1.9	7.9
CFW82	404	3.9	21.2	2.1	7.7
CFW94	147	3.7	19.5	2.4	5.7

[1] CFW15 = Clean fleece weight at 15 months of age, etc.

Table 7.4 The number of records (n), mean, coefficient of variation (CV), minimum and maximum of the different fibre diameter measures

Traits	Number of records	Mean (µm)	CV(%)	Minimum (µm)	Maximum (µm)
FD6[1]	1954	17.3	7.7	14.2	22.3
FD15	1954	18.5	7.9	14.5	24.0
FD22	1954	18.9	8.4	14.6	25.1
FD34	1541	19.2	8.1	15.0	28.9
FD46	1220	19.6	8.0	14.6	28.7
FD58	872	19.6	7.9	15.3	27.7
FD70	613	19.8	8.0	15.6	25.7
FD82	404	19.6	7.4	15.4	24.5
FD94	147	19.1	6.9	15.5	22.6

[1] FD6 = Fibre diameter at 6 months of age, etc.

It is evident from Table 7.4 that the mean fibre diameter ranges from 17.3 µm (FD6) to 19.8 µm (FD70). The high maximum fibre diameter measurements were recorded on the early progeny of the fine x strong line. The same tendency was observed in staple length (Table 7.5) as in fleece weight, with the mean staple length as well as the coefficient of variation decreasing with age. The staple strength of the ewes decreased with age from 50 N/Ktex (SS22) to 37.7 N/Ktex (Table 7.6) and was the trait with the highest coefficient of variation and also increased with age.

Table 7.5 The number of records (n), mean, coefficient of variation (CV), minimum and maximum of the different staple length measures

Traits	Number of records	Mean (mm)	CV(%)	Minimum (mm)	Maximum (mm)
SL15[1]	1954	107.3	15.7	61.0	167.3
SL22	1954	102.6	16.0	43.2	155.0
SL34	1541	95.1	15.0	43.2	144.1
SL46	1220	96.6	13.0	59.2	144.1
SL58	872	94.7	13.2	59.5	134.5
SL70	613	91.6	12.4	55.4	134.5
SL82	404	86.3	12.7	50.0	112.2
SL94	147	82.6	13.5	55.0	103.3

[1] SL15 = Staple length at 15 months of age, etc.

Table 7.6 The number of records (n), mean, coefficient of variation (CV), minimum and maximum of the different staple strength measures

Traits	Number of records	Mean (N/Ktex)	CV(%)	Minimum (N/Ktex)	Maximum (N/Ktex)
SS15[1]	867	43.7	24.4	9.0	77.0
SS22	867	50.0	25.9	11.0	80.0
SS34	687	46.9	25.6	6.0	82.0
SS46	565	48.7	25.8	8.0	79.0
SS58	460	45.8	32.0	5.0	80.0
SS70	337	45.4	34.4	5.0	86.0
SS82	248	44.1	32.4	3.0	78.0
SS94	117	37.7	40.9	6.0	72.0

[1] SS15 = Staple strength at 15 months of age, etc.

Repeatability model

The Log Likelihood values for the respective traits are presented as a deviation from the most suitable model in Table 7.7 for the repeatability analyses. The inclusion of either the maternal additive effect (σ^2_m), effect (σ^2_{pe}) or the maternal permanent environmental effect (σ^2_{mpe}) had a significant effect on the models of BW, GFW, CFW and FD. However, there was no significant difference between the models that included only one of these effects or the model that included both. It was therefore decided that the most suitable model for BW, GFW, CFW and FD include direct additive effect (σ^2_a), the animal permanent environmental (σ^2_{pe}), σ^2_m, and σ^2_{mpe}, while for SL and SS the most suitable model only included σ^2_a and σ^2_{pe}.

Table 7.7 Log Likelihood deviations from the most suitable model for the respective traits

Random effect	BW	GFW	CFW	FD	SL	SS
σ^2_a	40.26	24.48	29.44	31.72	0.40	0.20
$\sigma^2_a + \sigma^2_{mpe}$	25.18	7.04	6.6	17.78	0.14	0.14
$\sigma^2_a + \sigma^2_m$	36.06	9.20	9.00	19.74	-0.04	0.20
$\sigma^2_a + \sigma^2_m + \sigma_{am}$	19.48	5.38	5.94	15.64	-0.38	4.56
$\sigma^2_a + \sigma^2_m + \sigma^2_{mpe}$	25.18	3.92	3.30	14.68	-0.06	0.14
$\sigma^2_a + \sigma^2_m + \sigma^2_{mpe} + \sigma_{am}$	16.02	3.24	2.80	16.16	-0.38	2.90
$\sigma^2_a + \sigma^2_{pe}$	2.68	15.28	19.94	4.94	**0.00**	**0.00**
$\sigma^2_a + \sigma^2_{pe} + \sigma^2_{mpe}$	1.22	5.50	5.36	5.52	-0.08	0.00
$\sigma^2_a + \sigma^2_{pe} + \sigma^2_m$	0.12	0.56	1.10	0.04	-0.34	0.00
$\sigma^2_a + \sigma^2_m + \sigma^2_{pe} + \sigma_{am}$	-0.32	0.24	0.82	-0.04	-0.44	2.22
$\sigma^2_a + \sigma^2_{pe} + \sigma^2_m + \sigma^2_{mpe}$	**0.00**	**0.00**	**0.00**	**0.00**	-0.34	0.00
$\sigma^2_a + \sigma^2_{pe} + \sigma^2_m + \sigma^2_{mpe} + \sigma_{am}$	-0.40	-0.46	-0.36	-0.08	-0.44	12.36

σ^2_a - direct additive effect; σ^2_m - maternal additive effect; σ^2_{pe} - animal permanent environmental effect; σ^2_{mpe} - maternal permanent environmental effect; σ_{am} - covariation between the direct and maternal additive effects

The variance ratios for the respective traits are summarised in Table 7.8. The repeatability of body weight from weaning to 94 months of age was 0.26, which is in the same order as values obtained ranging from 0.19 to 0.26 in a study on three newly developed Canadian breeds (Hansen & Sherstha, 2002). The repeatability estimated for body weight in this study, is much lower than the range of 0.46 to 0.75 reported in the literature (Morley, 1951; 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). It is, however, important to note that most of these estimates were from records that ranged from pre-weaning to post weaning weights or between one lamb weight and one adult weight. The body weights in this study ranged from weaning to 94 months of age and included three lamb weights and seven adult weights. There was no reference found with the same data structure as in the current study for sheep.

Table 7.8 Repeatability (t), direct heritability (h^2_a), maternal heritability (h^2_m), animal permanent environmental effect (c^2_{pe}) and the maternal permanent environmental effect (c^2_{mpe}) for the six traits (± s.e.)

Trait	h^2_a	h^2_m	c^2_{pe}	c^2_{mpe}	t
BW	0.17 ± 0.03	0.02 ± 0.02	0.10 ± 0.02	0.01 ± 0.01	0.26 ± 0.02
GFW	0.26 ± 0.04	0.06 ± 0.03	0.05 ± 0.03	0.02 ± 0.02	0.31 ± 0.02
CFW	0.26 ± 0.04	0.06 ± 0.03	0.04 ± 0.02	0.02 ± 0.02	0.30 ± 0.02
FD	0.36 ± 0.04	0.04 ± 0.02	0.10 ± 0.03	0.01 ± 0.02	0.46 ± 0.02
SL	0.16 ± 0.01	-	0.01 ± 0.02	-	0.17 ± 0.01
SS	0.10 ± 0.02	-	0.01 ± 0.02	-	0.11 ± 0.02

"-" – not fitted; BW – body weight; GFW – greasy fleece weight; CFW – clean fleece weight; FD – fibre diameter; SL – staple length' SS – staple strength

The low repeatability for body weight indicates that the environment has a substantial effect on the expression of the adult body weight in this flock with a high reproductive rate (Chapter 4). This is also supported by the stabilised growth curve of the ewes mated in this stud from 34 months of age.

The repeatabilities estimated for greasy and clean fleece weight from 15 to 94 months of age were 0.31 and 0.30 respectively in this study. This is considerably lower than the range reported in the literature for both traits of 0.50 to 0.80 (Morley 1951; Young et al., 1960; Beattie, 1961; Turner & Young 1969; Lewer et al., 1983; Mortimer 1987; Saboulard et al., 1995; Hatcher & Atkins, 2000; Lee et al., 2000; Swan & Purvis, 2000; Hatcher et al., 2005).

The repeatability estimated for fibre diameter from 6 to 94 months of age was 0.46 and it is slightly lower than the values reported in the literature (0.50 to 0.76) (Turner & Young, 1969; Young et al., 1960; Mullaney et al., 1970; Lewer et al., 1983; Hatcher & Atkins, 2000; Ponzoni & Fenton, 2000; Swan & Purvis, 2000; Hatcher et al., 2005).

For staple length and strength from 15 to 94 months of age the respective repeatabilities estimated were 0.17 and 0.11. Both values are much lower than the values reported in the literature. Hatcher & Atkins (2000) and Hatcher et al. (2005) reported repeatabilities of 0.68 and 0.61 for staple length and 0.39 and 0.35 for staple strength respectively.

Random Regression (RR)

The log-likelihood values (LogL) as a deviation from the most suitable model, the Akaike's Information Criterion (AIC) and the Bayesian Information Criterion (BIC) for the different models evaluated for each trait are summarised in Table 7.9. None of the models that included the random maternal additive effect (σ^2_m), covariation between the direct and maternal additive effects (σ_{am}), animal permanent environmental effect (σ^2_{pe}) or the maternal permanent environmental effect (σ^2_{mpe}) converged. The Log L, AIC or BIC values for the models that included these effects are therefore not presented in Table 7.9. Therefore, only the random additive effect (σ^2_a) was included in the different random regression models. The Legendre polynomial was tested as a linear or quadratic function. The quadratic polynomial was the best fit for all six traits as indicated by the Log L, AIC and BIC values.

The heritability estimates (h^2_a) obtained with RR for body weight from 4 to 94 months of age are illustrated in Figure 7.1, while the genetic correlations among the different body weights are summarised in Table 7.10. The h^2_a increased with age ranging from 0.14 (4 months of age) to 0.84 (94 months of age).

Table 7.9 The log-likelihood values (LogL) as a deviation from the most suitable model, the Akaike's Information Criterion (AIC) and the Bayesian Information Criterion (BIC) for the different models evaluated for each trait

Trait	Polynomial level	Log L	AIC	BIC
Body weight	1	752.42	11474.76	11490.07
	2	0.00	10725.34	10749.83
Greasy fleece weight	1	108.04	7187.02	7201.42
	2	0.00	7081.98	7105.03
Clean fleece weight	1	123.16	4567.10	4581.50
	2	0.00	4446.94	4469.99
Fibre diameter	1	271.20	8143.56	8158.54
	2	0.00	7875.36	7899.33
Staple length	1	184.86	8301.78	8316.28
	2	0.00	8119.92	8143.12
Staple strength	1	17.08	4378.84	4391.90
	2	0.00	4364.76	4385.66

1 = Intercept + linear slope fitted; 2 = 1 + quadratic slope fitted

The same pattern was observed by Lewis & Brotherstone (2002), Fischer et al. (2004), Molina et al. (2007) and Wolc et al. (2011) with h^2_a increasing with age (15 to 180 days of age) with random regression models. Kariuki et al. (2010) also published similar findings for body weights ranging from 20 to 380 days of age. Genetic parameters obtained with random regression models for body weight in sheep are limited in the literature compared to the number of estimates obtained with single- or multi trait analysis (Safari & Fogarty, 2003).

The increase in h^2_a for body weight with age obtained with random regression models is in accordance with estimates obtained with single- or multi-trait analysis (Safari & Fogarty, 2003; Chapter 3). Snyman et

al. (1995) obtained similar trends in body weight at different ages in Afrino sheep with restricted maximum likelihood (REML) procedures. The h^2_a estimates obtained with random regression analysis in this study, as well as in the literature are comparable with the estimates obtained with REML for body weights at different ages (Fischer et al., 2004; Kebsi et al., 2008; Kariuki et al., 2010).
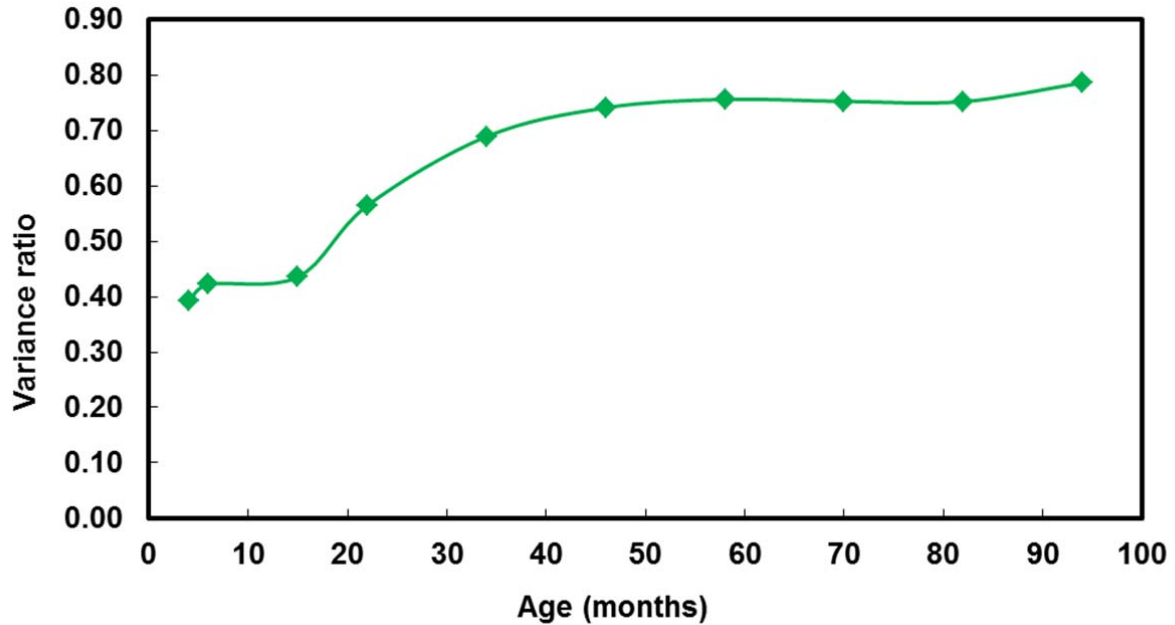
Figure 7.1 Direct heritability estimates for body weight of Merino ewes at different ages

The results from this study, supported by literature indicate a steep increase in h^2_a of body weight with age until about 30 months of age, after which it stabilises. 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 means that the direct additive genetic variance becomes a larger portion of the phenotypic variance resulting in a higher h^2_a.

Table 7.10 Estimated genetic correlations among the body weight measures in Merino sheep from 4 to 94 months of age

Trait	BW6	BW15	BW22	BW34	BW46	BW58	BW70	BW82	BW94
BW4[1]	0.977	0.724	0.598	0.487	0.428	0.387	0.340	0.265	0.150
BW6		0.855	0.755	0.660	0.605	0.558	0.493	0.375	0.191
BW15			0.986	0.951	0.918	0.871	0.778	0.588	0.279
BW22				0.989	0.968	0.927	0.837	0.641	0.315
BW34					0.993	0.966	0.888	0.704	0.382
BW46						0.989	0.933	0.774	0.472
BW58							0.976	0.858	0.595
BW70								0.950	0.756
BW82									0.923

[1] BW = Body weight at 4 months of age, etc.

From Table 7.10 it can be seen that r_g decreased between the different measurements with an increase in age and that adjacent measurements had the highest correlations. These results are supported by comparable findings published in the literature (Lewer et al., 1994; Vaez Torshizi et al., 1996; Wuliji et al., 2001; Fischer et al., 2004; Huisman & Brown, 2008; Wolc et al., 2011).

Wolc et al. (2011) reported a comparable range (-0.05 to 0.999) of correlations among several body weights between birth and 150 days of age, which also decreased with an increase in age. Fischer et al. (2004) and Huisman & Brown (2008) reported similar ranges of correlations (0.31 to 0.94) among different ages between early and adult body weights. In all these studies, as well as the current study it is clear that the correlations tend to decrease with an increase in age. The correlations estimated by Lewer et al. (1994), Vaez Torshizi et al. (1996) and Wuliji et al. (2001) between early growth traits are much lower than the values estimated in this study, as well as other studies using random regression models.

The correlations between early and adult body weight is low to moderate which implies that traits at different ages are not under exactly the same genetic control (Fischer et al., 2004). This means that an animal can be above average for body weight at selection age and can then be below average at adult weight or vice versa. Despite the above mentioned, the positive correlations between 15 month of age and adult body weights (22 to 94 months of age), as well as results from the literature, indicate that selection for increased 15 month body weight, will lead to an increase in adult body weight.

The heritability estimates for greasy and clean fleece weight from 15 to 94 months of age are illustrated in Figures 7.2 and 7.3, while the genetic correlations among the different fleece weights are summarised in Tables 7.11 and 7.12.
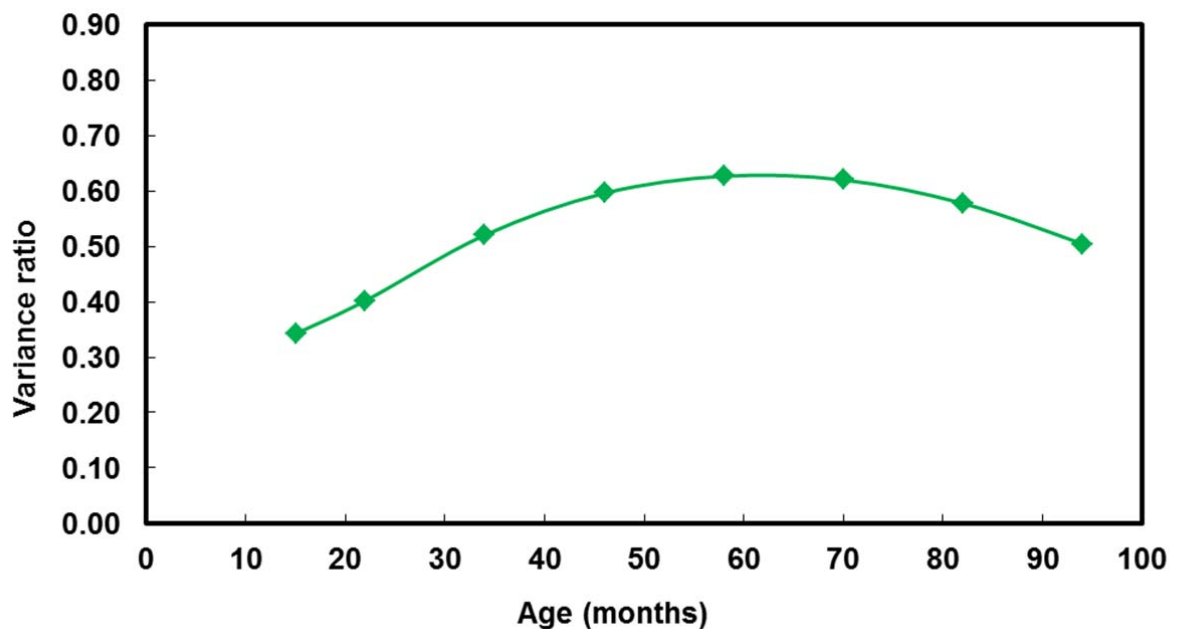
Figure 7.2 Direct heritability estimates for greasy fleece weight of Merino ewes at different ages
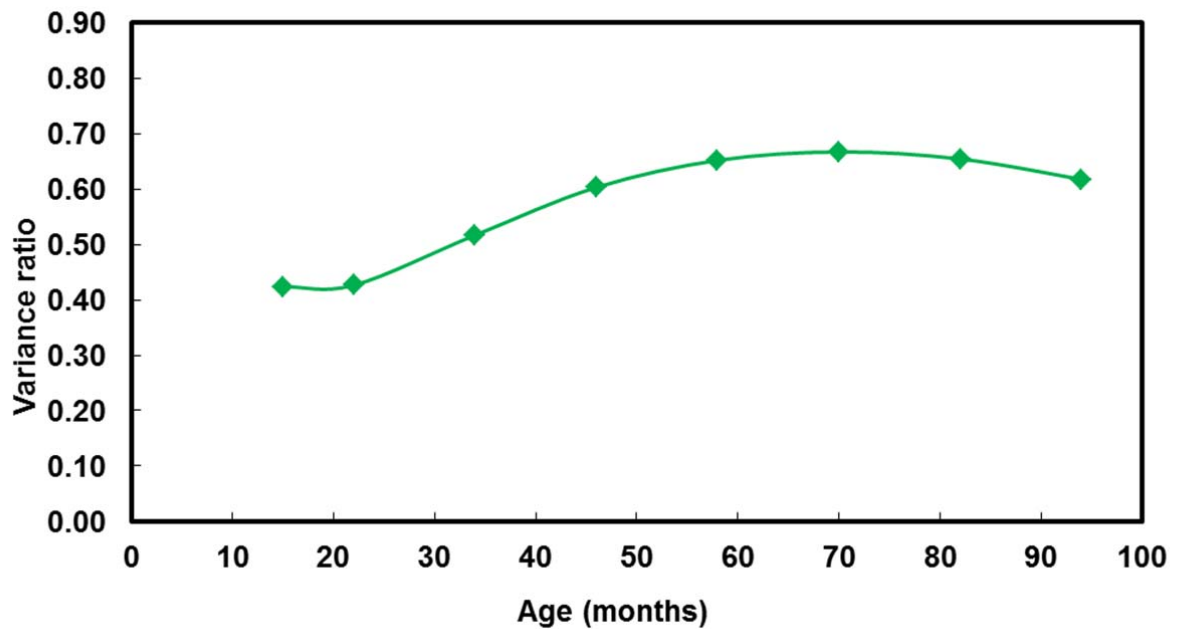
Figure 7.3 Direct heritability estimates for clean fleece weight of Merino ewes at different ages

Greasy and clean fleece weights' h^2_a estimates ranged from 0.14 (15 months of age) to 0.84 (94 months of age) and 0.42 (15 months of age) to 0.67 (70 months of age) respectively. Heritability estimates for adult fleece weight are scarce in the literature as most of the h^2_a are estimated for 10 to 16 months of age.

Huisman et al. (2008) estimated h^2_a for GFW of 0.46 to 0.33 (365 to 540 days of age) and these estimates decreased with age, which is in contrast to the trend observed in this study. The 15 month greasy fleece weight h^2_a of 0.14 is at the lower end of the range for estimates (10 to 18 months of age) reported in the literature that ranged from 0.12 to 0.55 (Lewer et al., 1994; Mortimer & Atkins, 1994; Swan & Hickson, 1994;Vaez Torshizi et al., 1995; Nagy et al., 1999; Cloete et al., 2002; Safari et al., 2007b; Chapter 3).

The 22 months of age h^2_a estimate is similar to the range reported for 10 to 18 months of age, while the other adult estimates (34 to 94 months of age) are similar or higher than the range of 0.45 to 0.57 reported in the literature for adult fleece weight (Bromley et al., 2000; Hill, 2001; Hanford et al., 2002; Van Vleck et al., 2003; Cloete et al., 2004). The h^2_a range reported by Huisman et al. (2008) for clean fleece weight ranged from 0.36 to 0.50 (365 to 540 days of age) and increased with age, as was also observed for CFW in the present study.

Heritability estimates for clean fleece weight from 15 and 22 months of age accords well with literature values from 10 to 18 months of age (0.27 to 0.57) (Lewer et al., 1994; Snyman et al., 1996; Lee et al., 2002a; Safari et al., 2007b; Chapter 3) The estimates obtained for the 34 to 94 month measurements are similar to the range of estimates reported in the literature (0.34 to 0.60) (Saboulard et al., 1995; Woolaston et al., 1995; Coelli et al., 1998; Hill, 2001; Cloete et al., 2003a).

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The increase in h^2_a estimates of both greasy and clean fleece weights suggests that there is an increase in the expression of the genes with direct additive effects. This is also accompanied with a decrease in the variance of the other random effects later in life.

Table 7.11 Estimated genetic correlations among the greasy fleece weight measures in Merino sheep from 15 to 94 months of age

Trait	GFW22	GFW34	GFW46	GFW58	GFW70	GFW82	GFW94
GFW15[1]	0.949	0.812	0.722	0.673	0.651	0.644	0.633
GFW22		0.955	0.903	0.869	0.849	0.829	0.775
GFW34			0.990	0.975	0.960	0.932	0.847
GFW46				0.996	0.987	0.960	0.869
GFW58					0.996	0.975	0.891
GFW70						0.990	0.924
GFW82							0.968

[1] GFW15 = Greasy fleece weight at 15 months of age, etc.

