GENETIC RELATIONSHIPS AFFECTING DUAL PURPOSE USE OF MERINO SHEEP

A thesis submitted in partial fulfilment
of the requirements for the degree of
Doctor of Philosophy

By

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Abstract

Data from the Turretfield Resource flocks was used to investigate the genetic relationship between reproduction traits in South Australian Merino sheep. Reproductive performance was recorded in females over four years and in males scrotal circumference was recorded at 5, 10 and 16 months of age. These records were used to calculate heritabilities, phenotypic and genetic correlations between and within female and male reproductive traits. Heritabilities of female reproductive traits were generally low, but genetic correlations between different ages of the same trait and between traits were very high. Heritabilities of the male trait and genetic correlations between the male and female traits were moderate to high. Litter size and scrotal circumference at 10 months of age were identified as the best options for genetic improvement of flock reproductive rate. Genetic parameters between reproduction and fleece traits were also estimated using the Turretfield Resource Flock data. Genetic correlations ranged from low to moderate between female reproductive traits and fleece traits. Genetic correlations between scrotal circumference and fleece traits were generally low. Genetic correlations indicated that reproduction and fleece traits could be improved simultaneously using appropriate selection methods.

Intensive measurement of live weight, fat depth and eye muscle depth was carried out over two years using the Selection Demonstration Flocks. Live weight measurements were taken at birth and weaning. Live weight, and ultrasound fat and eye muscle depth (at the C site) were measured at 6 weekly intervals from 4 to 10 months, at 13 months and 16 months of age. These traits were analysed to determine the genetic relationship between measurements at different ages and between the different traits. Heritabilities were generally low for live weights, and moderate for fat and eye muscle depth. Genetic correlations between ages indicated that selection at young ages will lead to improvements in that trait at older ages. Genetic correlations between the traits indicated that improvements to growth and carcase traits can be made in the Merino. The live weight and carcase measurements from the Selection Demonstration Flocks were used to estimate some of the first correlations with fleece traits. Genetic correlations indicated that there are no major genetic antagonisms between gains in wool, meat and reproduction traits. Recommendations for selection and implications for the Australian Merino Industry are discussed.

Declaration

I hereby declare that this work contains no material which has been accepted for that award of any other degree or diploma in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text.

I give consent to this copy of my thesis, when deposited in the University Library, being available for loan and photocopying.

Veronica Ingham

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List of Abbreviations

aFert	average fertility
aLS	average litter size
aNLW	average number of lambs weaned
Aod	age of dam
aRA	average rearing ability
BW	birth weight
c^2	permanent environmental heritability
CFW	clean fleece weight
Control	Control flock
CR	correlated response to selection
EMD	eye muscle depth
EWF	Elite wool flock
FAT	fat depth
FD	fibre diameter
Fert	fertility
FG	fat gain per month
Flock	flock of birth
FM+	Fibre meat plus flock
h^2	direct heritability
GFW	greasy fleece weight
HW	hogget weight
LS	litter size
MG	muscle gain per month
Mo.	months of age
MPR	Measured performance records flock
NLW	number of lambs weaned
OR	ovulation rate
PCA	Professional classer assessment flock
r	correlation
R	response to selection for single trait
RA	rearing ability
s.d.	standard deviation
s.e.	standard error
SC	scrotal circumference
SDF	Selection Demonstration Flock
SL	staple length
SS	staple strength
Tobr	type of birth and rearing
TRC	Turretfield Research Centre
TRF	Turretfield Resource Flock
Wean	weaning
V_p	phenotypic variance
WG	weight gain per month
WLW	weight of lamb weaned
WT	live weight
WW	weaning weight
Year	year of birth
YW	yearling weight

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Chapter 1

Literature Review

1.1 INTRODUCTION

The Australian sheep industry has been facing a constant decline in wool prices for many decades, with only periods in the 1950's, 1970's and late 1980's, where prices have risen. This is true for most agricultural products. However, recently, relative to wool, lamb and sheep meat prices have not declined as rapidly (ABARE 2002). The industry has responded by increasing lamb supply, with many producers placing a greater emphasis on meat production (Banks 2000). The above described situation has brought about much greater interest from both wool and meat producers in sound information regarding all aspects of sheep meat production. There are many factors involved in the