The genetic correlations among GFW (Table 7.11) and CFW (Table 7.12) decreased with an increase in age and the adjacent measurements are highly correlated. This finding is supported by estimates in the literature. The r_g among the clean fleece weight measurements ranged from 0.495 (15 and 94 months of age) to 0.998 (58 and 70 months of age). These correlations were higher than the corresponding correlations for GFW.

Huisman & Brown (2009) reported r_g estimates that ranged from 0.59 to 0.75 for greasy fleece weight at three different ages (365 to 540 days) and 0.56 to 0.66 for clean fleece weight. Lewer et al. (1983), Atkins & Mortimer (1987), Ponzoni et al. (1995), Vaez Torshizi et al. (1995), Brash et al. (1997) and Nagy et al. (1999) reported a correlation range of 0.41 to 0.88 for fleece weights measured at approximately 15 months of age and early adult measurements. These correlations are also lower than the corresponding correlations obtained in this study between the same age groupings.

Table 7.12 Estimated genetic correlations among the clean fleece weight measures in Merino sheep from 15 to 94 months of age

Trait	CFW22	CFW34	CFW46	CFW58	CFW70	CFW82	CFW94
CFW15[1]	0.936	0.715	0.563	0.491	0.475	0.506	0.584
CFW22		0.915	0.817	0.764	0.750	0.767	0.808
CFW34			0.980	0.959	0.949	0.949	0.942
CFW46				0.996	0.991	0.984	0.957
CFW58					0.998	0.991	0.958
CFW70						0.996	0.968
CFW82							0.986

[1] CFW15 = Clean fleece weight at 15 months of age, etc.

The estimates of the heritabilities of fibre diameter at the different ages are illustrated in Figure 7.4 and the genetic correlations among the age-specific fibre diameter measurements are presented in Table 7.13. Heritabilities estimated in the current study for FD ranged from 0.51 at 6 months of age to 0.81 at 94 months of age.

The heritability estimates (point estimates) reported in the literature for adult fibre diameter range from 0.62 to 0.77 (Coelli et al., 1998; Lee et al., 2002a; Cloete et al., 2003a; Huisman et al., 2008). Reported estimates of direct heritability for fibre diameter at a young age ranged from 0.44 to 0.68 (Lewer et al., 1994; Mortimer & Atkins, 1994; Swan & Hickson, 1994; Coelli et al., 1998; Lee et al., 2002a; Safari et al., 2007b; Chapter 3). The FD h^2_a estimates for 22 to 70 months of age were within the reported range, while the h^2_a at 82 and 94 months of age are higher than the reported values.

The increases in FD heritability estimates with age can probably be ascribed to lambs and hoggets that are still growing (body size) rather than wool yield. Later in life, given adequate nutrition, their genetic potential for fibre diameter may be expressed more accurately. It can also be attributed to some extent to the increase in the available genetic information on an individual with age. Therefore, the influence of the genetic makeup on the phenotype of an animal increases with age (Fischer et al., 2004; Kesbi et al., 2008).

Table 7.13 Estimated genetic correlations among the fibre diameter measures in Merino sheep from 6 to 94 months of age

Traits	FD15	FD22	FD34	FD46	FD58	FD70	FD82	FD94
FD6	0.878	0.739	0.582	0.510	0.489	0.501	0.527	0.532
FD15		0.971	0.898	0.853	0.827	0.804	0.750	0.621
FD22			0.977	0.950	0.927	0.891	0.806	0.625
FD34				0.994	0.978	0.939	0.838	0.628
FD46					0.994	0.963	0.870	0.663
FD58						0.986	0.915	0.733
FD70							0.969	0.834
FD82								0.998

[1] FD6 = Fibre diameter at 15 months of age, etc.
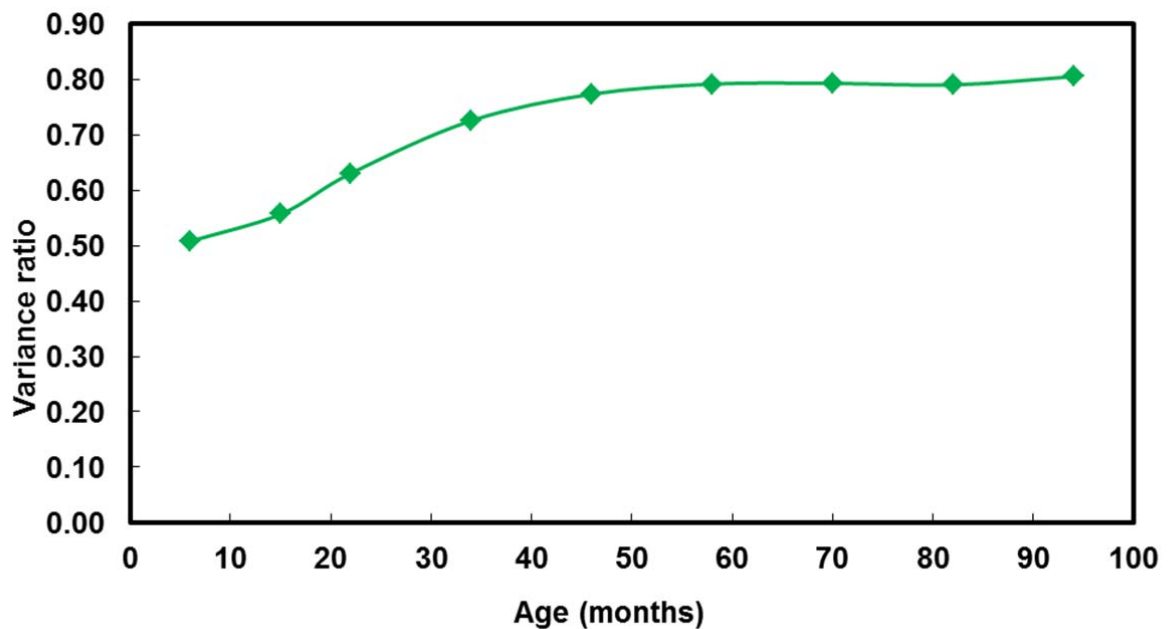
Figure 7.4 Direct heritability estimates for fibre diameter of Merino ewes at different ages

The genetic correlations among FD measurements at different ages ranged from 0.49 (between 6 and 58 months of age) and unity (between 82 and 94 months of age). Similar genetic correlations among fibre diameter at different ages are reported in the literature and ranged from 0.82 to 0.96 (Lewer et al. 1983; Atkins & Mortimer 1987; Hickson et al., 1994; Ponzoni et al. 1995; Vaez Torshizi et al. 1995; Brash et al. 1997; Coelli et al., 1998; Mortimer & Atkins 2003; Huisman & Brown, 2008).

The fact that fibre diameter is a highly heritable trait, as well as the high correlations between fibre diameter measured at different ages indicate that fibre diameter at selection age is an accurate indicator of adult fibre diameter. Therefore, selection for reduced fibre diameter at 15 months of age should lead to a lower adult fibre diameter.

The heritability estimates for SL are illustrated in Figure 7.5, while the genetic correlations among the different SL measures are summarised in Table 7.14. The heritabilities estimated in this study for SL ranged from 0.24 (34 months of age) to 0.55 (94 months of age) and these estimates decreased for the first three measurements, after which it increased steadily to 94 months of age.

The h^2_a estimates reported in the literature for adult SL ranged from 0.49 to 0.74 (Mortimer & Atkins, 1994; Hill, 2001; Cloete el al., 2003; Huisman et al., 2008), while the corresponding estimates for early SL ranged from 0.25 to 0.51 (Mortimer and Atkins 1994; Ponzoni et al., 1995; Cloete et al., 1998a; Greeff and Karlsson, 1998; Brown et al., 2002a; Cloete et al., 2002; Lee et al., 2002a; Olivier et al., 2014a). One of the major constraints with staple length measurements of wool with a short growth period is the accuracy with which a wool sample is taken, as well as differences in the length of residual wool left on the sheep by different shearers. The latter effect may affect consecutive SL measurements.
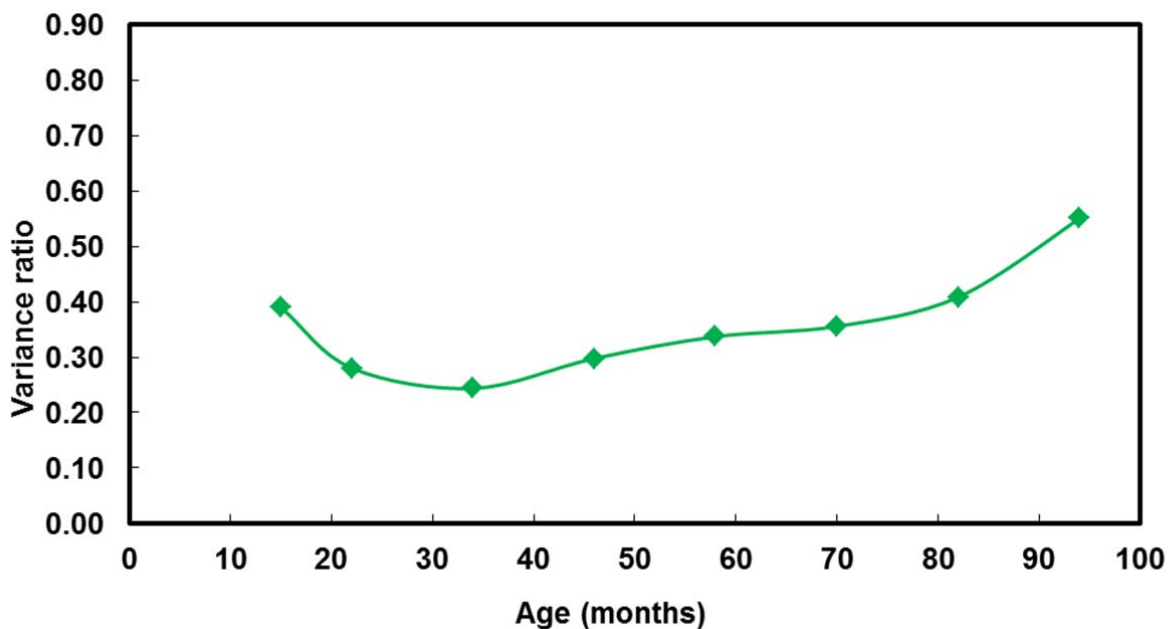
Figure 7.5 Direct heritability estimates for staple length of Merino ewes at different ages

Lewer et al. (1994) and Huisman & Brown (2008) reported correlations between young and adult staple length measures that ranged from 0.76 to unity, while estimates between two early measurements ranged from 0.71 to 0.78 (Ponzoni et al., 1995; Hill, 2001). These correlations are similar to the values estimated in this study for similar age groupings with the highest values between adjacent SL measurements and the r_g estimates decreasing with an increased time between measurements.

Table 7.14 Estimated genetic correlations among the staple length measures in Merino sheep from 15 to 94 months of age

Trait	SL22	SL34	SL46	SL58	SL70	SL82	SL94
SL15	0.939	0.519	0.147	-0.013	-0.030	0.070	0.101
SL22		0.780	0.469	0.300	0.225	0.199	0.188
SL34			0.915	0.800	0.663	0.435	0.161
SL46				0.967	0.853	0.583	0.218
SL58					0.950	0.730	0.376
SL70						0.904	0.635
SL82							0.904

[1] SL15 = Staple length at 15 months of age, etc.

The heritability estimates for and genetic correlations among the different SS measures are illustrated and presented in Figure 7.6 and Table 7.15 respectively. The h^2_a of SS generally increase with an increase of age, although the initial increments were smaller. The h^2_a estimates ranged from 0.10 (22 months of age) to 0.55 (94 months of age). Parameter estimates for SS are scarce in the literature.
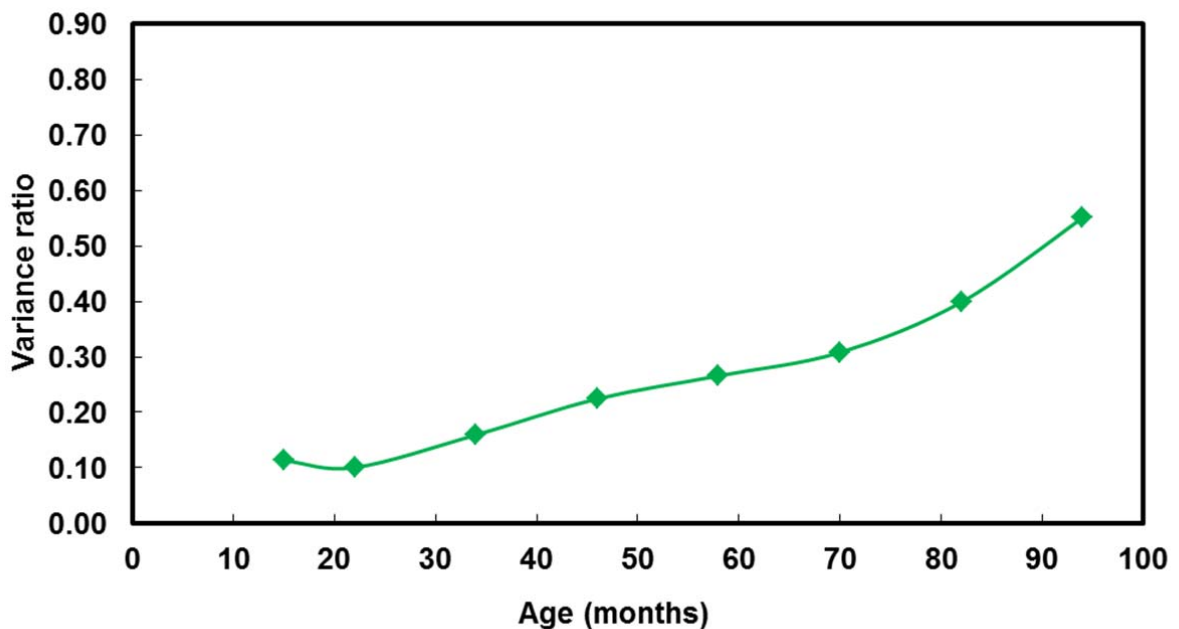
Figure 7.6 Direct heritability estimates for staple strength of Merino ewes at the different ages.

Huisman et al. (2008) reported h^2_a of 0.40 and 0.47 for two early staple strength measurements (365 and 450 days of age), which were higher than the corresponding estimates in this study. Hill (2001) reported a h^2_a of 0.33 at 40 months of age, which is higher than the estimates obtained in this study at 34 and 46 months of age. The estimate obtained in this study for an early staple strength measurement (15 months

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of age) was within the range of 0.13 to 0.47 reported in the literature (Ponzoni et al., 1995; Swan et al., 1995; Greeff & Karlsson, 1998; Wuliji et al., 2001; Chapter 3).

Staple strength r_g estimates are the highest at adjacent measurements and decrease with an increase in time intervals between measurements. The correlations reported in the literature for early or early adult measurements ranged from 0.68 to 0.86 (Ponzoni et al., 1995; Hill, 2001; Huisman & Brown, 2009).

Table 7.15 Estimated genetic correlations among the staple strength measures in Merino sheep from 15 to 94 months of age

Trait	SS22	SS34	SS46	SS58	SS70	SS82	SS94
SS15[1]	0.850	0.408	0.174	0.053	-0.010	-0.028	-0.015
SS22		0.824	0.646	0.500	0.328	0.124	-0.048
SS34			0.958	0.857	0.654	0.341	0.035
SS46				0.963	0.811	0.519	0.203
SS58					0.936	0.721	0.441
SS70						0.917	0.725
SS82							0.939

[1] SS15 = Staple strength at 15 months of age, etc.

The adult measurements of BW, fleece weight (GFW & CFW) and FD are highly correlated with 15 month performance data which implies that selection at 15 months of age will also improve the adult traits. Moreover, the genetic gain that can be achieved from selection for adult traits might be limited because these measurements are done after the main selection age and it is only recorded on ewes that were already selected for breeding. Swan & Brown (2013) found that the genetic gains from adult measurements were lower compared to the gain achieved at yearling traits in a simulation study. This was the case, despite the fact that higher heritabilities and phenotypic variances were obtained for the adult measurements than the yearling traits (Brown et al., 2013; Swan & Brown, 2013).

Selecting animals only on one year's records to improve the lifetime performance in a specific trait are a form of indirect selection (Lewer et al., 1983). This indirect selection together with the favourable r_g between measurements at 15 months of age and adult measurements will ensure that the adult ewe flock will improve.

The lower h^2_a and r_g of SL and SS compared to the other traits analysed in this study indicates that the environment at adult age plays a bigger role than in the other traits. Furthermore, one of the major factors influencing the environment of adult ewes is the number of lambs weaned. Cloete et al. (2000) and Scobie et al. (2012) found a significant decrease in staple tenacity with an increase in reproduction for Merino and Romney sheep respectively. The adult records of these two traits should therefore be rather included in selection programs as individual culling levels within year and reproduction status.

CONCLUSIONS

It can be concluded from this study that the heritability of fibre diameter increased with age, while the genetic relationships decreases in magnitude among fibre diameter measures as the time interval between measurements increase. The high genetic correlations of fibre diameter at 15 months of age,

which is performance testing age for Merino sheep in South Africa, with adult fibre diameter measures, indicate that selection for a reduced fibre diameter at 15 months will have a favourable effect on the fibre diameter of adult ewes.

Furthermore, it can be concluded from the results that body weight and fleece weight at performance testing age (15 months of age) of Merino sheep in South Africa is genetically highly correlated with the respective adult recordings. Selection to increase these two traits at 15 months will thus lead to an increased adult body weight and fleece weight. However, selection to increase body weight should be implemented with care, as it is not desirable to increase adult body weight unconditionally because of higher maintenance requirements of heavy adult ewes.

Fibre diameter had a much higher repeatability compared to the other traits analysed. In addition, the different FD measurements are higher correlated with less variation between the r_g which suggests that FD measurements at different ages are basically controlled largely by the same genes.

The estimates obtained with a random regression model are in the same order as values reported in the literature at specific ages using multi-trait analyses. Therefore, it can be concluded that random regression models are reliable and accurate for the estimation of genetic parameters for repeated records.

CHAPTER 8. EVALUATION OF FINE WOOL PRODUCTION OF MERINO SHEEP ON NATURAL PASTURES

INTRODUCTION

During the1980s until early 1990s substantial price premiums were paid for fine wools. Prior to this, the percentage of fine wool (defined as 20 µm and finer) in the national clip decreased from 69% in 1951 to 1955, to only 4% in 1976 to 1980 (Marx, 1981). This reduction was mainly due to more emphasis being placed on selection for the quantity of wool in the 1950s and 1960s. The price premium paid for finer wool during the 1980s led to more emphasis being placed on the production of fine wool, rather than simply the quantity of wool. The increased demand for finer wool and the associated price difference resulted in the proportion of fine wool in the national clip to increase to 43% in 2012/13 (Cape Wools SA, Personal communication, 2013).

This shift in the emphasis of wool production led to more attention being paid to the production of fine wool in South Africa and the establishment of fine wool projects at Cradock Experimental Station and Grootfontein Agricultural Development Institute, as set out in previous chapters.

Likewise, more producers in South Africa included reduced fibre diameter as one of the main breeding objectives in their selection programs (Olivier & Olivier, 2005). It is noteworthy that most woolled sheep in South Africa are kept under extensive farming conditions in the semi-arid and arid regions where seasonal droughts regularly occur, subjecting these animals to nutritional stress. Furthermore, most of these woolled sheep are medium to strong wool types (>20 µm). In the South African wool industry, as well as in Australia, medium wool sheep are regarded as a different strain than fine wool animals.

According to McGuirk (2009) different genotypes is normally defined as breeds, but in the context of Merinos it can also refer to strains or bloodlines. The different Merino strains are defined by their respective potentials for production, wool quality and reproduction (Short & Carter, 1955; Dunlop, 1962; 1963; Jackson & Roberts, 1970; Mortimer et al., 1985; Mortimer & Atkins, 1989; Kleemann et al., 2006; McGuirk, 2009). The latter literature sources reported that fine wool animals produced less, but finer wool compared to medium wool Merino strains.

Furthermore, Swan et al. (2001) stated that there is anecdotal evidence that fine wool Merinos are poorer reproducers compared to other Merino strains. This was also the popular believe in South Africa and is supported by findings from a study done by Mortimer et al. (1985) indicating that there was a substantial difference in number of lambs weaned per joining between fine wool strains (0.55) and medium wool Peppin (0.80) bloodlines. In contrast to this, Swan et al. (2001) found that the reproduction of fine wool animals is comparable with other Merino strains.

Olivier et al. (1989) stated that the performance of fine wool animals under different production environments in South Africa was not known and that it was important to determine the production

potential of these animals. A study where fine wool animals were evaluated on natural pastures in different wool producing areas was thus undertaken. This study was conducted in two phases. During the first phase animals were evaluated under a controlled environment on experimental farms and during the second phase on-farm evaluations were done at four localities in South Africa.

The aim of this study was to evaluate the production and reproduction of fine woolled animals under natural grazing conditions in five divergent environments. The study was motivated by perceptions among farmers that it would be infeasible to farm with finer Merino strains in part of South Africa dedicated to the production of medium to strong fleeces.

MATERIALS AND METHODS

This study was done in two phases. During the first phase fine woolled animals was evaluated against a control group on natural pastures at the Grootfontein Agricultural Development Institute (GADI). As the farming and grazing conditions at GADI are not representative of the entire South Africa, it prevents the extrapolation of these results to most other extensive sheep farming areas of South Africa. It was therefore decided to evaluate the production and reproduction performance of genetic fine wool Merinos under different veld conditions in South Africa during the second phase. The evaluation of the reproduction performance was very important because meat production is the main source of income for woolled sheep farmers in South Africa. Furthermore, some results in the literature has suggested that fine wool animals are poorer reproducers compared to other Merino strains (Mortimer et al., 1985; Kuchel & Lindsay, 1999; Safari et al., 2005; Kleemann et al., 2006)

<u>PHASE 1</u>

Data collected from 1989 to 1999 on the Grootfontein Merino flock (GMF) was used during this phase. This flock was maintained at GADI near Middelburg (31°28'S, 25°1'E) in the North-eastern Karoo region of South Africa. GADI is located in the False Upper Karoo (Acocks, 1988) and has an average annual rainfall of 360 mm.

Four hundred Merino ewes with an average fibre diameter of 23.6 µm were randomly divided into two groups of 200 each during 1989. These groups were labelled as a fine woolled (F) line and a control (C) line. The F-line was upgraded by mating to genetic fine wool rams from the Cradock fine wool Merino stud, while the C-line was mated to rams from the Grootfontein Merino stud. One of the main selection objectives in both sire studs was to maintain or reduce fibre diameter (Chapter 2; Olivier, 1989; Olivier et al., 1998). However, it is important to take note that the genetic makeup with regard to fibre diameter was widely divergent. The Grootfontein Merino stud was a medium wool flock, whereas the Cradock Merino stud (CMS) is a genetic fine wool flock. The CMS was established in 1988 with ewes with the lowest fibre diameter, purchased from producers throughout South Africa with the finest flocks (Chapter 2).

The production traits analysed for the lambs of the GMF included birth weight (BirthW), weaning weight (WW), 15-month body weight (BW), greasy fleece weight (GFW; corrected to 365 days wool growth), clean fleece weight (CFW), fibre diameter (FD), clean yield (CY), staple length (SL), wrinkle score (WS) and number of crimps per 25 mm (Crimps). The ewe flock was shorn annually and due to the fact that the ewes were in the process of being upgraded, only the production traits of the ewes born in 1997 and 1998 were used for this study. The same wool traits were analysed as for the lambs.

The reproduction traits over the life time of the ewes analysed were conception rate (number of ewes lambed / number of ewes mated), the total number of lambs born (NLB) and weaned (NLW) and the total weight of lambs weaned per ewe per year (TWW).

The least-squares means (LSM), standard errors and flock differences for the production traits and for NLB, NLW and TWW were obtained with the PROC GLM-procedure of SAS (SAS, 2009). The line difference in the binomially distributed conception rate data was tested for significance with the CHI-SQUARE-procedure of SAS (SAS, 2009).

The fixed effects tested for significance (P<0.05) to be included in the final models for the traits analysed in the first phase were sex (males and females), birth status (only BirthW), rearing status (all traits except BirthW), age of dam (years), year of birth, line (F or C) and the two-way interaction of sex by line. The age of the animals (linear regression) was also tested for significance. For the production traits of the ewe flock, year, line and year of birth were tested for significance (P<0.05). The fixed effects of year of birth, line and number of lambing opportunities were tested for significance (P<0.05) for NLB, NLW and TWW.

PHASE 2

The second phase of this study was conducted on the farms of four Merino producers in the non-traditional fine wool producing areas of South Africa. Ewes from the fine wool line of the GMF were used for comparison with ewes of the same age bred on the respective farms. The participating farms were located in Carnarvon (Goraas; 31º11'18''S, 21º31'10''E; 1224m above sea level (asl)), De Aar (Nuwejaarsfontein; 30º52'15''S, 24º00'26''E; 931m asl), Steynsburg (Geduldsfontein; 31º06'12''S, 25º50,01''E; 1517m asl) and Wakkerstroom (Oudehoutskraal; 27º20'22''S 30º12'33''E; 1844m asl) districts.

The feed on offer on the farms in the Carnarvon and De Aar districts mainly consisted of Karoo shrub veld, while grass veld was mostly utilised in Steynsburg and Wakkerstroom. Carnarvon is situated in the Arid Karoo, De Aar in the Central Upper Karoo and False Arid Karoo, Steynsburg in the False Upper Karoo and Karroid Merxmeullera Mountain Veld, while Wakkerstroom is situated in the Sour Grass Veld (Acocks, 1988). The respective grazing capacities for the Carnarvon, De Aar, Steynsburg and Wakkerstroom localities were 30, 18, 12 and 3 ha/large stock unit (LSU).

After completion of **Phase 1** in 2000, 200 ewes of the fine wool line of the GMF were randomly divided on a stratified body weight, fibre diameter and number of lambs scanned basis within dam age groups into

four groups of 50 ewes each. These ewes were transferred to the participants between August and September 2000 after being mated in May 2000 to rams from the Cradock fine wool Merino stud at GADI. The respective control flocks consisted of a group of 50 ewes from within the flocks of each participant (regarded as medium to strong wool animals). The latter ewes were mated to rams used at each farm at approximately the same time as the fine wool ewes. Fine wool and control ewes were maintained in the same flock throughout the project, except during mating.

The first **Phase 2** lambs were born during October or November 2000. In 2001, replacement ewes were obtained from the original flock at Grootfontein. From 2002 onwards, replacements were obtained from the progeny born on each location. The replacements for the participant's own flocks were also sourced from his own flock during 2001 and subsequently from within the control line at each locality. Rams from the Cradock fine wool Merino stud, were used as sires in the respective fine wool lines for the duration of the project, while the ewes of the control lines were mated to the same rams used by the respective participants in their own flocks.

The traits included in the analysis of **Phase 2** were weaning weight (WW; approximately 120 days of age) and 14-months BW, GFW, CFW, FD, SL, coefficient of variation of FD (CV) and staple strength (SS). The following subjectively assessed traits were recorded prior to shearing at approximately 14 months of age: wool quality (WQ), evenness over the fleece (EF), wool yolk (WY), staple formation (SF), belly and points (BP), conformation of the head (HEAD), pigmentation (Pigm), hocks, pasterns, conformation of the front quarter (FQ) and overall body conformation (BC) (See Chapter 6 for detailed explanation of subjective traits).

Body weight at mating (MW), greasy and clean fleece weight, fleece traits and total weight of lambs weaned per ewe per year (TWW) were recorded annually for the ewe flocks.

The profit per hectare for the progeny of the two groups at each locality in **Phase 2** was calculated for each 14-month old animal by using the model described by Herselman (2004) and Herselman & Olivier (2010).

Profit (R/SSU) $=983.37 + 3.61BW + 75.04CFW + 0.3SL - 123.26FD + 2.6116FD^2 + 8.46MP(1)$

Where: 983.37 is a constant, BW is the phenotypic body weight, CFW is the phenotypic clean fleece weight, SL is the phenotypic staple length, FD is the phenotypic mean fibre diameter, MP is the meat price (for these calculations the price for lamb was taken as R44.72/kg, which was the average for the last six years (2008 to 2012)).

The least-squares means (LSM), standard errors and flock differences within locality for the production traits and TWW were obtained with the PROC GLM-procedure of SAS (SAS, 2009).

The following fixed effects were tested for significance for inclusion in the final models for the production and subjective traits during **Phase 2**, as well as profit per hectare for the progeny: sex (males and females),

rearing status, year of birth, flock (combination of line (fine wool or control) and locality) and the two-way interactions of sex by flock and year of birth by flock. The age of the animals (linear regression) at weaning and performance testing age were included in the model for WW and the 14-month traits respectively. Only year and flock were testedfor the production and reproduction traits of the ewe flocks. Only the effects that had a significant effect on a specific trait were included in the final model, except for flock, which was included regardless of the significance level to obtain LSM and flock differences for the respective traits.

RESULTS AND DISCUSSION
PHASE 1

The significance level of the fixed effects tested for each trait are summarised in Table 8.1. It is evident from Table 8.1 that the age of the animal had a significant effect on the growth traits, as well as fleece weight and fibre diameter. Year of birth also had a significant effect on all the traits, while sex, birth or rearing status, dam age and line, were significant for most traits. The two way interaction between line and sex were not significant for any off the traits. For the purpose of this study only the effect of line will be discussed in detail.

The effect of line on the production traits of the progeny and the adult ewe flock of **Phase 1** (GMF) are summarised in Tables 8.2 and 8.3 respectively. It is evident from Table 2 that the control flock progeny were 2% heavier (P<0.05) than the fine wool flock at birth and at performance testing age. Furthermore, the fine wool flock progeny produced 11% less wool (P<0.05) than control animals, but their fleeces were 8% finer (P<0.05) compared to the control group. The control group progeny had a better clean yield (P<0.05) than their fine wool contemporaries and 54% less crimps per 25 mm (P<0.05) compared to the fine wool group.

Table 8.1 Significance level of the fixed effects tested for each trait

Traits	Age[1]	Sex	Bstat[2]/ RS[3]	DAGE[4]	Year of birth	Flock
Birth weight		**	**	**	**	**
Weaning weight	**	**	**	**	**	ns
15 Month body weight	**	**	**	**	**	**
Greasy fleece weight	**	**	**	**	**	**
Clean fleece weight	**	**	**	**	**	**
Fibre diameter	**	**	*	**	**	**
Clean yield	ns	*	*	ns	**	**
Staple length	ns	ns	**	ns	**	*
Wrinkle score	ns	**	**	**	**	*
No. of crimps / 25 mm	ns	ns	ns	**	**	**

** - P<0.01; * - P<0.05; ns – Not significant; [1]Age - age at weaning for WW, age at performance testing for other traits; [2]Bstat - birth status for birth weight; [3]RS - rearing status for other traits; [4]DAGE – age of the dam in years.

Table 8.2 The effect of flock on the production traits (± s.e.) of the fine wool and control progeny (animal numbers in brackets)

Traits	Fine wool (n=1996)	Control flock (n=1896)
Birth weight (kg)	4.3[a] ± 0.0	4.6[b] ± 0.0
Weaning weight (kg)	24.1[a] ± 0.2	24.1[a] ± 0.2
15 Month Body weight (kg)	37.9[a] ± 0.3	38.7[b] ± 0.3
Greasy fleece weight (kg)	4.1[a] ± 0.1	4.6[b] ± 0.1
Clean fleece weight (kg)	2.8[a] ± 0.0	3.1[b] ± 0.0
Fibre diameter (µm)	18.0[a] ± 0.1	19.6[b] ± 0.1
Clean yield (%)	66.6[a] ± 0.3	68.3[b] ± 0.3
Staple length (mm)	88.9[a] ± 0.5	89.9[a] ± 0.6
Wrinkle score	8.0[a] ± 0.1	7.8[a] ± 0.1
Number of crimps / 25 mm	16.8[a] ± 0.4	10.9[b] ± 0.4

[a,b] - Values with different superscripts differed significantly (P<0.05)

Table 8.3 The effect of flock on the production traits (± s.e.) of the fine woolled and control adult ewes (animal numbers in brackets)

Traits	Fine woolled ewes (n=377)	Control ewes (n=353)
Body weight at mating (kg)	50.5[a] ± 0.4	51.0[a] ± 0.4
Greasy fleece weight (kg)	5.0[a] ± 0.1	5.4[b] ± 0.1
Clean fleece weight (kg)	3.2[a] ± 0.0	3.5[b] ± 0.0
Fibre diameter (µm)	19.7[a] ± 0.1	21.6[b] ± 0.1
Clean yield (%)	66.3[a] ± 0.3	65.2[a] ± 0.3
Staple length (mm)	88.0[a] ± 0.8	87.6[a] ± 0.8
Wrinkle score	8.5[a] ± 0.1	8.5[a] ± 0.1
Number of crimps / 25 mm	13.8[a] ± 0.1	9.1[b] ± 0.1

[a,b] - Values with different superscripts differed significantly (P<0.05)

It is evident from Table 8.3 that there was no significant difference between the adult body weights of the two lines. The fine wool ewes produced 10% finer wool (P<0.05) but 9% less (P<0.05) wool compared to the control line ewes. The fine wool ewes also had 52% more crimps per 25 mm than the control ewes. There were no significant differences in clean yield, staple length or wrinkle score between the lines. The differences between the fine wool and control line of the progeny and the adult ewes were similar in sign and direction in most instances.

The reduction in the mean fibre diameter of the control flock can be ascribed to the fact that one of the main selection criteria in the Grootfontein Merino stud was also to reduce fibre diameter (see the genetic trends in Olivier et al., 1995). The average fibre diameter of the control line adult ewe flock decreased from 23.9 µm in 1989 to 22.0 µm in 1999 and from 23.9 µm to 19.7 µm in the fine wool line.

The effect of line on the conception rate, the lifetime number of lambs born and weaned and the total weight of lambed weaned are presented in Table 8.4. There were no significant differences in the reproduction of the two lines. The relative difference between NLB and NLW in both these lines can be ascribed to two main factors. Firstly, most of the deaths of lambs prior to weaning can be ascribed to a Chlamydia infection where the ewes lambed on small, irrigated pastures. Secondly, stray dogs, as well as damage-causing animals (jackal and caracal) also caused losses in some years. The average number of lambing opportunities of ewes in both lines was 3.69.

Table 8.4 The effect of flock on the reproductive performance (± s.e.) of the fine wool and control ewes (animal numbers in brackets). No significant differences were found.

Traits	Fine wool ewes (n=693)	Control ewes (n=659)
Conception rate (%)	90	89
Number of lambs born per ewe	5.5 ± 0.2	5.6 ± 0.2
Number of lambs weaned per ewe	3.7 ± 0.2	3.6 ± 0.2
Total weight of lamb weaned per ewe (kg)	92.6 ± 4.3	91.7 ± 4.2

PHASE 2

The significance level of the fixed effects tested for each trait are summarised in Table 8.5. It is evident from Table 5 that flock had a significant effect on all the traits. The two way interaction between flock and sex were also significant for all the traits, except for CVFD and EF. As flock is a concatenation of flock and locality, these results are difficult to interpret. However, results for lines within localities are reported in Tables 8.6, 8.7 and 8.8 to assist with interpretation. Year of birth also had a significant effect on all the traits except for Pigm and hocks. Age of the animal, sex and rearing status had a significant effect on most of the traits. Only significant effects were included in the final model for each trait, except for flock which was included regardless of the significance level to obtain LSM and flock differences for the respective traits. For the purpose of this study only the effect of flock within locality will be discussed in detail.

The effect of flock within locality on the production traits of all the lambs born from 2000 to 2004 is summarized in Table 8.6. It is evident from Table 8.6 that the WW of the control lambs at De Aar and Wakkerstroom, as well as the BW of control lambs at Carnarvon and De Aar, were approximately 10% and 4% heavier (P<0.05) respectively than that of their fine wool counterparts. These weights did not differ between the fine wool and control groups at the other localities. Fine wool progeny produced 8% to 17% finer and approximately 11% shorter wool (P<0.05) than the corresponding control groups at all four localities. The control group progeny at Carnarvon, De Aar and Wakkerstroom produced between 19% and 30% more wool (P<0.05) than the corresponding fine wool groups. The same tendency was observed in the first phase pertaining to the quantity of wool produced and fibre diameter.

The fine wool groups at De Aar and Wakkerstroom had a lower CVFD than their control group contemporaries (Table 8.6), whereas this trend was reversed at Steynsburg. The fine wool lambs at Steynsburg had a 18% better (P<0.05) staple strength than their control group counterparts. It is evident from Table 8.6 that there were no significant differences between the profit per ha of fine wool groups compared to their respective control group contemporaries at all four farms. The large variation in the profit per hectare (Table 8.6) can be ascribe to the differences in grazing capacity that ranged from 3ha/LSU at Wakkerstroom to 30ha/LSU at Carnarvon.

Table 8.5 Significance level of the fixed effects tested for each trait

Traits	Age[1]	Sex	RS[2]	Year of birth	Flock	Flock x Sex	Flock x Year
Weaning weight	*	*	*	*	*	*	*
Body weight	*	*	*	*	*	*	*
Clean fleece weight	*	*	*	*	*	*	*
Fibre diameter	*	ns	ns	*	*	*	*
Staple length	*	*	*	*	*	*	ns
Coefficient of variation fibre diameter	*	*	ns	*	*	ns	ns
Staple strength	*	*	*	*	*	*	*
Wool quality	ns	*	*	*	*	*	*
Evenness of the fleece	ns	ns	ns	*	*	ns	ns
Wool yolk	ns	*	*	*	*	*	*
Staple formation	*	*	ns	*	*	*	*
Bellies and points	*	*	*	*	*	*	*
Conformation of the head	*	*	*	*	*	*	*
Pigmentation	ns	ns	ns	ns	*	*	ns
Hocks	ns	ns	ns	ns	*	*	ns
Pasterns	*	*	ns	*	*	*	ns
Front quarters	*	*	*	*	*	*	*
Overall conformation	*	*	*	*	*	*	*

* - P<0.05; ns – Not significant; [1]Age - age at weaning for WW, age at performance testing for other traits; [2]RS - rearing status for other traits.

The effect of flock within locality on the subjectively assessed traits is presented in Table 8.7. It is evident from this table that the wool quality of all the groups tended to be above average. Control group progeny at De Aar and Steynsburg had approximately 10% better (P<0.05) wool quality than their fine wool counterparts. The evenness of the fleeces of all the groups was better than the average of the breed. At Carnarvon, De Aar and Wakkerstroom the fleeces of the fine wool groups were between 9% and 20% more even (P<0.05) than that of the control groups.

The control groups at the two localities located in the Karoo shrub veld (Carnarvon and De Aar) had an approximately 8% higher (P<0.05) WY score compared to the corresponding fine wool groups (Table 8.7). In contrast, at the two localities located in the grass veld (Steynsburg and Wakkerstroom), the fine wool groups had an approximately 5% higher (P<0.05) WY score. The fine wool groups at Carnarvon and De Aar had 4% and 20% thinner (P<0.05) staples respectively than their corresponding control groups. In contrast, the fine wool lines had 8% thicker (P<0.05) staples at Steynsburg than their control group contemporaries.

The means for conformation of the head and the pigmentation scores of the control group progeny were respectively 12% to 17% and 5% better (P<0.05) at Carnarvon, De Aar and Wakkerstroom in comparison to those of the comparable fine woolled groups.

The control group progeny had better (P<0.05) hocks at all four localities compared to the fine wool groups (Table 8.7). A significant difference in pasterns was observed at De Aar with the fine wool animals having higher scores compared to the control animals. In contrast, the control animals at Wakkerstroom had higher scores than their fine wool counterparts. The FQ and BC scores of the groups were average

and the control animals had respectively between 8% to 11% and 10% to 15% higher (P<0.05) average scores for both these traits than the fine wool groups.

The effect of flock within locality on the production and reproduction traits of the adult ewes from 2000 to 2004 at all four localities is summarised in Table 8.8. It is evident from this table that the fine wool ewes at Carnarvon and Steynsburg were respectively 3% and 10% heavier (P<0.05) than the corresponding control groups at mating, while at De Aar and Wakkerstroom the control ewes were respectively 2% and 4% heavier (P<0.05) than the fine wool ewes.

The fine wool ewes at De Aar and Wakkerstroom produced respectively 31% and 18% less wool (P<0.05) than their control group contemporaries, whereas the fine wool ewes at Steynsburg produced 15% more wool (P<0.05) than their control group counterparts. The fine wool ewes at all four localities were between 7% and 20% finer (P<0.05) than their contemporaries. At three of the localities the mean staple length of the fine wool ewes was between 6% and 13% shorter (P<0.05) than that of the corresponding control groups, except at Carnarvon where no difference was found. The staple strength of the wool of the adult ewes did not differ significantly, except at De Aar where the fine wool ewes had 14% stronger staples than the control group ewes. It is however, important to note that there was none of the flocks that had a staple strength of below 30 N/Ktex, which is generally accepted as the lower boundary for good processing. The same tendency was observed with the progeny.

There were no significant differences observed between the total weight of lamb weaned per ewe per lambing opportunity for the two lines within localities. Results of this study accorded with the results of the first phase pertaining to the quantity of wool produced, fibre diameter and total weight of lamb weaned per ewe mated.

The results from this study with regard to reproduction are consistent with findings from Swan et al. (2001), and in contrast to the results reported earlier by other researchers (Mortimer et al., 1985; Kleemann et al., 2006). Thus, the anecdotal evidence (Swan et al., 2001), as well as the popular belief in South Africa with regard to the reproduction potential of fine wool ewes, can be laid to rest. This is very important, because reproduction is the key to economic survival for local sheep enterprises.

Hatcher et al. (2004) demonstrated the economic advantage of selection for reduced fibre diameter, despite the unfavourable changes in BW and CFW. The reduced CFW and BW of fine wool lines were also demonstrated in the earlier line differences reported by Mortimer et al. (1989). These results are in accordance with the results of the current study, as well as in studies conducted by Hatcher et al. (2000) and Adams & Cronje (2003). According to Coelli et al. (2000) finer ewes had lower CFW and BW, as well as shorter staples, which is also in agreement with the current study.

Table 8.6 The effect of flock within locality on the production traits (± s.e.)of the lambs at the four participating farms (animal numbers in brackets)

Trait	Carnarvon		De Aar		Steynsburg		Wakkerstroom	
	Fine (n)	Control (n)	Fine (n)	Control (n)	Fine (n)	Control (n)	Fine (n)	Control (n)
Weaning weight (kg)	27.51^a ± 1.12 (293)	27.04^a ± 1.14 (256)	30.41^a ± 1.13 (265)	32.31^b ± 1.13 (277)	31.76^a ± 1.15 (204)	32.03^a ± 1.15 (197)	26.90^a ± 1.24 (188)	29.80^b ± 1.25 (182)
15 Month body weight (kg)	43.52^a ± 1.14 (265)	44.80^b ± 1.18 (240)	51.17^a ± 1.18 (250)	53.24^b ± 1.18 (261)	41.01^a ± 1.28 (107)	41.86^a ± 1.31 (95)	45.75^a ± 1.21 (216)	46.48^a ± 1.16 (203)
Clean fleece weight (kg)	2.81^a ± 0.12	3.33^b ± 0.12	3.42^a ± 0.12	4.46^b ± 0.12	2.26^a ± 0.13	2.25^a ± 0.13	2.59^a ± 0.12	3.28^b ± 0.12
Fibre diameter (μm)	17.74^a ± 0.22	19.10^b ± 0.23	18.18^a ± 0.23	21.29^b ± 0.23	16.03^a ± 0.25	17.54^b ± 0.25	17.54^a ± 0.23	18.91^b ± 0.22
Staple length (mm)	85.28^a ± 2.48	94.61^b ± 2.58	91.93^a ± 2.57	102.69^b ± 2.56	76.71^a ± 2.80	85.86^b ± 2.85	87.69^a ± 2.63	96.62^b ± 2.53
Coefficient of variation of fibre diameter (%)	18.88^a ± 0.38	19.03^a ± 0.39	18.94^a ± 0.39	20.65^b ± 0.39	21.00^a ± 0.43	20.00^b ± 0.44	19.56^a ± 0.40	20.38^b ± 0.39
Staple strength (N/Ktex)	40.05^a ± 1.60	41.28^a ± 1.66	46.06^a ± 1.65	45.65^a ± 1.65	51.40^a ± 1.79	43.52^b ± 1.81	34.90^a ± 1.72	33.27^a ± 1.65
Profit (R/ha)[1]	104.89^a ± 17.5	103.78^a ± 18.12	187.9^a ± 18.04	200.81^a ± 18.06	251.15^a ± 19.7	222.00^a ± 20.1	850.89^a ± 18.37	891.65^a ± 17.83

[a,b] - Values with different superscripts within locality differed significantly ($P<0.05$)

[1] Grazing capacity at Carnarvon is 30 ha/LSU, De Aar 18 ha/LSU, Steynsburg 12 ha/LSU and Wakkerstroom 3ha/LSU

Table 8.7 The effect of flock within locality on the subjectively assessed traits (± s.e.) of the lambs at the four participating farms

Trait	Carnarvon		De Aar		Steynsburg		Wakkerstroom	
	Fine	Control	Fine	Control	Fine	Control	Fine	Control
Wool quality	29.66^a	30.91^a	31.95^a	34.35^b	31.66^a	34.79^b	29.22^a	30.14^a
	± 1.48	± 1.53	± 1.52	± 1.52	± 1.62	± 1.65	± 1.55	± 1.50
Evenness of the fleeces	35.03^a	31.12^b	37.37^a	31.02^b	37.47^a	36.32^a	32.94^a	30.33^b
	± 1.25	± 1.29	± 1.28	± 1.28	± 1.37	± 1.39	± 1.31	± 1,27
Wool yolk	23.76^a	25.24^b	22.59^a	24.48^b	27.30^a	26.34^b	24.53^a	23.35^b
	± 0.64	± 0.66	± 0.66	± 0.66	± 0.70	± 0.71	± 0.67	± 0.65
Staple formation	29.75^a	30.71^b	27.58^a	32.98^b	33.81^a	31.46^b	27.80^a	28.05^a
	± 0.92	± 0.95	± 0.94	± 0.94	± 1.01	± 1.02	± 0.96	± 0.93
Bellies and points	25.28^a	27.63^b	23.42^a	27.29^b	32.33^a	30.43^b	27.71^a	29.00^b
	± 1.21	± 1.25	± 1.24	± 1.24	± 1.33	± 1.35	± 1.26	± 1.22
Conformation of the head	25.65^a	29.90^b	27.66^a	32.30^b	30.19^a	31.86^a	24.43^a	27.27^b
	± 1.40	± 1.44	± 1.43	± 1.43	± 1.53	± 1.55	± 1.46	± 1.41
Pigmentation	34.25^a	35.83^b	35.18^a	36.56^b	36.81^a	36.52^a	33.46^a	35.13^b
	± 1.37	± 1.42	± 1.41	± 1.41	± 1.51	± 1.53	± 1.44	± 1.40
Hocks	21.58^a	23.24^b	21.59^a	24.24^b	22.44^a	23.82^b	22.38^a	23.05^b
	± 0.77	± 0.79	± 0.79	± 0.79	± 0.84	± 0.86	± 0.80	± 0.78
Pasterns	38.57^a	37.98^a	38.78^a	38.08^b	40.73^a	40.03^a	35.11^a	36.68^b
	± 1.00	± 1.03	± 1.02	± 1.02	± 1.09	± 1.11	± 1.04	± 1.01
Front quarters	22.83^a	24.51^b	23.93^a	26.65^b	26.00^a	28.26^b	22.79^a	25.26^b
	± 0.98	± 1.01	± 1.01	± 1.01	± 1.08	± 1.09	± 1.03	± 1.00
Overall conformation	24.40^a	27.69^b	25.85^a	29.67^b	28.95^a	31.86^b	23.35^a	26.49^b
	± 1.15	± 1.18	± 1.17	± 1.17	± 1.25	± 1.27	± 1.20	± 1.16

[a,b] - Values with different superscripts within locality differed significantly (P<0.05)

Table 8.8 Wool production and reproduction data (± s.e.) of the ewe flocks at the four participating farms (animal numbers in brackets)

Trait	Carnarvon		De Aar		Steynsburg		Wakkerstroom	
	Fine (n)	Control (n)	Fine (n)	Control (n)	Fine (n)	Control (n)	Fine (n)	Control (n)
Mature weight (kg)	47.09^a ± 0.41 (232)	45.77^b ± 0.42 (224)	52.56^a ± 0.43 (215)	53.68^b ± 0.42 (225)	51.51^a ± 0.59 (117)	46.85^b ± 0.59 (119)	52.25^a ± 0.40 (231)	54.13^b ± 0.39 (251)
Clean fleece weight (kg)	3.06^a ± 0.05 (219)	3.13^a ± 0.05 (209)	3.41^a ± 0.05 (209)	4.47^b ± 0.05 (215)	3.49^a ± 0.07 (110)	3.04^b ± 0.07 (98)	3.37^a ± 0.05 (231)	3.96^b ± 0.05 (227)
Fibre diameter (μm)	19.45^a ± 0.11	21.24^b ± 0.11	20.03^a ±0.11	23.99^b ± 0.11	19.65^a ± 0.16	20.95^b ± 0.17	19.21^a ± 0.11	21.74^b ± 0.11
Staple length (mm)	89.39^a ± 0.84	91.63^a ± 0.86	88.65^a ± 0.86	96.31^b ± 0.85	79.18^a ± 1.24	89.06^b ± 1.31	91.70^a ± 0.82	97.46^b ± 0.82
Coefficient of variation of fibre diameter (%)	17.99^a ± 0.13	19.04^b ± 0.13	18.60^a ± 0.13	19.89^b ± 0.13	17.99^a ± 0.19	17.73^a ± 0.20	18.53^a ± 0.13	19.58^b ± 0.13
Staple strength (N/Ktex)	44.87^a ± 0.93	45.67^a ± 0.94	43.99^a ± 1.14	38.52^b ± 1.13	43.47^a ± 1.40	45.75^a ± 2.03	49.63^a ± 1.11	51.41^a ± 1.12
Total weight of lamb weaned (kg/ewe/year)[1]	27.72^a ± 1.00 (287)	25.65^a ± 1.02 (276)	27.26^a ± 1.04 (267)	30.00^a ± 1.02 (280)	26.39^a ± 1.13 (236)	25.46^a ± 1.11 (243)	23.31^a ± 1.12 (303)	23.84^a ± 1.11 (308)

a,b,c,d - Values with different superscripts within locality differed significantly (P<0.05)

[1] Weaning weight used for the calculation of TWW corrected to 120 days and sex, except at Wakkerstroom where weaning weight was corrected to 180 days

Furthermore, unfavourable correlations (Chapters 3 & 4) among FD and production and reproduction traits will hamper the progress in these traits if selection for reduced FD is unduly emphasised in the selection objective. It is therefore important that selection should not only be based solely on FD, but should also include the other economically important traits in the selection objective.

CONCLUSIONS

The study provides evidence that this specific genetic fine wool Merino strain adapted to the extensive farming conditions of South Africa at localities where medium to strong wool is traditionally produced. This conclusion is supported by the fact that the reproduction and body weight of the fine wool animals were mostly in the same range as that of the control animals during both phases. Consequently, the differences in meat production of the flocks were relatively small and would not impact negatively on the profitability of a fine wool enterprise in comparison with a medium to strong wool production system.

CHAPTER 9. GENOTYPE X ENVIRONMENT INTERACTIONS FOR PRODUCTION TRAITS IN FINE AND STRONG WOOL MERINO SHEEP OF SOUTH AFRICA

INTRODUCTION

Genotypes are normally defined as different breeds, however in Merino sheep different strains or bloodlines are often seen as different genotypes (McGuirk, 2009). These different strains are defined by differences in production and reproduction potential (Short & Carter 1955; Dunlop, 1962; 1963; Jackson & Roberts, 1970; Mortimer et al., 1985; Mortimer & Atkins, 1989; Kleemann et al., 2006; McGuirk, 2009).

This perception that different genotypes may perform differently in the same environment or that the same genotypes may perform differently in different environments has led to the concept of a genotype by environment (GxE) interaction. There are different approaches to investigate the GxE interaction. When the performances of same genotypes are recorded in different environments the most common method to evaluate this interaction is through the genetic correlation between the estimated breeding values in each environment (Falconer, 1952). In this case the performance of animals in different environments is regarded as separate traits. The animal breeding analogy with this model is the multi-trait model, where performances in different environments are regarded as different and genetically correlated traits.

A GxE interaction can be defined as the change in the performance in a specific trait of different genotypes in different environments. This implies that the animal with the best genetic merit in a specific environment will not necessarily be the best performer or produce the best offspring in another environment, i.e. some re-ranking of animals in different environments is expected (Falconer & Mackay, 1996; Lynch & Walsh, 1998; Cardoso & Tempelman, 2012).

This interaction may also be assessed by estimating the GxE variance as a variance ratio, expressed relative to the phenotypic variance (Dickerson, 1962). The phenotypes of animals across environments are therefore not always simply the sum of the genetic and environmental variation because it can also be affected by the interaction between the genotype and environment (Peaston & Whitelaw, 2006; Steinheim et al., 2008).

GxE interactions are considered to be present when the correlation between estimated breeding values for a specific trait expressed in different environments differs from unity ($r_G < 1$; Falconer, 1952). Because it becomes cumbersome to derive correlations for all GxE combinations, there is a tendency to assume that the genetic correlations between different environments for a trait affected by GxE are equal to unity and subsequently excluding the GxE (Bertrand et al., 1985; Woolaston, 1987; Cameron & Curran, 1995; Warner et al., 2010). The exclusion of such interactions can compromise selection efficiency (Dominik & Kinghorn, 2008; Huquet et al., 2012).

The optimum use of specific genotypes in different environments depends on knowledge of the effect of GxE interactions on the important production traits (Vostrý et al., 2008; Warner et al., 2010). Such interactions can potentially be important for wool sheep in South Africa, as production environments vary a lot from arid conditions with a low carrying capacity to high-potential irrigated pastures where high levels of production are sustained. It is also conceded that specific strains adapt better to specific environments/conditions than others (Dickerson, 1962).

The popular belief in South Africa is that fine wool cannot be produced successfully under the extensive and arid farming conditions. This contention resulted in a study where fine wool animals were evaluated on natural pastures (Chapter 8; Olivier & Olivier, 2007). The results of this study indicated that the production and reproduction potential of the fine wool animals were comparable to medium wool animals under veld conditions (Chapter 8; Olivier & Olivier, 2007).

The aim of this study was to estimate the GxE interaction and resulting breeding values in a dataset that consisted of two genotypes that were recorded within three divergent environments. GxE was assessed by using different methods.

MATERIALS AND METHODS

Data collected from 1989 to 1999 on the Grootfontein Merino flock (GMF), from 1989 to 2010 on the Cradock fine wool Merino stud (CMS) and from 1966 to 2010 on the Grootfontein Merino stud (GMS) were used for estimating the GxE interaction. The GMF was maintained at the Grootfontein Agricultural Development Institute (GADI) near Middelburg (31°28'S, 25°1'E) in the North-eastern Karoo region of South Africa. GADI is located in the False Upper Karoo (Acocks, 1988) and has an average annual rainfall of 360 mm.

During 1989, 400 Merino ewes of the Grootfontein Merino flock with an average fibre diameter of 23.6 μm were randomly divided into two groups of 200 ewes each, subsequently labelled as a fine woolled (F) line and a control (C) line. The F-line was upgraded to produce finer wool by being mated to genetic fine wool rams from the Cradock fine wool Merino stud, while the C-line was mated to rams from the GMS.

The CMS was run on irrigated pastures at the Cradock Experimental Station near Cradock in the Eastern Cape province of South Africa. See Chapter 2 for a detailed description of the management and selection practices of this stud. The GMS was run on a combination of Karoo veld and irrigated pastures at GADI. Olivier (1989) and Olivier et al. (1998) give a detailed description of management and selection practices of this stud.

The production traits included in the analysis of the GxE interaction were weaning weight (WW), 15-month body weight (BW), greasy fleece weight (GFW; corrected to 365 days wool growth), clean fleece weight (CFW), fibre diameter (FD) and staple length (SL). The least-squares means (LSM) and the standard errors for these production traits were obtained with the PROC GLM-procedure and the significance

levels of differences among the flocks were obtained with the PDIFF-option under the PROC GLM-procedure of SAS (SAS, 2009).

The fixed effects tested for significance included stud (CMS, GMS, fine wool line GMF (GMFF) and control line GMF (GMFC)), sex (males and females), year of birth, age of the dam (2 to 6 years), rearing status (single/multiple) and age of the animal (linear regression) at weaning and 15 months of age.

The estimation of the genetic parameters was done with ASREML (Gilmour et al., 2009) by fitting single-trait animal models. These models included different combinations of the direct additive, maternal additive and maternal permanent environmental effects, as well as the covariation between the direct and maternal additive effects. The GxE variance ratio (ge^2) was calculated from the sire x flockyear variance and expressed as a proportion of the total phenotypic variance. These different combinations led to the following six models fitted:

$$y = Xb + Z_1a + e \qquad\qquad (1)$$
$$y = Xb + Z_1a + Z_3mpe + e \qquad\qquad (2)$$
$$y = Xb + Z_1a + Z_2m + e; \text{ with } cov(a,m) = 0 \qquad\qquad (3)$$
$$y = Xb + Z_1a + Z_2m + e; \text{ with } cov(a,m) = A\sigma_{am} \qquad\qquad (4)$$
$$y = Xb + Z_1a + Z_2m + Z_3mpe + e; \text{ with } cov(a,m) = 0 \qquad\qquad (5)$$
$$y = Xb + Z_1a + Z_2m + Z_3mpe + e; \text{ with } cov(a,m) = A\sigma_{am} \qquad\qquad (6)$$

where **y** is a vector of observed traits of animals; **b**, **a**, **m** and **mpe** are vectors of fixed effects, direct additive effects, maternal additive effects and the maternal permanent environmental effects; X, Z_1, Z_2, and Z_3 are the corresponding incidence matrices relating the effects to **y**; **e** is the vector of residuals; A is the numerator relationship matrix and σ_{am} is the covariance between the direct and maternal additive effects.

The most suitable random effects model was determined as described in Chapter 3. The GxE was subsequently estimated for the respective traits by adding sire x flockyear as an additional random effect ($I\sigma^2_{ge}$) to the most suitable model for each trait.

It was assumed that $V(a) = A\sigma^2_a$; $V(m) = A\sigma^2_m$; $V(c) = I\sigma^2_{mpe}$; $V(g) = I\sigma^2_{ge}$; $V(e) = I\sigma^2_e$, where I is an identity matrix, σ^2_a, σ^2_m, σ^2_{mpe}, σ^2_{ge} (sire x flockyear effect) and σ^2_e are the direct additive variance, maternal additive variance, maternal permanent environmental variance, sire x flockyear variance and environmental variance respectively. All components, with the phenotypic variance (σ^2_p), being the sum of σ^2_a, σ^2_m, $\sigma_{am,}\sigma^2_{mpe}$, σ^2_{ge} and σ^2_e were derived at convergence.

Animal solutions reflecting breeding values (EBV) for the sires were obtained from two trait analyses including or excluding GxE. The sire effects for each environment were calculated as 0.5*EBV_i + S*F_ij where EBV_i was for sire_i and S*F_ij was the sire*flock interaction term for sire_i and flock_j. The

Spearman ranking correlation under the PROC CORR-procedure of SAS (SAS, 2009) was used to estimate the correlations between the ranks of the estimated breeding values so derived.

The investigation into the possible effect of GxE was extended by estimating the genetic correlation between the different environments for the respective traits. These genetic correlations were estimated using two-trait models with ASREML (Gilmour et al., 2009).

RESULTS AND DISCUSSION

The production data of the progeny from the three flocks, as well as the number of records, sires and dams are summarised in Table 9.1. The animals in the GMS and CMS were both heavier and produced more and longer wool than the two GMF lines. The two lines of the GMF and CMS produced finer wool than the GMS. Year of birth, sex, rearing status and age of the dam also affected the body weight and wool characteristics of the three studs.

Table 9.1 Least squares means depicting the effect of flock on weaning weight (WW), body weight (BW), greasy fleece weight (GFW), clean fleece weight (CFW), fibre diameter (FD) and staple length (SL) (± s.e.) of the three flocks and the number of records, sires and dams

Trait	GMS (n=13392)	CMS (n=7770)	GMFF (n=1996)	GMFC (n=1896)
WW (kg)	$26.7^a \pm 0.2$	$26.7^a \pm 0.2$	$21.1^b \pm 0.3$	$21.9^c \pm 0.3$
BW (kg)	$51.0^a \pm 0.5$	$62.2^b \pm 0.5$	$44.2^c \pm 1.1$	$47.4^{c,d} \pm 1.3$
GFW (kg)	$11.4^a \pm 0.3$	$11.3^a \pm 0.3$	$8.3^b \pm 0.3$	$8.7^{b,c} \pm 0.3$
CFW (kg)	$5.0^a \pm 0.1$	$5.3^a \pm 0.1$	$3.1^b \pm 0.1$	$3.3^{b,c} \pm 0.1$
FD (µm)	$21.1^a \pm 0.1$	$19.5^{b,d} \pm 0.1$	$18.3^c \pm 0.1$	$19.6^d \pm 0.1$
SL (mm)	$97.4^a \pm 0.7$	$100.6^b \pm 0.7$	$79.3^c \pm 0.9$	$76.6^d \pm 0.9$
Number of records	13392	7770	671	572
Number of sires	335	142	36	36
Number of dams	3709	1933	291	283

[a,b,c,d] - Values with the different superscripts differed significantly (P<0.05); GMS = Grootfontein Merino stud; CMS = Cradock fine wool Merino stud; GMFF = fine wool line of the Grootfontein Merino flock; GMFC = control line of the Grootfontein Merino flock

The Log likelihood (Log L) values for WW, BW, GFW, CFW, FD and SL are presented as a deviation from the most suitable model in Table 9.2. Log L values for the inclusion of σ^2_{ge} are presented in Table 9.3 as a deviation from the most suitable for each trait. The final model for WW included all the other random effects and for BW, GFW and CFW only the direct additive and maternal additive variance. For FD and SL only the direct additive variance was included in the final model. The Log L values in Table 9.3 indicated that the inclusion of sire x flockyear had a significant (P<0.05) effect on the estimation of the genetic parameters.

The (co)variances and variance components and ratios for WW, BW, GFW, CFW, FD and SL are summarised in Table 9.4. The ge^2 effect for WW, BW, GFW, CFW, FD and SL amounted to 0.01, 0.08, 0.10, 0.05, 0.02 and 0.03 respectively. It is evident from these results that BW and GFW are subjected to a higher level of GxE interaction compared to the other traits. Hagger (1998) and Maniatis & Pollott

(2002) reported ge^2 values of 0.04 to 0.06 for pre-weaning growth rate and 0.02 to 0.03 for pre- and post-weaning body weights respectively. Pollott & Greeff (2004) and Van Wyk et al. (2008) reported ge^2 values of about 0.02 for body weight. The ge^2 value obtained in this study for WW corresponds with these results in the literature. However, the ge^2 value for BW estimated in this study is slightly higher than the other values published in the literature.

Table 9.2 Log Likelihood deviations from the most suitable model (bold) for weaning weight (WW), body weight (BW), greasy fleece weight (GFW), clean fleece weight (CFW), fibre diameter (FD) and staple length (SL) (GxE excluded)

Trait	σ^2_a	$\sigma^2_a + \sigma^2_{mpe}$	$\sigma^2_a + \sigma^2_m$	$\sigma^2_a + \sigma^2_m + \sigma_{am}$	$\sigma^2_a + \sigma^2_m + \sigma^2_{mpe}$	$\sigma^2_a + \sigma^2_m + \sigma^2_{mpe} + \sigma_{am}$
WW	454.88	73.18	93.08	89.88	7.04	**0.00**
BW	414.08	47.58	**0.00**	-3.74	-5.74	-5.96
GFW	194.14	6.02	**0.00**	-2.82	-3.30	-3.70
CFW	54.10	42.24	**0.00**	-3.06	0.00	-3.06
FD	**0.00**	4.72	2.54	-0.74	0.04	4.72
SL	**0.00**	6.02	4.70	5.58	1.12	3.46

σ^2_a - direct additive variance; σ^2_m - maternal additive variance; σ^2_{mpe} - maternal permanent environmental variance; σ_{am}- covariance between the direct and maternal additive effects

Table 9.3 Log Likelihood deviations from the most suitable model (bold) for weaning weight (WW), body weight (BW), greasy fleece weight (GFW), clean fleece weight (CFW), fibre diameter (FD) and staple length (SL) (GxE excluded)

Trait	Most suitable model	Including σ^2_{ge} (sire x flockyear effect)
WW	**0.00**	-17.12
BW	**0.00**	-271.64
GFW	**0.00**	-174.60
CFW	**0.00**	-145.58
FD	**0.00**	-53.36
SL	**0.00**	-73.60

Pollott & Greeff (2004) estimated ge^2 values of 0.03, 0.02 and 0.005 for CFW, FD and SL respectively. Van Wyk et al. (2008) reported GxE variances amounting to 0.025 for CFW and 0.02 for FD. The values estimated in this study are in accordance with these published values. However, the ge^2 estimated for GFW (0.10) in this study is slightly higher that the value of 0.04 estimated by Pollott & Greeff (2004).

The h^2_a estimates reported by Pollott & Greeff (2004) including the GxE interaction in the model for BW (0.39), GFW (0.44) and FD (0.50) were similar to the values obtained in this study. However, their analysis did not include the maternal variance in the final models for BW and GFW. The values that were reported by Pollott & Greeff (2004) for CFW and SL are much higher than the corresponding values estimated in this study for these two traits. Maniatis & Pollott (2002) reported h^2_a, h^2_m, r_{am} and c^2_{mpe} that are in the same order for pre- and post-weaning weights than the values estimated in this study for WW.

The h^2_a and h^2_m estimates reported in the literature for 120d WW excluding ge^2 ranged from 0.10 to 0.26 and 0.05 to 0.17 respectively (Snyman et al., 1996; Rao & Notter, 2000; Cloete et al., 2001a; Duguma et al., 2002b, Van Vleck et al., 2003, Cloete et al., 2009; Chapter 3). Both these estimates obtained in this study fall in the lower end of these ranges. The c^2_{mpe} estimated in this study for WW is similar to the

values reported in the literature (Snyman et al., 1996; Rao & Notter, 2000; Duguma et al., 2002b; Van Vleck et al., 2003; Chapter 3). The r_{am} estimates reported in the literature ranged from -0.10 to 0.57 (Snyman et al., 1996; Rao & Notter, 2000; Duguma et al., 200b2; Van Vleck et al., 2003; Chapter 3) which is higher than the estimate (-0.33) obtained in this study

Table 9.4 (Co)variances and variance components and ratios (± s.e.) for weaning weight (WW), body weight (BW), greasy fleece weight (GFW), clean fleece weight (CFW), fibre diameter (FD) and staple length (SL)

Trait	WW	BW	GFW	CFW	FD	SL
σ^2_a	2.58	15.02	0.54	0.22	1.32	45.29
σ^2_m	1.12	2.03	0.06	0.03	-	-
σ_{am}	-0.33	-	-	-	-	-
σ^2_{mpe}	1.60	-	-	-	-	-
σ^2_{ge}	0.22	3.46	0.14	0.04	0.06	3.87
σ^2_e	12.81	20.58	0.7	0.4	1.01	88.99
σ^2_p	17.99	41.1	1.44	0.68	2.39	138.15
h^2_a	0.14 ± 0.02	0.37 ± 0.05	0.38 ± 0.02	0.33 ± 0.02	0.55 ± 0.02	0.33 ± 0.02
h^2_m	0.06 ± 0.01	0.05 ± 0.01	0.04 ± 0.01	0.04 ± 0.01	-	-
r_{am}	-0.19 ± 0.01	-	-	-	-	-
c^2_{mpe}	0.09 ± 0.01	-	-	-	-	-
ge^2	0.01 ± 0.00	0.08 ± 0.01	0.10 ± 0.01	0.05 ± 0.01	0.02 ± 0.00	0.03 ± 0.00

σ^2_a = direct additive variance, σ^2_m = maternal additive variance, σ_{am} = direct additive and maternal covariance, σ^2_{mpe} = maternal permanent environmental variance, σ^2_{ge} = sire by flockyear variance, σ^2_e = environmental (residual) variance, σ^2_{p-} = phenotypic variance, h^2_a = direct heritability, h^2_m = maternal heritability, r_{am} = genetic correlation between the animal effects, c^2_{mpe} = maternal permanent environmental effect, ge^2 = GxE variance ratio; "-" – Not fitted

Estimates for h^2_a and h^2_m of body weight (without GxE) reported in the literature ranged from 0.13 to 0.56 and 0.01 to 0.10 respectively (Brown et al., 2005; Safari et al., 2005; Matebesi et al., 2009a; See Chapter 3). The corresponding values for fleece weight ranged from 0.17 to 0.59 (Ponzoni et al., 1995; Safari et al., 2005; Matebesi et al., 2009a; Chapter 3) and 0.00 to 0.14 (Swan & Hickson, 1994; Lewis & Beatson, 1999; Safari et al., 2005; Matebesi et al., 2009a; Chapter 3). The h^2_a for FD and SL in the literature ranged from 0.44 to 0.77 and 0.32 to 0.63 respectively (Ponzoni et al., 1995; Swan et al., 1995; Brash et al., 1997; Purvis & Swan, 1997; Cloete et al., 1998; Hill, 2001; Wulijiet al., 2001; Matebesi et al., 2009a; Chapter 3).

The Spearman ranking correlations between the ranks for models including or excluding the sire x flockyear variance are summarised in Table 9.5. It is evident from this table that the inclusion of a sire by flockyear variance component will not lead to a substantial re-ranking of the animals in this analysis.

The genetic correlations between the same traits expressed in different environments are summarised in Table 9.6. The genetic correlation for SL between GMS and GMFC (0.98) were not different from unity

through association with the corresponding standard errors. A GxE interaction is of agriculture importance when the genetic correlation for a trait between different environments is below 0.80 (Robertson, 1959). The genetic correlations, through association with the standard errors, for WW (GMSxGMFC), FD and SL (CMSxGMFF) were higher than 0.80. These results suggest that GxE is probably not too important for these traits. The magnitude of the genetic correlations for BW and the fleece weights between the different environments indicates that there is a GxE present.

Table 9.5 Spearman rank-order correlations between the ranks obtained from models including or excluding sire x flockyear variance for the different traits

Trait	Spearman rank correlation
Weaning weight (WW)	0.996
Body weight (BW)	0.974
Greasy fleece weight (GFW)	0.961
Clean fleece weight (CFW)	0.984
Fibre diameter (FD)	0.983
Staple length (SL)	0.992

Table 9.6 Genetic correlations (± s.e.) between the same trait expressed in different environments

Trait	Flock	
	GMS x GMFC	**CMS x GMFF**
WW	0.73 ± 0.19	0.95 ± 0.10
BW	0.55 ± 0.21	0.40 ± 0.23
GFW	0.54 ± 0.17	0.52 ± 0.19
CFW	0.42 ± 0.30	0.42 ± 0.32
FD	0.74 ± 0.14	0.80 ± 0.12
SL	0.98 ± 0.08	0.80 ± 0.13

WW – Weaning weight; BW – body weight; GFW – greasy fleece weight; CFW – clean fleece weight; FD – fibre diameter; SL – staple length; GMS x GMFC = Genetic correlation between Grootfontein Merino stud (GMS) and control line of the Grootfontein Merino flock (GMFC); CMS x GMFF = Genetic correlation between Cradock Merino stud (GMS) and fine wool line of the Grootfontein Merino flock (GMFF)

Very few reports of GxE effects on wool traits are available. It was suggested by Robertson (1959) that when the genetic correlation between two genotypes is less than 0.8, the GxE interaction is of biological and agricultural importance. Dominik et al. (1999) reported genetic correlations that ranged from 0.62 ± 0.20 (CFW) to 1.00 ± 0.05 (BW and SL) between related animals kept in two specific environments for a range of production traits. It was concluded that there was not a GxE effect present for WW, FD and SL because most of the estimates were close to or higher than 0.8. The exceptions were GFW, CFW and LW where the genetic correlations between environments were all below 0.6. Results from the present study accord well with these findings. Dominik et al. (1999) stated that their genetic correlation estimates for CFW was not significantly different from 0.8, through association with the standard error. In contrast, the correlations obtained in the current study for BW, GFW, CFW and FD were higher than those reported by MacLeod et al. (1990).

In summary, the estimates obtained in the current study, as well as those in the literature indicated that the magnitude of ge^2 for body weight and fleece traits of sheep were generally below 0.10 and often

below 0.05. Furthermore, the within-trait genetic correlations among most of the traits expressed in different environments were above 0.80 which implies that GxE for that trait was not of agricultural importance. The Spearman ranking correlations support the above mentioned results, as these values were not indicative of marked re-ranking of animals. Re-ranking is assumed to be more likely in mediocre sires than in those performing best or worse for a specific trait. However, across-flock evaluation of production traits in the Merinoplan (South African performance testing scheme for Merinos) may be subject to GxE of larger magnitude.

CONCLUSIONS

It is evident from the results of this study that BW and GFW are subject to a higher level of GxE compared to the other traits. Furthermore, accounting for these relatively small GxE effects did not result in a substantial re-ranking of sires in different production environments.

However, it is important to note that the possibility of GxE needs to be considered when breeding values are estimated on a national basis where a wider range of different genotypes and environments are included in the same analysis. Ignoring GxE may lead to the estimation of biased breeding values which can have a detrimental effect on the selection of replacement animals.

CHAPTER 10. THE COMBINATION OF RECORDS OF PRODUCTION, REPRODUCTION AND SUBJECTIVE TRAITS IN A PROVISIONAL SELECTION INDEX

The indices and estimated breeding values derived for different production and reproduction traits forms the basis of the National Small Stock Improvement Scheme (NSSIS) in South Africa. The net result of such selection is an increase in production and reproduction or income per head as set out by Olivier (1999). It has to be stressed that specific production traits may contribute positively as well as negatively towards farm income. Increased body weight, for example, has a direct positive influence on income through higher carcass weight of culled ewes. It also has an indirect positive influence on income as the faster-growing progeny of such ewes can be marketed earlier. Having the lambs on the farm for a shorter period allows the farmer to keep more ewes on the same area of land. However, increased body weight of the ewe breeding flock also has an indirect negative influence on income, as heavier animals require more food. Fewer of the larger animals can therefore be kept on the same area of land when compared to smaller animals. Increased weaning percentage directly increases income as a result of more lambs available for marketing but it also has an indirect negative influence on income because a higher number of lambs require more grazing which in turn dictate that fewer ewes can be kept. Increased clean fleece weight has a direct positive influence on income through increasing the quantity of product while a decreased fibre diameter has a positive influence on income through a price premium for finer wool.

It has been shown that marked responses in different production traits of sheep can be achieved through selection based on BLUP of breeding values in Afrino sheep (Snyman, 2009) and also in two flocks of Merino sheep (Olivier, 1989; Chapter 3).

The general goal in animal breeding is to obtain a new generation of animals that will produce more efficiently than the present generation (Groen, 1990). The first steps in the development of a breeding program are the definition of the production system and the establishment of the selection objective. The objective for individual animals should be to maximise the economic benefit (profit) of the production enterprise (Charfeddine, 2000). To obtain maximum economic gain from selection, an expression of the goal for individual animals is needed and most scientists approached this problem by formulating a profit function (Harris, 1970; Ponzoni, 1988).

A profit function is a procedure or rule that describes the change in net economic returns as function of a series of physical, biological and economic parameters. The role of the profit function in animal breeding is principally to define economic weights of traits contributing to economic improvement. Therefore, profit should be defined as a function of additive genetic values of aggregate genotype traits. Other inputs such as management contributions and economic parameters should be considered as fixed. Therefore the profit function should consist of genotypic values for a given set of management and economic circumstances (Charfeddine, 2000).

The selection goal can be defined as an objective function of several traits, each with its own discounted economic value, called the aggregate genotype (Hazel, 1943) and used to represent the genetic merit of an animal. The aggregate genotype, H, for a given individual is the sum of its genotypes for different traits, each genotype being weighted by their predicted contribution to the increase in the overall objective.

H = a1BV1 + a2BV2 + …. + anBVn

where
H is the aggragate genotype
BVi: is the breeding value for trait i
ai: is the discounted economic value for trait i

Selectin for improved production and reproduction can be supported with the establishment of an index that is a combination of the production and reproduction traits and their respective economic cntribution. Herselman & Olivier (2010) derived such a model for Merino sheep that combined a five year rolling average of the wool and meat prices and the estimated breeding values of the production and reproduction traits. The objective of this study was therefore firstly to determine the economic contribution of the production and reproduction traits under different selection scenarios. Secondly, to assess and (if possible) validate the relative economic value encompassed in the present selection index prescribed by Merino SA as a selection aid for stud breeders and commercial farmers in identifying the best animals for their stud or flock.

The following information is needed to construct a selection index: the phenotypic standard deviations for each trait, the phenotypic and the relative economic value for each trait (Hazel, 1943). The economic value of a trait was defined from the wool and meat prices of the 2012-2013 wool auction season, as well as the 2000-2001 season. This was done to compare two different wool pricing scenarios, namely substantial price premiums for fibre diameter and for high wool prices, without an excessive premium for fibre diameter.

The quantification of the economical contribution of each trait under different selection scenarios were determined with the MTINDEX Excel spreadsheet for the calculation of selection index calculations (Van der Werf, 2008). Genetic information was combined with economic information to investigate the impact of a limited number of plausible selection strategies, involving a combination of qualitative and quantitative production traits.

The traits that are normally included in selection programs for Merino sheep in South Africa were used for this analysis. These traits included body weight (BW), clean fleece weight (CFW), fibre diameter (FD), staple length (SL) and staple strength (SS) measured at 15 months of age, number of lambs weaned (NLW), wool quality (WQ) and overall body conformation (BC). The phenotypic standard deviation, prices, and heritabilities of the tratis as well as the genetic and phenotypic correlations are summarised in Table

10.1. The phenotypic standard deviations, heritabilities and correlations for and among the respective traits were obtained from Chapter 3, 4 and 6.

Table 10.1 (Co)variance ratios, phenotypic standard deviations (SD) and economic weights according to prices in 2000-2001 (EW1) and in 2012-2013 (EW2) (both in ZAR) for the production, reproduction and subjective traits

Trait	BW	CFW	FD	SL	SS	NLW	WQ	BC
SD	11.69	1.35	1.59	17.16	11.11	44.65	7.72	6.99
EW1	R 19.80	R 417.10	-R 35.00	R 0.50	R 0.50	R 24.00	R 1.80	R 2.00
EW2	R 6.79	R 183.35	R 220.00	R 0.50	R 0.50	R 12.00	R 0.50	R 0.75
Heritabilities (bold on the diagonal), genetic correlations (below) and phenotypic correlations (below)								
BW	**0.49**	0.29	0.21	0.12	0.17	0.05	0.03	0.59
CFW	0.03	**0.55**	0.20	0.34	0.18	-0.06	0.17	0.24
FD	0.30	0.24	**0.63**	0.07	0.30	0.05	-0.32	0.17
SL	0.10	0.48	0.08	**0.41**	0.12	-0.04	0.17	0.26
SS	0.20	0.27	0.51	0.06	**0.26**	0.07	0.06	0.22
NLW	0.31	-0.23	0.56	0.16	0.19	**0.02**	-0.05	0.07
WQ	-0.01	0.28	-0.45	0.30	0.13	-0.21	**0.54**	0.72
BC	0.82	0.06	0.27	0.45	0.35	0.35	0.93	**0.48**

Trait definitions: BW – body weight, CFW – clean fleece weight, FD – fibre diameter, SL – staple length SS – staple strength, NLW – number of lambs weaned, WQ – wool quality, BC – body conformation

The sources of information available for selection are summarised in Table 10.2. The different selection scenarios that were considered were as follows:

1. All the information on all traits was utilised,

2. Only own body weight records were used from available replacements,

3. All body weight records from live animals were available,

4. All body weight and fibre diameter records from live animals were available,

5. Only own fibre diameter records from replacement animals were available,

6. All fibre diameter records from all live animals were available,

7. All body weight, clean fleece weight and fibre diameter records from live animals were available,

8. All number of lambs weaned records from live animals were available (by implication all female relatives in production, as the replacement animal woud not have a record of its own),

9. All body weight, clean fleece weight, fibre diameter and number of lambs weaned records from live animals were available (the closest scenario to the relative economic values provided by the NSSIS),

10. Only own wool quality and body conformation scores from live replacement animals were available,

11. All wool quality and body conformation scores from live animals were available.

The responses were predicted at a selection intensity of 1 when ~38% of the animals are selected overall. Outcomes from the calculations are expressed as responses per generation and were therefore divided by 4 years to get the response per year. The genetic gains expressed in ZAR per year for 2012/2013 are presented in Table 10.3, while the gains for 2000/2001 are presented in Table 10.4. The gains of the scenarios 2 to 11 were expressed as a percentage of the gain of scenario when using scenario 1.

Clean fleece weight had the highest contribution to the monetary gain per year for scenario 1 using the present price structure (Table 10.3). This can be expected with the current situation a very high wool price, without excessive price premiums for fibre diameter. This is also a further indication that farmers are currently making more money out of wool production than mutton or meat production. The negative contribution of fibre diameter can be ascribed to the fact that the price premium for a decrease of 1 μm is relatively small while fibre diameter is also unfavourably correlated to clean fleece weight.

Table 10.2 Sources of information used in the selection index for the production, reproduction and subjective traits

Traits	Number of records				
	Own	**Dam**	**Sire**	**Full sibs**	**Half sibs**
BW	1	1	1	0	20
CFW	1	1	1	0	20
FD	1	1	1	0	20
SL	1	1	1	0	20
SS	1	1	1	0	20
NLW	0	4	0	0	1
WQ	1	1	1	0	20
BC	1	1	1	0	20

Trait definitions: BW – body weight, CFW – clean fleece weight, FD – fibre diameter, SL – staple length
SS – staple strength, NLW – number of lambs weaned, WQ – wool quality, BC – body conformation

It is evident form Table 10.3 that the expected gains from scenarios 7 and 9 that include information on clean fleece weight are similar (>90%) to gains from scenario 1. Scenario 8 had the lowest genetic gain of all the scenarios, which were ~25% of the expected gain from scenario 1. Selection based only on body weight and/or fibre diameter information (scenarios 2 to 6) will lead to genetic gains that varied from 47.5% (scenario 2) to 67.6% (scenario 4). When selection is only based on information of subjective traits (scenarios 10 & 11) the expected genetic gains amounted to respectively 60.3% and 66.9%.

The effect of price premiums for fibre diameter is clearly visible in Table 10.4, where fibre diameter had the largest contribution to genetic gains per year in all 11 scenarios. NLW had the second highest contribution in all the scenarios, even if no selection was done for this trait. This can be attributed to the correlations among these traits. Scenarios 4 to 7 and scenario 9 will result in almost similar genetic gains (>90%) when compared to scenario 1 under the 2000-2001 pricing regime.

These calculated selection responses from the 2000-2001 and 2012-2013 wool and meat prices corresponded with the relative economic values estimated for Merino sheep in the early 2000's and currently. It can therefore be concluded that breeders and producers can use these values to identify animals that will have a positive influence on the profitability of their farming enterprises. However, it is important that care should be taken when replacement animals are selected under the current selection regime because fleece weight is presently overemphasised due to the favourable wool price. This can have a detrimental effect on the reproduction potential of the enterprise due to generally unfavourable genetic correlations between reproduction traits and fleece weight (Table 10.1; Chapter 4).

Table 10.3 Output from MTINDEX summarising the genetic gain in monetary terms for each trait under the 11 different scenarios using the 2012-2013 price structure

Trait	Scenarios monetary gain per year (ZAR)										
	1	2	3	4	5	6	7	8	9	10	11
	All traits[1]	BW[2]	BW[1]	BW & FD[1]	FD[2]	FD[1]	BW, CFW & FD[1]	NLW[1]	BW, CFW, FD & NLW[1]	WQ & BC[2]	WQ & BC[1]
BW	16.03	28.19	30.92	25.64	10.23	10.72	15.13	4.87	14.93	24.35	27.22
CFW	58.91	0.45	0.49	10.32	14.38	15.07	64.66	-9.39	62.28	5.05	4.79
FD	-5.56	-2.51	-2.75	-7.98	-9.09	-9.52	-5.87	-2.40	-5.96	-2.76	-3.24
SL	0.65	0.10	0.10	0.12	0.09	0.09	0.42	0.08	0.44	0.33	0.35
SS	0.24	0.49	0.11	0.26	0.28	0.29	0.26	0.05	0.25	0.16	0.17
NLW	23.48	17.23	18.9	35.5	34.71	36.36	11.24	30.98	16.7	28.14	32.12
WQ	0.33	0.03	0.04	-0.49	-0.73	-0.77	0.00	-0.20	-0.01	0.57	0.54
BC	1.21	1.28	1.40	1.01	0.25	0.26	0.8	0.32	0.83	1.65	1.78
Total (R)	95.28	45.26	49.21	64.38	50.11	52.5	86.64	24.31	89.47	57.48	63.72
Total (%)[3]	100.0	47.50	51.65	67.57	52.59	55.10	90.93	25.51	93.90	60.33	66.88
Accuracy	0.74	0.35	0.38	0.50	0.39	0.41	0.67	0.19	0.70	0.45	0.50

[1] – all pedigree information and records; [2] – only own record; [3] – expressed as a percentage from scenario 1; BW – body weight at 15 months of age; FD – fibre diameter at 15 months of age; CFW – clean fleece weight; SL – staple length; SS – staple strength; NLW – number of lambs weaned; WQ – wool quality; BC – body conformation; Total – total response

Table 10.4 Output from MTINDEX summarising the genetic gain in monetary terms for each trait under the 11 different scenarios using the 2000-2001 price structure

Trait	Monetary gain per year (ZAR) according to different scenarios										
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**
	All traits[1]	**BW[2]**	**BW[1]**	**BW & FD[1]**	**FD[2]**	**FD[1]**	**BW, CFW & FD[1]**	**NLW[1]**	**BW, CFW, FD & NLW[1]**	**WQ & BC[2]**	**WQ & BC[1]**
BW	5.01	9.67	10.6	5.45	3.51	3.68	4.75	1.67	4.73	8.01	9.13
CFW	15.06	0.20	0.22	6.24	6.32	6.62	15.76	-4.13	15.33	-1.53	-1.40
FD	56.73	15.76	17.28	59.29	57.14	59.87	57.1	15.1	57.4	26.31	29.07
SL	0.35	0.10	0.10	0.11	0.09	0.09	0.23	0.08	0.25	0.17	0.20
SS	0.3	0.10	0.11	0.29	0.28	0.29	0.31	0.05	0.31	0.12	0.14
NLW	18.9	8.61	9.45	18.8	17.35	18.18	15.22	15.49	17.18	16.67	18.69
WQ	-0.12	0.01	0.01	-0.2	-0.2	-0.21	-0.15	-0.06	-0.15	-0.12	-0.41
BC	0.26	0.48	0.52	0.19	0.09	0.1	0.19	0.12	0.2	0.34	1.09
Total (R)	96.49	34.92	38.3	90.17	84.58	88.61	93.4	28.33	95.26	49.95	56.51
Total (%)[3]	100.00	36.19	39.69	93.45	87.66	91.83	96.80	29.36	98.73	51.77	58.57
Accuracy	0.83	0.30	0.33	0.77	0.73	0.76	0.80	0.24	0.82	0.43	0.48

[1] – all pedigree information and records; [2] – only own record; [3] – expressed as a percentage from scenario 1; BW – body weight at 15 months of age; FD – fibre diameter at 15 months of age; CFW – clean fleece weight; SL – staple length; SS – staple strength; NLW – number of lambs weaned; WQ – wool quality; BC – body conformation; Total – total response

Furthermore, the fact that a large proportion of Merino sheep in South Africa are still selected on subjective traits will hamper the genetic progress of the Merino breed. This practice will have a negative effect on the contribution that the Merino breed can have in food security and wealth creation in South Africa. It is therefore imperative that Merino ram breeders in South Africa should start to select replacement animals on production and reproduction performance and to make these types of animals available to the broader industry for commercial production.

GENERAL CONCLUSIONS

This study set out to determine (co)variance components for the important production, reproduction and conformation traits of a South African fine wool resource flock that was established at the request of the South African wool industry. A secondary aim was to assess progeny of these animals under pastoral conditions in areas where the production of fine wool is uncommon.

The moderate to high heritability estimates in the present study linked to sufficient phenotypic variation of all the economically important production traits confirm that these traits would respond to purposeful selection should a desire for genetic change be present. The traits can also be included in well-designed selection programs based on an economic index to improve the production of fine wool Merino sheep. However, it is important to consider unfavourable genetic correlations, in particular with fibre diameter, the trait of primary interest.

The high heritability estimated obtained in the current study, as well as supporting estimates reported in the literature imply that selection for reduced fibre diameter can have an immediate and large effect in improving the fineness of a flock, thereby largely impacting on wool income. However, the low levels of phenotypic variation that can be exploited in a genetic fine wool flock will constrain genetic progress in fibre diameter. However, reducing fibre diameter in medium to strong wool flocks through the use of genetically fine sires could possibly progress at a faster rate, by upgrading with genetically fine wool rams. This is important for local Merino breeders as a large portion of wool produced in South Africa (Figure 1.1) is still above 20 µm. These breeders can therefore realise a quick and almost immediate effect in the fibre diameter of their flocks to benefit from the higher wool prices paid for finer wool. These changes should, however, be balanced against the lower wool production shown to be typical to fine wool animals compared to animals with broader wool.

As reproduction is the key to survival for South African wool farmers, improvement through selection is very important. It can be concluded from the results of this study that selection for increased reproduction is achievable. The traits that can be considered for selection are number of lambs weaned or total weight of lamb weaned per lambing opportunity. However, the reproduction potential of a flock must be considered before a decision is taken with regard to the trait that will be included in the selection objective. As a rule-of-thumb, if a flock has a poor reproduction rate (i.e. number of lambs born or weaned; <1 lamb/ewe joined), the quickest and easiest method for improvement of reproduction would be through the inclusion of number of lambs weaned as a selection criterion.

In contrast, for flocks with a high reproduction rate (>1 lamb/ewe joined) selection for TWW will be the best option, as both the quantity and quality of the lambs produced will be improved. Moreover, this option may also be important for breeders in South Africa in the harsh and arid environments where most of the sheep are kept (Cloete & Olivier, 2010). Selection for an increase in the number of lambs born to the point where a substantial number of lambs born are triplets or higher order births, can potentially adversely affect lamb survival under extensive, pastoral conditions. This is particularly true in harsh environments where lambs need to survive with the minimum assistance from the stockman.

Selection for increased reproduction can further be supported by current flock gains derived from discriminating against ewes that were barren or that produce lambs that do not survive. This selection can be augmented by selecting for traits directly related to lamb survival in ewes (i.e. rearing ability or multiple rearing ability) by culling of unproductive ewes that failed to rear lambs. The possible indirect selection options to increase survival rate are limited as genetic correlations with potential indicator traits for lamb survival rate were generally low and not significant.

Despite the economic importance of reproduction breeders are to a large extent reluctant to record the necessary data required to calculate valuable information pertaining to the reproduction potential of their flocks. The Merinoplan (Merino performance testing scheme) in South Africa generates reports that will assist breeders to identify the good reproducing ewes, as well as the poor reproducing ewes on their farms. In the current economic environment can a relative small change in reproduction result in a substantial effect on the income generated from the enterprise.

It can therefore not be emphasised enough that South African sheep farmers must start to record accurate reproduction data to ensure that they, as well as the next generation farmers, be able to satisfy the increase demand for food. This is a twofold process, unreproductive ewes should be identified and culled to allow current-flock gains, while selection for increased reproduction should be practiced to further genetically improve the reproductive ewes in the flock.

Selection for body weight, fleece weight and fibre diameter, which are the most important economic production traits, at 15 months of age will result in the desired selection gains in the expression of these traits in the adult ewe flock. This is especially important since a large proportion of the wool produced on a farm comes from adult ewes. Therefore, the reduction of fibre diameter through selection at performance testing age will have a favourable effect on the income derived from wool production. However, increasing body weight without considering the effect on the adult body weight can have a detrimental effect on the profitability of a farm. The limiting factor for Merino breeders in South Africa is the available resources for sheep production. An unconditional increase in body weight would lead to heavier ewes that will result in the reduction of the number of animals that can be maintained on a farm. Breeders should therefore take great care when body weight is a selection criterion. Selection for body weight should rather be done indirectly through selection for TWW, as these two traits are strongly and favourably correlated. It can therefore be said that larger is not always better.

The higher repeatability of fibre diameter compared to the other traits analysed and the high correlations (Random regression model) among fibre diameter measurements at different ages suggest that fibre diameter is basically controlled by the same genes throughout the lifespan of animals. It can also be suggested that genetic parameters estimated with random regression models are reliable and accurate when traits with repeated records are considered.

The relative importance of selection of replacement animals in South Africa via subjectively assessed wool and conformation traits makes it imperative that the relationships of these traits with production traits are considered. It can be concluded from the results of this study that fibre diameter will be decreased as

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an indirect response to selection for wool quality, which is the most important subjective wool trait. Moreover, selection for body weight or conformation will not have an adverse effect on the improvement of wool quality. However, the major concern with the subjective wool traits are the unfavourable correlations of belly and points, especially with creeping belly in mind, with indicators of wool price (FD and CVFD) and reproduction. These correlations imply that the finer animals will tend to have a poorer belly and points and a larger chance of being culled on creeping belly. Furthermore, discrimination against creeping belly will potentially result in potentially reproductive ewes being culled.

The relationship of BP and reproduction needs to be investigated further, as reproduction is the most important trait for small stock farmers in South Africa and the rest of the world. A possible solution may be for sheep classers to be more lenient towards ewes with creeping belly depending on subsequent research. The practice of selection or culling of animals on subjective wool and conformation traits should be implemented with great care and should not be the main selection method. Selection through subjective traits as the main selection objective will hamper selection progress in the economically important traits. It is therefore concluded that selection should rather be aimed firstly at improving the economically important traits and secondly to use extreme deviations of the subjective traits as individual culling levels.

The most important findings of the current study was the results that are in contrast to the anecdotal evidence in Australia (Swan et al., 2001) and the perceptions in South Africa that fine wool animals are appreciably smaller en poorer reproducers than medium and strong wool ewes. Body weight and reproduction is important for South African Merino breeders, as a substantial portion (70%; Olivier, 1999) of the income derived from their flocks are derived from the slaughter of surplus animals. It is evident from the results of this study that the production potential of fine wool animals is comparable with medium wool strains in South Africa under normal grazing and farming conditions. This implies that breeders can successfully produce fine wool, without compromising the growth or reproduction of animals in their flocks. This can be achieved by developing breeding plans that include the economically important traits as part of the selection objective, while also monitoring other traits of interest for unwanted changes.

The genetic progress that was achieved in the fine wool genetic resource flock that formed the basis of this study is further support that fine wool animals can be bred without adversely affecting the genetic progress in body weight, fleece weight and reproduction (Figure 3.1 and Figure 4.1). These genetic trends were achieved despite unfavourable correlations of fibre diameter with these traits. Substantial amounts of gain were achieved in the traits during the second selection stage (1996 to 2003) when the main selection criteria were to decrease fibre diameter. However, it is important to note that this was achieved by including the other traits in the selection objective. The same conclusions can be made from the selection progress made during the other two stages, where changes were desirable (albeit slower) despite the unfavourable correlations of fibre diameter with the other traits.

It can therefore be concluded that selection for fibre diameter is a viable selection objective and that substantial genetic progress can be achieved if phenotypic variation is available for exploitation. This can have a positive effect on the income derived from wool production as the market trend is towards the

production of lightweight and easy-care garments (Hatcher et al., 2010). However, selection for production and reproduction traits should not be implemented without considering other economically important wool traits. The use of estimated breeding values and genetic correlations far below unity will make it possible for breeders to select finer animals with good growth and reproduction potential, which will lead to an enhanced body weight and reproduction while also reducing fibre diameter in the next generation.

The current practices in the Merino industry through the performance testing scheme would ensure that breeders that do selection in a balanced way to allow improvement of their animals in overall profitability in the long run. This may be achieved as long as the unfavourable correlations are taken into consideration. The possible genotype by environment interaction for the production traits must be considered in the across-flock evaluation for the production and reproduction traits recorded in the Merino performance testing scheme.

The results of this study indicates that selection based on the use of estimated breeding values (EBV) in the selection of replacement animals had a profound effect on the genetic progress made over the past 22 years. It is therefore strongly recommended that sheep farmers in South Africa join the small stock improvement scheme to gain participation and access to valuable selection information to aid their selection decisions. The current generation of breeders are privileged, as they live in a technologically advanced era and on farm decisions can be made with a lot of information at hand.

For breeders to be part of this, it is important to implement selection based on EBV of economically important traits rather than just to rely on the visual appraisal of animals. However, it is important that data recording are accurate and done according to the rules and regulations of the small stock improvement schemes. Furthermore, the use of visual appraisal of animals should be limited to the identification of animals with functional cull faults and extreme deviations from expectations.

The current study intends to provide an extensive overview of the Cradock fine wool stud as a valuable resource population for the South African Merino industry. A number of key recommendations need to be made at the completion thereof. Firstly, one needs to consider the further maintenance of a resource such as this in the present era where across-flock genetic evaluations became a commonplace occurrence. It is envisaged that this flock, together with other similar South African resource flocks, may be instrumental in setting up a reference population for possible future genomic selection projects for Merinos in South Africa (Van Marle-Köster et al., 2013). Moreover, one could argue that the flock may play an important role in continued research of some issues raised in this study, such as the suggestion of deleterious genetic relationships of belly and points with key traits of economic importance, such as fibre diameter and reproduction. If this issue is to become of paramount interest for the South African sheep and wool industry, it is possibly opportune to redefine the use of the Cradock fine wool stud for doing further research on this contentious topic. Based on these arguments, the continuation of this resource flock is strongly recommended.

REFERENCES

Abegaz, S., Van Wyk, J.B. & Olivier, J.J., 2005. Model comparisons and genetic and environmental parameter estimates of growth and the Kleiber ratio in Horro sheep. S. Afr. J. Anim. Sci. 35, 30-40.

Acocks, J.P.H., 1988. Veld Types of South Africa.3rd ed. Botanical Research Institute, Dept. of Agric. and Water Supply, South Africa.

Adams, N.R. & Cronje, P.B., 2003.A review of the biology linking fibre diameter with fleece weight, liveweight, and reproduction in Merino sheep. Aust. J. Agric. Res. 54, 1-10.

Alexander, G., 1964. Lamb survival: physiological considerations. Proc. Aust. Soc. Anim. Sci. 5, 113-122.

Alexander, G., 1984. Constraints to lamb survival.In: Reproduction in sheep. Eds. D. R. Lindsay and D. T. Pearce. Australian Academy of Science in conjunction with the Australian Wool Corporation, Canberra, Australia. pp. 199-209.

Allden, W.G., 1968. Undernutrition of the Merino sheep and its sequelae. II. The influence of finite periods of arrested growth on the subsequent wool growth, fleece development and utilization of feed for wool production of lambs. Aust. J. Agric. Res.19, 639-648.

Al-Shorepy, S.A. & Notter, D.R., 1996. Genetic variation and covariation for ewe reproduction, lamb growth, and lamb scrotal circumference in a fall-lambing sheep flock. J. Anim. Sci. 74, 1490-1498.

Amer, P.R., McEwan, J.C., Dodds, K.G. & Davis, G.H., 1999. Economic values for ewe prolificacy and lamb survival in New Zzealand sheep. Livest. Prod. Sci. 58, 75-90.

Analla, M. & Serradilla, J.M., 1998. Estimation of correlations between ewe litter size and maternal effects on lamb weights in Merino sheep. Genet. Sel. Evol. 30, 493-501.

Atchley, W.R., 1998. Developmental quantative genetics: Age-specific response to selection. Proc. 6th World Congr. Genet. Appl. Livest. Prod., Armidale, NSW, Australia, 26, 505-512

Atchley, W.R., Xu, S. & Cowley, D.E., 1997. Altering developmental trajectories in mice by restricted index selection. Genet. 146, 629-640

Atkins, K.D., 1995. Strategies to reduce the average fibre diameter of the Australian wool clip. Proc. Aust. Assoc. Anim. Breed. Genet. 11, 580-586.

Atkins, K.D., Murray, J.I., Gilmour, A.R. & Luff, A.L., 1991. Genetic variation in liveweight and ultrasonic fat depth in Australian Poll Dorset Sheep. Aust. J. Agric. Res. 42, 629-640.

Bahri Binabaja, F., Tahmoorespura, M., Aslaminejada, A.A. & Vatankhah, M., 2013. The investigation of non-genetic factors affecting survival of Karakul lambs from birth to one year of age using linear and nonlinear models. Small Rumin.Res. In Press.

Baker, R.L., 1980. The role of maternal effects on the efficiency of selection in beef cattle: a review. Proc. N. Z. Soc. Anim. Prod. 40, 285-303.

Barazandeh, A., Moghbeli, S.M., Vatankhah, M. & Hossein-Zadeh, N.G., 2012. Lamb survival analysis from birth to weaning in Iranian Kermani sheep. Trop. Anim. Health Prod. 44, 929-934.

Barwick, S.A., Leymaster, K.A., Keele, J.W. & Harvey, W.R., 1990. Estimates of genetic parameters for lamb survival to weaning and birth weight in the U.S. Suffolk. Proc. Aust. Soc. Anim. Breed. Gen. 8, 331–334.

Beattie, A.W., 1961. Relationships among production characters of Merino sheep in north-western Queensland. I. Estimates of phenotypic parameters. Qld. J. Agric. Sci. 18, 437-445.

Bertrand, J.K., Berger, P.J. & Willham, R.L., 1985. Sire x environment interactions in beef cattle weaning weight field data. J. Anim. Sci. 60, 1396–1402.

Bezuidenhout, A.G., Greyling, A.C. & Jansen van Rensburg, J.M., 1994. Changes in production traits of a genetic strong-woolled Merino flock mated to genetic fine woolled rams. Karoo Agric 6 (1), 17-19.

Boligon, A.A., Mercadante, M.E.Z., Baldi, F., Lobo, R.B. & Albuquerque, L.G., 2010. Covariance functions for body weight from birth to maturity in Nellore cows. J. Anim. Sci. 88, 849-859.

Boligon, A.A., Mercadante, M.E.Z., Lobo, R.B., Baldi, F. & Albuquerque, L.G., 2012. Random regression analyses using B-spline functions to model growth of Nellore cattle. Anim. 6, 212-220.

Borg, R.C., Notter, D.R. & Kott, R.W., 2009. Phenotypic and genetic associations between lamb growth traits and adult ewe body weights in western range sheep. J. Anim. Sci. 87, 3506-3514.

Boujenane, I., Chikhi, A., Sylla, M. & Ibnelbachyr, M., 2013. Estimation of genetic parameters and genetic gains for reproductive traits and body weight of D'man ewes. Small Rumin. Res. 113, 40-46.

Brand, T.S. & Franck, F., 2000. Production responses of two genetic different types of Merino sheep to different nutritional levels. Small Rumin. Res. 37, 85-91.

Brash, L.D., Fogarty, N.M., Barwick, S.A. & Gilmour, A.R., 1994a. Genetic parameters for Australian maternal and dual-purpose meatsheep breeds. I. Liveweight, wool production and reproduction in Border Leicester and related types. Aust. J. Agric. Res. 45, 459-468.

Brash, L.D., Fogarty, N.M. & Gilmour, A.R., 1994b. Genetic parameters for Australian maternal and dual-purpose meatsheep breeds. II. Liveweight, wool and reproduction in Corriedale sheep. Aust. J. Agric. Res. 45, 469-480.

Brash, L.D., Fogarty, N.M. & Gilmour, A.R., 1994c. Genetic parameters for Australian maternal and dual-purpose meatsheep breeds. III. Liveweight, fat depth and wool production in Coopworth sheep. Aust. J. Agric. Res. 45, 481-486.

Brash, L.D., Fogarty, N.M. & Gilmour, A.R., 1994d. Reproductive performance and genetic parameters for Australian Dorset Sheep. Aust. J. Agric. Res.45, 427-441.

Brash, L.D., Taylor, P.J. & Gilmour, A.R., 1997. Estimates of genetic parameters and environmental effects for production traits in young Merino rams. Proc. Assoc. Advmt. Anim. Breed. Genet. 12, 529-533.

Brien, F.D., Hebart, M.L., Smith, D.H., Hocking Edwards, J.E., Greeff, J.C., Hart, K.W., Refshauge, G., Bird-Gardiner, T.L., Gaunt, G., Behrendt, R., Robertson, M.W., Hinch, G.N., Geenty, K.G. & Van der Werf, J.H.J., 2010. Opportunities for genetic improvement of lamb survival. Anim. Prod. Sci. 50, 1017-1025.

Bromley, C.M., Snowder, G.D. & Van Vleck, L.D., 2000. Genetic parameters among weight, prolificacy, and wool traits of Columbia, Polypay, Rambouillet, and Targhee sheep. J. Anim. Sci. 78, 846-858.

Bromley, C.M., Van Vleck, L.D. & Snowder, G.D., 2001. Genetic correlations for litter weight weaned with growth, prolificacy, and wool traits in Columbia, Polypay, Rambouillet and Targhee sheep. J. Anim. Sci. 79, 339-346.

Brown, D.J., Atkins, K. & Huisman, A.E., 2005. Expression of body weight, fleece weight and fibre diameter in across flock genetic evaluation. Proc. Assoc. Advmt. Anim. Breed. Genet. 16, 481-491.

Brown, D.J., Ball, A., Mortimer, R. & Oppenheimer, M., 2002a. Incorporating subjectively assessed sheep and wool traits into genetic evaluations for Merino sheep 1: Phenotypic variation and heritabilities. Wool Tech. Sheep Breed. 50, 373-377.

Brown, D.J., Ball, A., Mortimer, R. & Oppenheimer, M., 2002b. Incorporating subjectively assessed sheep and wool traits into genetic evaluations for Merino sheep 2: Phenotypic and genetic correlations. Wool Tech. Sheep Breed. 50, 378-382.

Brown, D.J., Swan, A.A. & Gill, J.S., 2010. Within- and across-flock genetic relationships for breech flystrike resistance indicator traits. Anim. Prod. Sci. 50, 1060-1068.

Brown, D.J., Swan, A.A. & Gill, J.S., 2013. Genetic correlations across ages for greasy fleece weight and fibre diameter in Merino sheep. Proc. Assoc. Advmnt. Anim. Breed. Genet. 20, 110-113.

Brown, G.H., Turner, H.N. & Dolling, C.H.S., 1968. Vital statistics for an experimental flock of Merino sheep V. The effects of age of ram, maternal handicap, and year of measurement on 10 wool and body characteristics for unselected rams. Aust. J. Agric. Res. 19, 825-835.

Brown, G.H., Turner, H.N., Young, S.S.Y. & Dolling, C.H.S., 1966. Vital statistics for an experimental flock of Merino sheep III.Factors affecting wool and body characteristics, including the effect of age of ewe and its possible interaction with method of selection. Aust. J. Agric. Res. 17, 557-581.

Bunge, R., Thomas, D.L. & Stookey, J.M., 1990. Factors affecting productivity of Rambouillet ewes mated to ram lambs. J. Anim. Sci. 68, 2253-2262.

Cameron, N.D. & Curran, M.K., 1995. Genotype with feeding regime interaction in pigs divergently selected for components of efficient lean growth rate. Anim. Sci. 61, 123–132.

Cardoso, F.F. & Tempelman, R.J., 2012. Linear reaction norm models for genetic merit prediction of Angus cattle under genotype by environment interaction. J. Anim. Sci. 90, 2130-2141.

Casellas, J., Caja, G. & Piedrafita, J., 2007. Genetic determinism for within-litter birth weight variation and its relationship with litter weight and litter size in the Ripollesa ewe breed. Anim. 1, 637-644.

Ceyhan, A., Sezenler, T. & Erdoğan, I., 2009. The estimation of variance components for prolificacy and growth traits of Sakız sheep. Livest.Sci.122, 68-72.

Chapman, R.E. & Bassett, J.M., 1970. The effects of prolonged administration of cortisol on the skin of sheep on different planes of nutrition. J. Endocrin. 48, 649-663.

Clarke, B.E., Brown, D.J. & Ball, A.J., 2003. Preliminary genetic parameters for live weight and ultrasound scan traits in Merinos. Proc. Assoc. Advmt. Anim. Breed. Genet. 15, 326-330.

Cloete, S.W.P., Gilmour, A.R., Olivier, J.J. & Van Wyk, J.B., 2003a. Age trends in economically important traits of Merino ewes subjected to 10 years of divergent selection for multiple rearing ability. S. Afr. J. Anim. Sci. 33, 43-51.

Cloete, S.W.P., Gilmour, A.R., Olivier, J.J. & Van Wyk, J.B., 2004. Genetic and phenotypic trends and parameters in reproduction, greasy fleece weight and liveweight in Merino lines divergently selected for multiple rearing ability. Aust. J. Exp. Agric. 44, 745-754.

Cloete, S.W.P., Greeff, J.C. & Lewer, R.P., 2001a. Genetic and phenotypic relationships of reproduction with live weight and wool traits in a Mediterranean environment. Proc. Assoc. Advmt. Anim. Breed. Genet. 14, 425-428.

Cloete, S.W.P., Greeff, J.C. & Lewer, R.P., 2002a. Direct and maternal genetic (co)variances for hogget liveweight and fleece traits in Western Australian Merino sheep. Aust. J. Agric. Res. 53, 271-279.

Cloete, S.W.P., Greeff, J.C. & Lewer, R.P., 2002b. Genetic and environmental variances in lamb production traits of Merino ewes in a Mediterranean environment. Wool Tech. Sheep Breed. 50, 395-400.

Cloete, S.W.P., Greeff, J.C. & Lewer, R.P., 2002c. Heritability estimates and genetic and phenotypic correlations of lamb production parameters with hogget liveweight and fleece traits in Western Australian Merino sheep. Aust. J. Agric. Res. 53, 281-286.

Cloete, S.W.P., Misztal, I. & Olivier, J.J., 2009. Genetic parameters and trends for lamb survival and birth weight in a Merino flock divergently selected for multiple rearing ability. J. Anim. Sci. 87, 2196-2208.

Cloete, S.W.P. & Olivier, J.J., 2010. South African Sheep and Wool Industry.In: The International Sheep and Wool Handbook.Ed. D.J. Cottle.Nottingham University Press, Manor Farm, Thrumpton, Nottingham NG11 0AX, United Kingdom. pp. 95-1120

Cloete, S.W.P., Olivier, J.J. & Du Toit, E., 1992. Linear type traits in a Merino flock subjected to selection for increased clean fleece mass and unselected control flock. S. Afr. J. Anim. Sci. 22, 70-73.

Cloete, S.W.P., Olivier, J.J. & Du Toit, E., 2013. Genetic trends in a Merino line selected for a reduced fibre diameter relative to an unselected control flock.Proc. Assoc. Advmt. Anim. Breed. Genet. 20, 377-380.

Cloete, S.W.P., Olivier, J.J., Snyman, M.A. & Du Toit, E., 1998a. Genetic parameters and trends in a selection experiment for increased clean fleece weight involving South African Merinos. Aust. J. Exp. Agric. 38, 427-432.

Cloete, S.W.P., Olivier, J.J. & Van Wyk, J.B., 2006. Twenty years of divergent selection for reproduction-genetic parameter and genetic change. Proc. 41[St] S. Afr. Soc. Anim. Sci. 3-6 April 2006, Bloemfontein, South Africa, 131.

Cloete, S.W.P., Olivier, J.J., Van Wyk, J.B., Erasmus, G.J. & Schoeman, S.J., 2003b. Genetic parameters and trends for birth weight, birth coat score and weaning weight in Merino lines divergently selected for ewe multiple rearing ability. S. Afr. J. Anim. Sci. 33, 248–256.

Cloete, S.W.P., Schoeman, S.J., Coetzee, J. & Morris, J.D., 2001b. Genetic variances for liveweight and fleece traits in Merino, Dohne Merino and South African Mutton Merino sheep. Aust. J. Exp. Agric. 41, 145-153.

Cloete, S.W.P., Scholtz, A.J. & Aucamp, B.B., 1998b. Environmental effects, heritability estimates and genetic trends in a Western Cape Dohne Merino nucleus flock. S. Afr. J. Anim. Sci. 28, 185-195.

Cloete S.W.P. & Scholtz, A.J., 1998. Lamb survival in relation to lambing and neonatal behaviour in medium wool Merino lines divergently selected for multiple rearing ability. Aust. J. Exp. Agric. 38, 801-811.

Coelli, K.A., Atkins, K.D., Casey, A.E. & Semple, S.J., 2000. 'Merino Bloodlines: The Comparisons: 1989-1999.' (Agnote DAI-52, NSW Agriculture: Orange, NSW.)

Coelli, K.A., Gilmour, A.R. & Atkins, K. D., 1998. Comparison of genetic covariance models for annual measurements of fleece weight and fibre diameter. Proc. 6th World Congr. Genet. Appl. Livest. Prod. 24, 31-34.

Conington, J., Bishop, S.C., Waterhouse, A.W. & Simm, G., 2004. A bioeconomic approach to derive economic values for pasture based sheep genetic improvement programs. J. Anim. Sci. 82, 1290-1304.

Corbett, J.L., 1979. In "Physiological and environmental limitations to wool growth" Eds. J.L. Black and P.J. Reis, The University of New England, Armidale Australia.p.79.

Cottle, D.J., 1994. Wool prices and sheep breeding objectives - a historical perspective. Aust. J. Agric. Res. 45, 1671-1681.

Cundiff, L.V., Gregory, K.E., & Koch, R.M., 1982. Selection for increased survival from birth to weaning. Proc. 2nd World Congr. Genet. Appl. Livest. Prod. Madrid, Spain. 310-337.

Dalton, D.C., Knight, T.W. & Johnson, D.L., 1980. Lamb survival in sheep breeds on New Zealand hill country. N. Z. J. Agric. Res. 23, 167-173.

Davis, G.P., 1987. Genetic relationships between lamb growth and lifetime productivity in Merino sheep. Ph.D. dissertation, University of New England, Australia.

Di, J., Zhang, Y., Tian, K., Lazate, K.C., Liu, J., Xu, X., Zhang, Y. & Zhang, T., 2011. Estimation of (co)variance components and genetic parameters for growth and wool traits of Chinese superfine Merino sheep with the use of a multi-trait animal model. Livest. Sci. 138, 278-288.

Dickerson, G.E., 1962. Implications in genetic-environmental interaction in animal breeding. Anim. Prod. 4, 47-63.

Dohm, M.R., 2002. Repeatability estimates do not always set an upper limit to heritability. Func. Ecol. 16, 273-280.

Dominik, S., Crook, B.J. & Kinghorn, B.P., 1999. Genotype x management interaction on wool production traits and bodyweight in Western Australian Merino sheep. Proc. Assoc. Advmt. Anim. Breed. Genet. 13, 98-101.

Dominik, S. & Kinghorn, B.P., 2008. Neglecting genotype x environment interaction results in biased predictions from selection index calculations. Livest. Sci. 114, 233-240.

Donoghue, K.A., Rekaya, R., Bertrand, J.K. & Misztal, I., 2004. Threshold-linear analysis of measures of fertility in artificial insemination data and days to calving in beef cattle. J. Anim. Sci. 82, 987–993.

Duerden, J. E., 1929. Standards of thickness and crimps in Merino grease wools. J. Text. Inst. 20, T 93-100.

Duguma, G., Cloete, S.W.P., Schoeman, S.J. & Jordaan, G.F., 2002a. Genetic parameters of testicular measurements in Merino rams and the influence of scrotal circumference on total flock fertility. S. Afr. J. Anim. Sci. 32, 76-82.

Duguma, G., Schoeman, S.J., Cloete, S.W.P. & Jordaan, G.F., 2002b. Genetic parameter estimates of early growth traits in the Tygerhoek Merino flock. S. Afr. J. Anim. Sci. 32, 66-75.

Dunlop, A.A., 1962. Interactions between heredity and environment in the Australian Merino. I. Strain X location interactions in wool traits. Aust. J. Agric. Res. 13, 503-531.

Dunlop, A.A., 1963. Interactions between heredity and environment in the Australian Merino. 11. Strain X location interactions in body traits and reproductive performance. Aust. J. Agric. Res. 14, 690-703.

Dwyer, C.M., 2007. Genetic and physiological determinants of maternal behaviour and lamb survival: implications for low-input sheep management. J. Anim. Sci. 86 (Suppl. E), E246–E258.

Dwyer, C.M., 2008. The welfare of the neonatal lamb. Small Rumin. Res. 76, 31-41.

Dwyer, C.M. & Morgan, C.A., 2006. Maintenance of body temperature in the neonatal lamb: effects of breed, birth weight and litter size. J. Anim. Sci. 84, 1093–1101.

Eales, F.A., Small, J. & Gilmour., J., 1983. Neonatal mortality of lambs and its causes. In: Sheep Production. Ed. W. Haresign. Butterworths, London, UK. pp. 289-298.

Ebenman, B., & Persson, L., 1988. The Dynamics of Size-Structured Populations. Springer-Verlag, Berlin.

Echternkamp, S.E., Thallman, R.M., Kappes, S.M. & Gregory, K.E., 2002. Increased twinning and cow productivity in beef cattle selected for ovulation and twinning rate. In: Proc. 7th World Congr. Genet. Appl. Livest. Prod.CD-ROM communication no. 08-12, 4, pp., Cedex, France.

Eler, J.P., Van Vleck, L.D., Ferraz, J.B. & Lôbo, R.B., 1995. Estimation of variances due to direct and maternal effects for growth traits of Nelore cattle. J. Anim. Sci. 73, 3253-3258.

Erasmus, G.J. & Delport, G.J., 1987. Factors influencing the price of greasy fleece wool in South Africa. S. Afr. J. Anim. Sci. 17, 111-115.

Ercanbrack, S.K. & Knight, A.D., 1998. Responses to various selection protocols for lamb production in Rambioullet, Targhee, Columbia and Polypay sheep. J. Anim. Sci. 76, 1311-1325.

Everett-Hincks, J.M., Lopez-Villalobos, N., Blair, H.T. & Stafford, K.J., 2005. The effect of ewe maternal behaviour score on lamb and litter survival. Livest. Prod. Sci. 93, 51–61.

Falconer, D.S., 1952. The problem of environment and selection. Am. Nat. 86, 293–298.

Falconer, D.S., 1989. Introduction to quantative genetics.3rd Ed. p 139.

Falconer, D.S. & Mackay, T.F.C., 1996. Introduction to quantitative genetics. 4th Ed Longman Group Ltd. Harlow, UK.

Fischer, T.M., Van der Werf, J.H.J., Banks, R.G. & Ball, A.J., 2004. Description of lamb growth using random regression on field data. Livest. Prod. Sci. 89, 175-185

Fitzhugh, H.A., 1976. Analysis of growth curves and strategies for altering their shapes. J. Anim. Sci. 33, 1036-1051.

Fogarty, N.M., Brash, L.D., Gilmour, A.R., 1994.Genetic parameters for reproduction and lamb production and their components and liveweight, fat depth and wool production in Hyfer sheep. Aust. J. Agric. Res. 45, 443-457.

Fogarty, N.M., Dickerson, G.E. & Young, L.D., 1985. Lamb production and its components in pure breeds and composite lines. III. Genetic parameters. J. Anim. Sci. 60, 40–57.

Fogarty, N.M., Hopkins, D.L. & Van de Ven, R., 2000. Lamb production from diverse genotypes. 1. Lamb growth and survival and ewe performance. Anim. Sci. 70, 135–145.

Fogarty, N.M., Safari, E., Gilmour, A.R., Ingham, V.M., Atkins, K.D., Mortimer, S.I.,Swan, A.A., Brien, F.D., Greeff, J.C. & Van der Werf , J.H.J., 2006. Wool and meat genetics — the joint possibilities. Proc. Aust. Sheep Indust. CRC Conf. 36-41.

Galpin, N., 1948. A Study of wool growth.II Mean fibre thickness, density of fibre population, the area of skin covered by fibre and the mean fibre length. J. Agric. Sci. 38, 303-314.

Gama, L.T., Dickerson, G.E., Young, L.D. & Leymaster, K.A., 1991. Effects of breed, heterosis, age of dam, litter size, and birth weight on lamb mortality. J. Anim. Sci. 69, 2727–2743.

Garnsworthy, R.H., Gully, R.L., Kandian. R.P., Kenins, P., Mayfield, RJ. & Westerman, R.A., 1988. Report G64 CSIRO Division of Wool Technology.

Gilmour, A.R., Gogel, B.J., Cullis, B.R. & Thompson, R., 2009.ASReml User Guide Release 3.0 VSN International Ltd, Hemel Hempstead, HPI 1ES, UK.

Greeff, J.C. & Karlsson, L.J.E., 1998. The genetic relationship between faecal consistency, faecal worm egg counts and wool traits in Merino sheep. Proc. 6th World Congr. Genet. Appl. Livest. Prod., Armidale, Australia 24, 63-66.

Greeff, J.C. & Karlsson, L.J.E., 1999. Will selection for decrease faecal worm egg count result in an increase in scouring? Proc. Assoc. Advmt. Anim. Breed. Genet. 13, 508-511.

Greeff, J.C., Karlsson, L.J.E. & Schlink, C.A., 2013. Identifying indicator traits for breech strike in Merino sheep in a Mediterranean environment. Anim. Prod. Sci. http://dx.doi.org/10.1071/AN12233

Green, L.E. & Morgan, K.L., 1993. Mortality in early born, housed lambs in south-west England. Prev. Vet. Med. 17, 251–261.

Gregory, I.P., 1982. Genetic studies of South Australian Merino sheep. III. Heritabilities of various wool and body traits. Aust. J. Agric. Res. 33, 355-362.

Groenewald, P.G.J., Olivier, J.J. & Olivier, W.J., 1999. Heritability estimates for Merino sheep obtained from a national progeny test. S. Afr. J. Anim. Sci. 29, 174-178

Gudex, B.W., Hickford, J.G.H. & Frampton, C.M., 2005. Sireline differences in lamb losses from starvation-exposure. Proc. N. Z. Soc. Anim. Prod. 65, 186–190.

Hagger, C. 1998. Litter, permanent environmental, ram-flock and genetic effects on early weight gain of lambs. J. Anim. Sci. 76, 452–457.

Hall, D.G., Gilmour, A.R. & Fogarty, N.M., 1994. Variation in reproduction and production of Poll Dorsets. Aust. J. Agric. Res. 45, 415-426.

Hanford, K.J., Van Vleck, L.D. & Snowder, G.D., 2002. Estimates of genetic parameters and genetic change for reproduction, weight, and wool characteristics of Columbia sheep.J. Anim. Sci. 80, 3086-3098.

Hanford, K.J., Van Vleck, L.D. & Snowder, G.D., 2006.Estimates of genetic parameters and genetic trends for reproduction, weight and wool characteristics of Polypay sheep. Livest. Prod. Sci. 102, 72-82.

Hansen, C. & Shrestha, J.N.B., 1999. Estimates of genetic and phenotypic correlations for ewe productivity traits of three breeds under 8-month breeding cycles and artificial rearing of lambs. Small Rumin. Res. 32, 1-11.

Hansen, C. & Shrestha, J.N.B., 2002. Consistency of genetic parameters of productivity for ewes lambing in February, June and October under an 8-month breeding management. Small Rumin. Res. 44, 1-8.

Hatcher, S. & Atkins, K.D., 2000. Breeding objectives which include fleece weight and fibre diameter do not need fibre curvature. Asian-Aus. J. Anim. Sci. 13 Supplement A, 293-296.

Hatcher, S., Atkins, K.D., Coelli, K.A. & Thornberry, K.J., 2000. In 'Finewool 2000 Breeding for Customer Needs.'Eds A.A. Swan & L.R. Piper. CSIRO Livestock Industries and The Woolmark Company: Australia. pp. 37-44.

Hatcher, S., Atkins, K.D. & Safari, E., 2010. Lamb survival in Australian Merino sheep: A genetic analysis. J. Anim. Sci. 88, 3198-3205.

Hatcher, S., Atkins, K.D. & Thornberry, K.J., 2004. 'Extreme ewes' - an investigation of the relationship between clean fleece weight, fibre diameter and bodyweight. Anim. Prod. Aust. 25, 81-84.

Hatcher, S., Atkins, K.D. & Thornberry, K.J., 2005. Age changes in wool traits of Merino sheep in Western NSW. Proc. Assoc. Advmt. Anim. Breed. Genet. 16, 314-318.

Hatcher, S., Hynd, P.I., Thornberry, K.J. & Gabb, S. 2010. Can we breed Merino sheep with softer, whiter, more photostable wool? Anim. Prod. Sci. 50, 1089-1097.

Haughey, K.G., 1983. Selective breeding for rearing ability as an aid to improving lamb survival. Aust. Vet. J. 60, 361-363.

Haughey, K.G., 1991. Perinatal lamb mortality—Its investigation, causes and control. J. S. Afr. Vet. Assoc. 62,78-91.

Herselman, M.J., 2002. The role of simulation models in agricultural extension. Proc. GSSA/SASAS Joint Congress.46, Christiana Aventura, 13-17 May.

Herselman, M.J., 2004.Description of a model for the calculation of breeding values for profitability. Proc. 40th S. Afr. Soc. Anim. Sci., 28 June – 1 July, Goudini, South Africa, 101

Herselman, M.J. & Olivier, W.J., 2010. Description of a model for the calculation of breeding values for profitability. Grootfontein Agric. 10, 67-75.

Herselman, M.J., Olivier, W.J. & Snyman, M.A., 2006. Determining the relationship between staple strength and production and subjectively assessed wool traits. Proc. 41 st S. Afr. Soc. Anim. Sci. 3-6 April 2006, Bloemfontein, South Africa.41, 95.

Herselman, M.J. & Van Heerden, M, 2013. Lamb survival in intensive vs. extensive lambing systems with Dohne Merino sheep. Proc. 46th S. Afr. Soc. Anim. Sci., 23-26 June 2013, Bloemfontein, 28.

Hickson, J., Kinghorn, B., Swan, A. & Piper, L., 1994. The relationship between hogget and adult production traits in Merino sheep. Proc. 5th World Congr. Genet.Appl. Livest. Prod. 18, 139-142.

Hight, G.K. & Jury, K.E., 1970. Hill country sheep production. II. Lamb mortality and birth weights in Romney and Border Leicester × Romney flocks. N. Z. J. Agric. Res. 13, 735–752.

Hill, J.A., 2001. Phenotypic and genetic parameters for the S.A. strongwool Merino strain with an emphasis on skin characters as early indicators of wool productivity. PhD Thesis, University of Adelaide, Adelaide, Australia.

Hinch, G.N., Kelly, R.W., Owens, J.L. & Crosbie, S.F., 1983. Patterns of lamb survival in high fecundity Booroola flocks. Proc. N. Z. Soc. Anim. Prod. 43, 29-32.

Huisman, A.E. & Brown, D.J., 2008. Genetic parameters for bodyweight, wool, and disease resistance and reproduction traits in Merino sheep. 2. Genetic relationships between bodyweight traits and other traits. Aust. J. Exp. Agric. 48, 1186-1193.

Huisman, A.E. & Brown, D.J., 2009. Genetic parameters for bodyweight, wool, and disease resistance and reproduction traits in Merino sheep. 4. Genetic relationships between and within wool traits. Anim. Prod. Sci. 49, 289-296.

Huisman, A.E., Brown, D.J., Ball, A.J. & Graser, H.-U., 2008. Genetic parameters for bodyweight, wool, and disease resistance and reproduction traits in Merino sheep. 1. Description of traits, model comparison, variance components and their ratios. Aust. J. Exp. Agric. 48, 1177-1185.

Huisman, A.E., Veerkamp, R.F. & Van Arendonk, J.A.M., 2002. Genetic parameters for various random regression models to describe the weight data of pigs. J. Anim. Sci. 80, 575-582.

Hunter, L., Van Wyk, J.B., De Wet, P.J., Grobbelaar, P.D., Pretorius, P.S., Morris, J. de V. & Leeuner, W., 1990. The effect of nutritional and lambing stress on wool fibre and processing characteristics. Wool Technol. Sheep Breed. (Sep., 1990 / Oct., 1990 & Dec., 1990 / Jan., 1991), 89-91d.

Huquet, B., Leclerc, H. & Ducrocq, V., 2012. Modelling and estimation of genotype by environment interactions for production traits in French dairy cattle. Gen. Sel. Evol.44, 35-48.

Hynd, P.I., Hughes, A., Earl, C.R. & Penno, N.M., 1997. Seasonal changes in the morphology of wool follicles in Finewool and Strongwool Merino strains at different stocking rates in southern Australia. Aust. J. Agric. Res. 48, 1089-1097.

Ingham, V.M. & Ponzoni, R.W., 2002. Genetic parameters for reproduction and fleece traits for South Australian Merino sheep. Proc. 7th World Congr. Genet. Appl. Livest. Prod.Montpellier, France, August 19-23, CD-ROM Communication No 12-04.

Ingham, V.M., Ponzoni, R.W., Gilmour, A.R. & Pitchford, W., 2003. Genetic parameters for weight, fat and eye muscle depth in South Australian Merino sheep. Proc. Assoc. Advmt. Anim. Breed. Genet. 15, 322-325.

Interbull, 2000. National Genetic Evaluation Programmes for Dairy Production Traits Practised in Interbull Member Countries, 1999-2000. Department of Animal Breeding and Genetics, Uppsala, Bulletin 24.

Jackson, N. & Roberts, E.M., 1970. Comparison of three Australian Merino strains for wool and body traits. I. Genetic means of studs and strains and their interactions with years and sexes. Aust. J. Agric. Res. 21, 815-835.

James, P.J., Ponzoni, R.W., Walkley, J.R.W. & Whiteley, K.J., 1990. Genetic parameters for wool production and quality traits in South Australian Merinos of the Collinsville family group Aust. J. Agric. Res. 41, 583–594.

Jamrozik, J., Schaeffer, L.R. & Dekkers, J.C., 1997. Genetic evaluation of dairy cattle using test day yields and random regression model. J. Dairy Sci. 80, 1217-1226.

Kariuki, C.M., Ilatsia, E.D., Wasike, C.B., Kosgey, I.S. & Kahi, A.K., 2010.Genetic evaluation of growth of Dorper sheep in semi-arid Kenya using random regression models. Small Rumin. Res. 93, 126-134.

Kebsi, F.G., Eskandarinasab, M. & Shahir, M.H., 2008. Estimation of direct and maternal effects on body weight in Mehraban sheep using random regression models. Arch. Tierz. 51, 235-246.

Kemper, K.E., Smith, J.L. & Purvis, I.W., 2003. The value of birth coat score as an early selection criterion for superfine Merino sheep. Proc. Assoc. Advmt Anim. Breed. Genet. 15, 139-142.

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

Kleemann, D.O., Grosser, T.I. & Walker, S.K., 2006. Fertility in South Australian commercial Merino flocks: aspects of management. Theriogen. 65, 1649-1665.

Knight, T.W., Lynch, P.R., Hall, D.R.H. & Hockey, H.U.P., 1988. Identification of factors contributing to the improved lamb survival in Marshall Romney sheep. N. Z. J. Agric. Res. 31, 259–271.

Konstantinov, K.V., Beard, K.T., Goddard, M.E. & Van der Werf, J.H.J., 2009. Genetic evaluation of Australian dairy cattle for somatic cell scores using multi-trait random regression test-day model. J. Anim. Breed. Genet. 126, 209–215.

Krejcova, H., Mielenz, N., Pribyl, J., Schuler, L., 2007. Comparison of breeding values for daily gains of bulls estimated with multi-trait and random regression models. Arch. Tierz. 2, 147-154.

Kuchel, R.C. & Lindsay, D.R., 1999. Maternal behaviour and the survival of lambs in superfine wool sheep. Reprod. Fert. Dev. 11, 391-394.

Lang, W.R., 1945. Growth in tender wool. J. Text. Inst. 36, T243-252.

Lee, G.J. & Atkins, K.D., 1994. The use of reproductive performance in early life to predict lifetime reproductive rate in Australian Merinos. Proc. 5th World Congr. Genet. Appl. Livest. Prod. 18, 87–90.

Lee, G.J., Atkins, K.D. & Sladek, M.A., 2009. Genetic parameters for lifetime reproductive performance of Merino ewes. Proc. Assoc. Advmt. Anim. Breed. Genet. 18, 382-385.

Lee, G.J., Atkins, K.D. & Swan A.A., 2002a. Pasture intake and digestibility by young and non-breeding adult sheep: the extent of genetic variation and relationships with productivity. Livest. Prod. Sci. 73, 185-198.

Lee, D., Misztal, I., Bertrand, J.K. & Rekaya., R., 2002b. National evaluation for calving ease, gestation length and birth weight by linear and threshold model methodologies. J. Appl. Genet. 43, 209–216.

Lee, J.W., Waldron, D.F. & Van Vleck, L.D., 2000. Parameter estimates for greasy fleece weight of Rambouillet sheep at different ages. J. Anim. Sci. 78, 2108-2112.

Lewer, R.P. & McLeod, I.M., 1990. One-and two-stage selection indexes for Australian Merino sheep incorporating visual selection criteria. Proc. 4th World. Congr. Genet. Appl. Livest. Prod. XV, 61-64.

Lewer, R.P., Rae, A.L. & Wickham, G.A., 1983. Analysis of records of a Perendale flock. V. Repeatabilities and genetic correlations between ages. N. Z. J. Agric. Res. 26, 315-319.

Lewer, R.P., Woolaston, R.R. & Howe, R.R., 1994. Studies on Western Australian Merino sheep 2. Genetic and phenotypic parameter estimates for objectively measured traits on ram and ewe hoggets using different model types. Aust. J. Agric. Res. 45, 829-840.

Lewer, R.P., Woolaston, R.R. & Howe, R.R., 1995. Studies of Western Australian Merino sheep. III Genetic and phenotypic parameter estimates for subjectively assessed and objectively measured traits in ewe hoggets. Aust. J. Agric. Res. 46, 379-388.

Lewis, R.M. & Beatson, P.R., 1999. Choosing maternal-effect models to estimate (co)variances for live and fleece weight in New Zealand Coopworth sheep. Livest. Prod.Sci. 58, 137-150.

Lewis, R.M. & Brotherstone, S., 2002. A genetic evaluation of growth in sheep using random regression techniques. Anim. Sci. 74, 63-70.

Li, Y., Swan, A.A. & Purvis I., 1999. Genetic variation in resistance to fleece rot in CSIRO's fine wool flock. Proc. Assoc. Advmt. Anim. Breed. Genet. 13, 524-527.

Lindner, H.R. & Ferguson, K.A., 1956. Influence of the adrenal cortex on wool growth and its relation to break and tenderness of the fleece. Nature (London) 177, 188-189.

Lindsay, D.R., Nowak, R., Gede Putu I. & McNeill, D., 1990. Behavioural interactions between the ewe and her young at parturition: a vital stop for the lamb. In: Reproductive Physiology of Merino Sheep. Concepts and Consequences. Eds Oldham, C.M., Martin, G.B. & Purvis, I.W. The University of Western Australia: Perth, pp. 191-205.

Lopez-Villalobos, N. & Garrick., D.J., 1999. Genetic parameter estimates for lamb survival in Romney sheep. Proc. N. Z. Soc. Anim. Prod. 59, 121-124.

Lupton, C.J., Huston, J.E., Craddock, B.F., Pfeiffer, F.A. & Polk, W.L., 2007. Comparison of three systems for concurrent production of lamb meat and wool. Small Rumin. Res. 72, 133-140.

Lush, J.L., 1937. Animal Breeding Plans. Collegiate Press, Inc., Ames.

Lynch, M. & Walsh, B., 1998. Genetics and analysis of quantitative traits.1st Ed. Sinauer Associates, Inc. Sunderland, MA.

Lyne, A.G., 1964. Effect of adverse nutrition on the skin and wool follicles in Merino sheep. Austr. J. Agric. Res. 15, 788-801.

MacLeod, I.M., Howe, R.R., Lewer, R.P. & Woolaston, R.R., 1990. Genotype by environment interactions among Merino sheep in Western Australia. Proc. Aust. Assoc. Anim. Breed Genet. 8, 303-306.

Malik, R.C. & Acharya, R.M., 1972. A note on factors affecting lamb survival in Indian sheep. Anim. Prod. 14, 123-125.

Mandal, A., Prasad, H., Kumar, A., Roy, R. & Sharma, N., 2007. Factors associated with lamb mortalities in Muzaffarnagari sheep. Small Rumin. Res. 71, 273-279.

Maniatis, N. & Pollott, G.E., 2002. Genotype x environment interactions in lamb weight and composition traits. Anim. Sci. 75, 3-14.

Marx, B.D. & Eilers, P.H.C., 1998. Direct generalized additive modelling with penalized likelihood. Comp. Stat. Data Anal. 28, 193-209.

Marx, F.E., 1981. Die gehalte van die Suid-Afrikaanse Merinoskeersel oor dertig jaar. Karoo Agric 2, 13-14 (in Afrikaans).

Matebesi, P.A., Cloete, S.W.P. & Van Wyk, J.B., 2009a. Genetic parameter estimates of 16-month live weight and objectively measured wool traits in the Tygerhoek Merino flock. S. Afr. J. Anim. Sci. 39, 73-82.

Matebesi, P.A., Van Wyk, J.B. & Cloete, S.W.P., 2009b. Relationships of subjectively assessed wool and conformation traits with objectively measured wool and live weight traits in the Tygerhoek Merino flock. S. Afr. J. Anim. Sci. 39, 188-196.

Matebesi, P.A., Van Wyk, J.B. & Cloete, S.W.P., 2009c. Genetic parameters for subjectively assessed wool and conformation traits in the Tygerhoek Merino flock. S. Afr. J. Anim. Sci. 39, 176-187.

Matika, O., Van Wyk, J.B., Erasmus, G. & Baker, R.L., 2003. Genetic parameter estimates in Sabi sheep. Livest. Prod. Sci. 79, 17-28.

Matos, C.A.P., Thomas, D.L., Young, L.D. & Gianola, D., 2000. Genetic analyses of lamb survival in Rambouillet and Finnsheep flocks by linear and threshold models. Anim. Sci. 71, 227-234.

Maxa, J., Shrifi, A.R., Pedersen, J., Gauly, M., Simianer, H. & Norgerg, E., 2009. Genetic parameters and factors influencing survival to twenty-four hours after birth in Danish meat sheep breeds. J. Anim. Sci. 87, 1888-1895.

McGuirk, B.J., 2009. Genotype x environment interactions and Merino breeding programmes for wool production. Proc. Assoc. Advmt. Anim. Breed. Genet. 18, 42-47.

Meyer, H.H. & Clarke, J.N., 1978. Genetic and environmental effects on incidence and causes of lamb mortality. Proc. N. Z. Soc. Anim. Prod. 38, 181-184.

Meyer, K., 2004. Scope for a random regression model in genetic evaluation of beef cattle for growth. Livest. Prod. Sci. 86, 69-83.

Miraei-Ashtiane, S.R., Seyedalian, S.A.R. & Shahrbabak, M.M., 2007. Variance components and heritabilities for body weight traits in Sangsari sheep using univariate and multivariate animal models. Small Rumin. Res. 73, 108-114.

Misztal, I., 2006. Properties of random regression model using linear splines. J. Anim. Breed. Genet. 123, 73-144.

Misztal, I., Tsuruta, S., Strabel, T., Auvray, B., Druet, T. & Lee, D.H., 2002. BLUPF90 and related programs (BGF90). Proc. 7th World Congr. Genet. Appl. Livest. Prod. 33, 743-744. Montpellier, France.

Molina, A., Menendez-Buxadera, A., Valera, M. & Serradilla, J.M., 2007. Random regression model of growth during the first three months of age in Spanish Merino sheep. J. Anim. Sci. 85, 2830-2839.

Morley, F.H.W., 1951. Selection for economic characters in Australian Merino sheep (I) Estimates of phenotypic and genetic parameters. Sci. Bull. Dep. Agric. N.S.W. No.73.

Morley, F.H.W., 1955a. Selection for economic characters in Australian Merino sheep. V. Further estimates of phenotypic and genetic parameters. Aust. J. Agric. Res. 6, 77-90.

Morley, F.H.W., 1955b. Selection for economic characters in Australian Merino sheep. VI. Inheritance and interrelationships of some subjectively graded characteristics. Aust. J. Agric. Res. 6, 873-881.

Morrell, C.H., 1998. Likelihood ratio testing of variance components in the linear mixed effects model using restricted maximum likelihood. Biomet. 54, 1560-1568.

Morris, C.A., Hickey, S.M. & Clarke, J.N., 2000. Genetic and environmental factors affecting lamb survival at birth and through to weaning. N. Z. J. Agric. Res. 43, 515–524.

Mortimer, S.I., 1987. In "Merino Improvement Programs in Australia", Australian Wool Corporation, Melbourne Australia. p. 159.

Mortimer, S.I. & Atkins, K.D., 1989. Genetic evaluation of production traits between and within flocks of Merino sheep. I Hogget fleece weights, body weight and wool quality. Aust. J. Agric. Res. 40, 433-443.

Mortimer, S.I. & Atkins, K.D., 1994. Direct additive and maternal genetic effects on wool production in Merino sheep.Proc. 5th World Congr. Genet. Appl. Livest. Prod. Guelph, Canada, August 18, 103-106.

Mortimer, S.I. & Atkins, K.D., 1995. Maternal effects influence growth traits in Merino sheep. Proc. Aust. Assoc. Anim. Breed. Genet. 11, 421-424.

Mortimer, S.I. & Atkins, K.D., 2003. Genetic parameters for clean fleece weight and fibre diameter in young Merino sheep. Proc. Assoc. Advmt. Anim. Breed. Genet. 15, 143-146.

Mortimer, S.I., Atkins, K.D. & Rogan, I.M., 1985. Reproductive performance of Merino strains and bloodlines. Proc. Aust. Assoc. Anim. Breed. Genet. 5, 218-219.

Mortimer, S.I., Atkins, K.D., Semple, S.J.&. & Fogarty, N.M., 2010. Predicted responses in Merino sheep from selection combining visually assessed and measured traits. Anim. Prod. Sci. 50, 976-982.

Mortimer, S.I., Robinson, D.L., Atkins, K.D., Brien, F.D., Swan, A.A., Taylor, P.J. & Fogarty, N.M., 2009.Genetic parameters for visually assessed traits and their relationships to wool production and liveweight in Australian Merino sheep. Anim. Prod. Sci. 49, 32-42

Mrode, R.A. & Kennedy B.W., 1993. Genetic variation in measures of food efficiency in pigs and their relationships with growth rate and backfat. Anim. Prod. 56, 225-232.

Mullaney, P.D., Brown, G.H., Young, S.S.Y. & Hyland, P.G., 1969. Genetic and phenotypic parameters for wool characteristics in fine-wool Merino, Corriedale, and Polwarth sheep I. Influence of various factors on production. Aust. J. Agric. Res. 20, 1161-1176.

Mullaney, P.D., Brown, G.H., Young, S.S.Y. & Hyland, P.G., 1970. Genetic and phenotypic parameters for wool characteristics in fine-wool Merino, Corriedale, and Polwarth sheep II.Phenotypic and genetic correlations, heritability, and repeatability. Aust. J. Agric. Res. 21, 527-540.

Murphy, P.M. & Lindsay, D.R., 1996. The contribution of the activity of the newborn Merino lambs to the attachment to its mother and subsequent survival. Proc. Aust. Soc. Anim. Prod. 21, 486.

Nagy, I., Solkner, J., Komlosi, I. & Safar, L., 1999. Genetic parameters of production and fertility traits in Hungarian Merino sheep. J. Anim. Breed. Genet. 116, 399-413.

Naidoo, P., Cloete, S.W.P. & Olivier, J.J., 2004. Heritability estimates and correlations between subjectively assessed and objectively measured fleece traits in Merino sheep. S. Afr. J. Anim. Sci. 34 (SASAS congress 2004), 38-40.

Nash, M.L., Hungerford, L.L., Nash, T.G. & Zinn, G.M., 1996. Risk factors for perinatal and postnatal mortality in lambs. Vet. Rec. 139, 64–67.

Nasholm, A. & Danell, O., 1996. Genetic relationships of lamb weight, maternal ability, and mature ewe weight in Swedish finewool sheep. J. Anim. Sci. 74, 329-339.

Nephawe, K.A., 2004. Application of random regression models to the genetic evaluation of cow weight in Bonsmara cattle of South Africa. S. Afr. J. Anim. Sci. 34, 166-173.

Neser, F.W.C., Erasmus, G.J. & Van Wyk, J.B., 2001. Genetic parameter estimates for pre-weaning weight traits in Dorper sheep. Small Rumin. Res. 40, 197-202.

Nichols, J.E., 1933. Fibre growth phases in a sample of Australian Merino wool. J. Text. Inst. 24, T333-T340.

Nobre, P.C.R., Misztal, I., Tsuruta, S., Bertrand, J.K., Silva, L.O.C. & Lopez, P.S., 2002.Genetic evaluation of growth in beef cattle with a RR model.Proc. 7th World Congr. Genet. Appl. Livest. Prod. Communication No. 20-10.

Notter, D.R., 2008. Genetic Aspects of Reproduction in Sheep. Reprod. Dom. Anim. 43 (Supp. 2), 122-128.

Notter, D.R., 2012. Genetic improvement of reproductive efficiency of sheep and goats. Anim. Reprod. Sci. 130, 147-151.

Notter, D.R., Kuehn, L.A. & Kott, R.W., 2007. Genetic analysis of fibre characteristics in adult Targhee ewes and their relationship to breeding value estimates derived from yearling fleeces. Small Rumin. Res. 67, 164-172.

Nowak, 1990. Lamb's bleats: important for the establishment of a mother-young bond. Behav. 155, 14-29.

Okut, H., Bromley, C.M., van Vleck, L.D. & Snowder, G.D., 1999. Genotypic expression at different ages: 1. Prolificacy traits of sheep. J. Anim. Sci. 77, 2357-2365.

Olivier, J.J., 1989. Genetic and environmental trends in the Grootfontein Merino stud. Ph.D. thesis, University of the Orange Free State, Bloemfontein, South Africa.

Olivier, J.J., 1999. The South African Merino performance testing scheme. In: 'Rising to the challenge – Breeding for the 21st Century Customer'. Beef Industry and CRC for Premium Quality Wool Industry Symposia. Suppl. Proc. Assoc. Advmt Anim. Breed. Genet. 13, 119-124.

Olivier, J.J., 2002. The South African National Small Stock Improvement Scheme. http://agtr.ilri.cgiar.org/index.php?option=comcontent&task=view&id=86&Itemid=103   (last accessed 05.12.12).

Olivier, J.J., Bezuidenhout, A.G., Greyling, A.C. & Cloete, S.W.P., 1999. Evaluation of genetic fine and strong x fine wool Merinos on irrigated pastures. Proc. Assoc. Advmt. Anim. Breed. Genet. 13, 62-65

Olivier, J.J. & Cloete, S.W.P., 2007. Genetic change in South African Merino studs participating in the Merino Plan. Proc. Assoc. Advmt. Anim. Breed. Gen. 17, 324-327.

Olivier, J.J., Delport, G.J., Erasmus, G.J. & Eksteen, T.J., 1987. Linear type scoring in Merino sheep. Karoo Agric 3, 1-4.

Olivier, J.J., Erasmus, G.J., Van Wyk, J.B. & Konstantinov, K.V., 1995. Response to selection on BLUP of breeding values in the Grootfontein Merino stud. S. Afr. J. Anim. Sci. 25, 13-15.

Olivier, J.J., Steynberg, H. & Wentzel, D., 1989. Vestiging van `n genetiese fynwolkudde.Merino Joernaal, 52, http://gadi.agric.za/articles/Agric/fynwolkudde.php (in Afrikaans).

Olivier, W.J., 1998. Evaluation of ewe productivity measures. M.Sc. Agric. Thesis, University of the Orange Free State, Bloemfontein, South Africa.

Olivier, W.J., 2009. Is selection for decreased fibre diameter in a Merino flock with overstrong wool viable? Grootfontein Agric. 9, 27-33.

Olivier, W.J. & Greyling, A.C., 2009. Is selection for decreased fibre diameter in a Merino flock with overstrong wool viable? Proc. 43rd Cong. S. Afr. Soc. Anim. Sci. Alpine Heath 28 to 30 July 2009, 84

Olivier, W.J. & Olivier, J.J., 2005. Effect of feeding stress on the wool production of strong and fine wool Merino sheep. S. Afr. J. Anim. Sci. 35, 273-281.

Olivier, W.J. & Olivier, J.J., 2007. Evaluation of genetic fine wool animals under natural conditions in the non-traditional fine wool producing areas of the areas. Grootfontein Agric. 7, 35-38.

Olivier, W.J., Olivier J.J., Snyman M.A., Pretorius A.P. & Van Heerden M., 2002. Production and reproduction norms of fine woolled Merino sheep on natural pastures in the Karoo. Grootfontein Agric. 5, 29-31.

Olivier, W.J., Olivier, J.J., Cloete, S.W.P. & Van Wyk, J.B., 2006a. Genetic analysis of the Cradock fine wool Merino stud. Proc. 8th World Congr. Genet. Appl. Livest. Prod., Belo Horizonte, 13-18 Augustus, 599-602.

Olivier, W.J., Olivier, J.J. & Greyling, A.C., 2006b. Correlations of subjectively assessed traits of fine wool Merino sheep with production and reproduction traits. Proc. 41st Cong. S. Afr. Soc. Anim. Sci. 3-6 April 2006, Bloemfontein, South Africa, 98.

Olivier, W.J. & Roux, J.A., 2007. Production and reproduction norms of fine woolled Merino sheep on natural pastures in the Karoo. S. Afr. J. Anim. Sci. 37, 31-34.

Olivier, W.J., Snyman, M.A., Olivier, J.J., Van Wyk, J.B. & Erasmus, G.J., 2001. Direct and correlated responses to selection for total weight of lamb weaned in Merino sheep. S. Afr. J. Anim. Sci. 31, 115-121.

Olivier, W.J., Snyman, M.A., Van Wyk, J.B. & Erasmus, G.J., 1998. Genetic parameter estimates for fitness traits in South African Merino sheep. Livest. Prod. Sci. 56, 71-77.

Peaston, A. & Whitelaw, E., 2006. Epigenetics and phenotypic variation in mammals. Mammalian Genome, 17, 365−374.

Piper, L.R., Hanrahan, J.P., Evans, R., & Bindon, B.M., 1982. Genetic variation in individual and maternal components of lamb survival in Merinos. Proc. Aust. Soc. Anim. Prod. 14, 29-30.

Plush, K.J., Hebart, M.L., Brien, F.D. & Hynd, P.I., 2011. The genetics of temperament in Merino sheep and relationships with lamb survival. Appl. Anim. Behav. Sci. 134, 130-135.

Pollott, G.E. & Greeff, J.C., 2004. Genotype × environment interactions and genetic parameters for fecal egg count and production traits of Merino sheep. J. Anim. Sci. 82, 2840-2851.

Ponzoni, R.W. & Fenton, M.L., 2000. Phenotypic and genetic parameters from fine, medium and strong wool Australian Merino strains. SARDI and The Woolmark Company.

Ponzoni, R.W., Grimson, R.J., Jaensch, K.S., Smith, D.H., Gifford, D., Ancell, P., Walkley, J. & Hynd, P., 1995. The Turretfield sheep breeding project: Messages on phenotypic and genetic parameters for South Australian Merino sheep. Proc. Assoc. Advmt. Anim. Breed. Genet. 11, 303-313.

Ponzoni, R.W., Grimson, R.J., Jaensch, K.S., Smith, D.H. & Hynd, P.I., 1996. Birth coat: is it worth taking it into consideration in Merino sheep genetic improvement programs? Demands of wool and wool growers beyond 2000. SARDI Research Report Series, No 11. pp. 44.

Purvis, I.W., 1995. Strategies for improving wool quality and productivity in fine and superfine woolled Merino flocks. Proc. Aust. Assoc. Anim. Breed. Genet. 11, 510-515.

Purvis, I.W. & Piper, L.R., 1993. The development of an ultra-fine strain of Merino sheep. Proc. Aust. Assoc. Anim. Breed. Genet. 10, 109-113.

Purvis, I.W. & Swan, A.A., 1997. Can follicle density be used to enhance the rate of genetic improvement in Merino flocks? Proc. Assoc. Advmt. Anim. Breed. Genet. 12, 512-515.

Raadsma, H.W. & Wilkinson, B.R., 1990. Fleece rot and body strike in Merino sheep. IV. Experimental evaluation of traits related to greasy wool colour. Aust. J. Agric. Res. 41, 139-153.

Rao, S. & Notter, D.R., 2000. Genetic analysis of litter size in Targhee, Suffolk, and Polypay sheep. J. Anim. Sci. 78, 2113-2120.

Reis, P.J. & Sahlu, T., 1994. The nutritional control of the growth and properties of mohair and wool fibres: A comparative review. J. Anim. Sci. 72, 1899-1907.

Riggio, V., Finocchiaro, R. & Bishop, S.C., 2008. Genetic parameters for early lamb survival and growth in Scottish Blackface sheep. J. Anim. Sci., 86, 1758-1764.

Robertson, A., 1959. The sampling variance of the genetic correlation coefficient. Biomet., 15, 469-485.

Roman, R.M., Wilcox, C.J.& Martin, F.G., 2000. Estimates of repeatability and heritability of productive and reproductive traits in a herd of Jersey cattle.Genet. Mol. Biol. 23, 113-119.

Rosati, A., Mousa, E., Van Vleck, L.D. & Young.L.D., 2002. Genetic parameters of reproductive traits in sheep. Small Rumin. Res. 43, 65-74.

Rose, M. & Pepper, P., 1999. Genetic parameters for production traits in Queensland Merinos. Proc. Assoc. Advmt. Anim. Breed. Genet. 13, 114-117.

Ryder, M.L. & Stephenson, S.K., 1968. Wool Growth. Academic Press. pp. 562-592.

Saboulard, M., Russell, W.C. & Riley, M.L., 1995. Selection for lambing rate and clean fleece weight in sheep. J. Anim. Sci. 73, 3195-3198.

Safari, A. & Fogarty, N.M. 2003. Genetic Parameters for Sheep Production Traits: Estimates from the Literature. Technical Bulletin 49, NSW Agriculture, Orange, Australia.

Safari, E., Fogarty, N.M. & Gilmour, A.R., 2005. A review of genetic parameter estimates for wool, growth, meat and reproduction traits in sheep. Livest. Prod. Sci. 92, 271-289.

Safari, E., Fogarty, N.M., Gilmour, A.R., Atkins, K.D., Mortimer, S.I., Swan, A.A., Brien, F.D., Greeff, J.C., & Van der Werf, J.H.J., 2007a. Across population genetic parameters for wool, growth, and reproduction traits in Australian Merino sheep. 2. Estimates of heritability and variance components. Aust. J. Agric. Res. 58, 177-184.

Safari, E., Fogarty, N.M., Gilmour, A.R., Atkins, K.D., Mortimer, S.I., Swan, A.A., Brien, F.D., Greeff, J.C., & Van der Werf, J.H.J., 2007b. Genetic correlations among and between wool, growth and reproduction traits in Merino sheep. J. Anim. Breed. Genet. 124, 65-72.

Said, S.I., Muwalla, M.M., & Hanrahan, J.P., 1999. Sources of variation and repeatability and repeatability for litter size, body weight and matured performance of Awassi ewes. Turk. J. Vet. Anim. Sci. 23, 461-465.

SAS Institute Inc., 2009. SAS Online Doc® 9.2.Cary, NC, SAS Institute Inc.

Sawahla, R.M., Conington, J., Brothersone, S. & Villanueva, B., 2007. Analyses of lamb survival of Scottish Blackface sheep. Anim. 1, 151–157.

Scales, G.H., Burton, R.N. & Moss, R.A., 1986. Lamb mortality, birthweight, and nutrition in late pregnancy. N. Z. J. Agric. Res. 29, 75–82.

Schaeffer, L.R., 2004. Application of random regression models in animal breeding. Livest. Prod. Sci. 86, 35-45.

Schaeffer, L.R. & Jamrozik, J., 2008.Random regression models: a longitudinal perspective.J. Anim. Breed. Genet. 125, 145-146.

Schaeffer, L.R., Swalve, H.H. & Dekkers, J.C.M., 1994. Random Regressions in Animal Models for Test-day Production in Dairy Cattle. Proc. 5th World Congr. Genet. Appl. Livest. Prod. Guelph, 433-446.

Schlink, A.C. & Dollin, A.E., 1995. Abnormal shedding contributes to the reduced staple strength of tender wool in Western Australian Merinos. Wool Technol. Sheep Breed.43, 268-84.

Schlink, A.C., Masters, D.G. & Dollin, A.E., 1992. Effects of animo acids on fibre shedding in reproducing ewes. Proc. Nutr. Soc. Aust. 17, 80.

Scholtz, A.J., Cloete, S.W.P., Van Wyk, J.B., Misztal, I., Du Toit, E. & Van der Linde, T.C.de K., 2010. Genetic covariances between wrinkle score and absence of breech strike in mulesed and unmulesed Merino sheep, using a threshold model. Anim. Prod. Sci. 50, 201-218.

Scobie, D.R., Bray, A.R., Smith, M.C., Woods, J.L., Morris, C.A. & Hickey, S.M., 2012. Wool staple tenacity in New Zealand Romney sheep: heritability estimates, correlated traits, and direct response to selection. Anim. Prod. Sci. 52, 448-455.

Shelton, M., & Menzies, J.W., 1970.Repeatabilities and heritabilities of components of reproductive efficiency in fine-wool sheep. J. Anim. Sci. 30, 1-5.

Sherlock, R., Lopez-Villalobos, N. & Garrick, D., 2003. Genetic parameters for wool traits in ultra-fine New Zealand Merinos. Proc. Assoc. Advmt. Anim. Breed. Genet. 15, 277-280.

Short, B.F. & Carter, H.B., 1955. Analysis of Merino stud flocks. CSIRO Aust. Bull. No. 276.

Smith, G.M., 1977. Factors affecting birth weight, dystocia and preweaning survival in sheep. J. Anim. Sci. 44, 745-753.

Snowder, G.D. & Fogarty, N.M., 2009. Composite trait selection to improve reproduction and ewe productivity: a review. Anim. Prod. Sci. 49, 9-16.

Snyman, M.A., Cloete, S.W.P. & Olivier, J.J., 1998a. Genetic and phenotypic correlations of total weight of lamb weaned with body weight, clean fleece weight and mean fibre diameter in three South African Merino flocks. Livest. Prod. Sci. 55, 157-162.

Snyman, M.A., Erasmus, G.J. & Van Wyk, J.B., 1998b. The possible improvement of reproduction and survival rate in Afrino sheep using a threhold model. S. Afr. J. Anim. Sci. 28, 120-124.

Snyman, M.A., Erasmus, G.J., Van Wyk, J.B. & Olivier, J.J., 1995. Direct and maternal (co)variance components and heritability estimates for body weight at different ages and fleece traits in Afrino sheep. Livest. Prod. Sci. 44, 229-235.

Snyman, M.A., Erasmus, G.J., Van Wyk, J.B. & Olivier, J.J., 1998c.Genetic and phenotypic correlations among production and reproduction traits in Afrino sheep. S. Afr. J. Anim. Sci. 28, 74-81.

Snyman, M.A., Olivier, J.J., Erasmus, G.J., Van Wyk, J.B., 1997. Genetic parameter estimates for total weight of lamb weaned in Afrino and Merino sheep. Livest. Prod. Sci. 48, 111-116.

Snyman, M.A., Olivier, J.J. & Olivier, W.J., 1996. Variance components and genetic parameters for body weight and fleece traits of Merino sheep in an arid environment. S. Afr. J. Anim. Sci. 26, 11-14.

Snyman, M.A. & Olivier, W.J., 2002. Correlations of subjectively assessed fleece and conformation traits with production and reproduction in Afrino sheep. S. Afr. J. Anim. Sci. 32, 88-96.

Speidel, S.E., Enns, R.M. & Crews Jr., D.H., 2010. Genetic analysis of longitudinal data in beef cattle: a review. Genet. Mol. Res. 9, 19-33.

Steinheim, G., Ødega rd, J., A dnøy, T. & Klemetsdal, G., 2008. Genotype by environment interaction for lamb weaning weight in two Norwegian sheep breeds. J. Anim. Sci. 86, 33-39.

Stewart, A.M., Moir, R.J. & Schinckel, P.G., 1961. Seasonal fluctuations in wool growth in south western Australia. Aust. J. Exp. Agric.1, 85-91.

Steyn, O.P.J., 1996. Die Merino praktiese handleiding. Merino Sheep and Wool Experts' Association of South Africa, pp 83-147 (in Afrikaans).

Sumner, R.M.W., Clarke, J.N., Pearson, A.J. & Speedy, P.M., 1994. Repeatability of seasonal wool growth in Merino sheep. Proc. N. Z. Soc. Anim. Prod. 54, 163-165.

Sumner, R.M.W. & Wickham, G.A., 1969. Some effects of an increased stocking level on wool growth. Proc. N. Z. Soc. Anim. Prod. 29, 208-217.

Swalve, H.H., 1993. Estimation of direct and maternal (co)variance components for growth traits in Australian Simmental beef cattle. J. Anim. Breed. Genet. 110, 241-252.

Swan A.A. & Brown, D.J., 2013. The impact of measuring adult fleece traits with genomic selection on economic gain in Merino selection indexes. Proc. Assoc. Advmt. Anim. Breed. Genet. 20, 233-236.

Swan, A.A. & Hickson, J., 1994. Maternal effects in Australian Merinos. Proc. 5th World Congr. Genet. Appl. Livest. Prod., Guelph, Canada 18, 143-146.

Swan, A.A., Lax, J. & Purvis, I.W., 1995. Genetic variation in objectively measured wool traits in CSIRO's fine wool flock. Proc. Assoc. Advmt. Anim. Breed. Genet. 11, 516-520.

Swan, A.A., Piper, L.R., Brewer, H.G. & Purvis, I.W., 2001. Genetic variation in reproductive performance of fine wool Merinos. Proc. Assoc. Advmt. Anim. Breed. Genet. 14, 417-420.

Swan, A.A. & Purvis, I.W., 2000. Opportunities for genetic improvement of fine wool Merinos. Asian-Aust. J. Anim. Sci. 13 Supplement July 2000, 13-16.

Swan, A.A. & Purvis, I.W., 2005. Genetic progress in the T13 Merino breeding program. Proc. Assoc. Advmt. Anim. Breed. Genet. 16, 165-168.

Swan, A.A., Purvis, I.W., Hansford, K. & Humphries, W., 1997. The genetics of measured and assessed style traits in Merino sheep. Proc. Assoc. Advmt. Anim. Breed. Genet. 12, 153-157.

Swan, A.A., Purvis, I.W. & Piper, L.R., 2008. Genetic parameters for yearling wool production, wool quality and bodyweight traits in fine wool Merino sheep. Aust. J. Exp. Agric. 48, 1168-1176.

Taylor, P.J., Atkins, K. & Gilmour, A.R., 1999. Genetic association between fibre curvature, staple crimp and wool production and quality of Merino sheep. Proc. Assoc. Advmt. Anim. Breed. Genet. 13, 456-459.

Taylor, P.J., Gilmour, A.R., Crowe, D., Jackson, N. & Atkins, K., 1997. Genetic parameters for objectively measured style traits of Merino fleeces. Proc. Assoc. Advmt. Anim. Breed. Genet. 12, 149-152.

Thompson, A.N., Schlink, A.C., Peterson, A.D. & Hynd, P.I., 1998. Follicle abnormalities and fibre shedding in Merino weaners fed different levels of nutrition. Aust. J. Agric. Res. 49, 1173-1179.

Thwaites, C.J., 1972. The effects of short-term undernutrition and adrenocortical stimulation on wool growth. Aust. J. Biol. Sci. 32, 317-327.

Turner, H.N. & Young, S.S.Y., 1969. Quantitative Genetics in Sheep Breeding. Macmillan, Australia.

Vaez Torshizi R., Nicholas, F.W. & Raadsma, H.W., 1996. REML estimates of variance and covariance components for production traits in Australian Merino sheep using an animal model 1. Body weight from birth to 22 months. Aust. J. Agric. Res. 47, 1235-1249.

Vaez Torshizi, R., Raadsma, H.W. & Nicholas, F.W., 1995. An investigation of the potential for early (indirect) selection in Australian Merino sheep. Proc. Assoc. Advmt. Anim. Breed. Genet. 11, 314-317.

Valera, M., Arrebola, F., Juárez, M. & Molina, A., 2009. Genetic improvement of wool production in Spanish Merino sheep genetic parameters and simulation of selection strategies. Anim. Prod. Sci. 49, 43-47.

Van der Werf, J.H.J., 2005. Mixed models for genetic analysis. NSW, Armidale, http://genstat.com/products/asreml/user/geneticanalysis.pdf

Van Marle-Köster, E., Neser, F.W.C., Van Wyk, J.B., Visser, C. & Cloete, S.W.P., 2013. Genomic selection for the South African livestock industry. Proc. 46th Cong. S. Afr. Soc. Anim. Sci. 23-26 July 2013, Bloemfontein, South Africa. Pages 1-6.

Van Vleck, L.D., Snowder, G.D. & Hanford, K.J., 2003. Models with cytoplasmic effects for birth, weaning, and fleece weights, and litter size, at birth for a population of Targhee sheep. J. Anim. Sci. 81, 61-67.

Van Wyk, J.B., Fair, M.D. & Cloete, S.W.P., 2003. Revised models and genetic parameter estimates for production and reproduction traits in the Elsenburg Dormer sheep stud. S. Afr. J. Anim. Sci. 33, 213-222.

Van Wyk, J.B., Swanepoel, J.W., Cloete, S.W.P., Olivier, J.J. & Delport, G.J., 2008. Across flock genetic parameters for yearling body weight and fleece traits in the South African Dohne Merino population. S. Afr. J. Anim. Sci. 38, 31-37.

Vatankhah, M. & Talebi, M.A., 2008. Heritability estimates and correlations between production and reproductive traits in Lori-Bakhtiari sheep in Iran. S. Afr. J. Anim. Sci. 38, 110-118.

Vostrý, L. & Milerski, M., 2013.Genetic and non-genetic effects influencing lamb survivability in the Czech Republic. Small Rumin. Res. 113, 47-54.

Vostrý, L., Přibyl, J., Jakubec, V., Vesela, Z. & Majzlik, I., 2008. Selection of a suitable definition of environment for the estimation of genotype x environment interaction in the weaning weight of beef cattle. Czech J. Anim. Sci., 53, 407-417.

Wang, C.T. & Dickerson, G.E., 1991. Simulation of life-cycle efficiency of lamb and wool production for genetic levels of component traits and alternative management options. J. Anim. Sci. 69, 4324-4337.

Warner, R.D., Greenwood, P.L., Pethick, D.W. & Ferguson, D.M., 2010. Genetic and environmental effects on meat quality. Meat Sci. 86, 171-183.

Welsh, C.S., Garrick, D.J., Ens, R.M. & Nicoll., G.B., 2006. Threshold model analysis of lamb survivability of Romney sheep. N. Z. J. Agric. Res. 49, 411-418.

Wentzel, D., 1991. Veredeling van `n genetiese fynwol Merinokudde. Progress report 1991 of project K5312/07/4/3. Department of Agriculture (in Afrikaans).

Willham, R.L., 1972. The role of maternal effects in animal breeding: III. Biometrical aspects of maternal effects in animals. J. Anim. Sci. 35, 1288-1293.

Wolc, A., Barczak, E., Wójtowski, J., Slósarz, P. & Szwaczkowski, T., 2011. Genetic parameters of body weight in sheep estimated via random regression and multi-trait animal models. Small Rumin. Res. 100, 15-18.

Woolaston, R.R., 1987. Genotype x environment interactions and their possible impact on breeding programs. In: Merino Improvement Programs in Australia. Ed. B.J. McGuirk. Australian Wool Corporation, Melbourne, pp. 421-435.

Woolaston, R., Ward, J.L., Arnold, G.W., Charlick, A.J. & Clune, G., 1995. Fitness and production in Merinos - is there an antagonism? Proc. Assoc. Advmt. Anim. Breed. Genet. 11, 134-137.

Wuliji, T.D.K., Andrews, R., Turner, P. & Wheeler, R., 1998. Responses to fleece weight selection and heritability estimates of wool characteristics in Romney sheep. Proc. 6th World Congr. Genet. Appl. Livest. Prod., Armidale, Australia 24, 55-58.

Wuliji, T.D.K., Dodds, K.G., Land, J.T.J., Andrews, R.N. & Turner, P.R., 2001. Selection for ultrafine Merino sheep in New Zealand: heritability, phenotypic and genetic correlations of live weight, fleece weight and wool characteristics in yearlings. Anim. Sci. 72, 241-250.

Yapi, C.V., Boylan, W.J. & Robinson, R.A., 1990. Factors associated with causes of preweaning lamb mortality. Prev. Vet. Med. 10, 145-152.

Yazdi, M.H., Nasholm, A., Johansson, K., Jorjani, H. & Liljedahl, L.E., 1997. Population parameters for birth and ewe fleece weight at different parities in Baluchi sheep. J. Anim. Breed. Genet. 114, 323-332.

Young, S.S.Y., Turner, H.N. & Dolling, C.H.S., 1960. Comparison of estimates of repeatability and heritability for some production traits in Merino rams and ewes I. Repeatability. Aust. J. Agric. Res. 11, 257-275.

Young, S.S.Y., Turner, H.N. & Dolling, C.H.S., 1963. Selection for fertility in Australian sheep. Aust. J. Agric. Res. 14, 460-482.

Zishiri, O.T., Cloete, S.W.P., Olivier, J.J. & Dzama, K., 2013. Genetic parameters for growth, reproduction and fitness traits in the South African Dorper sheep breed. Small Rumin. Res. 112, 39-48.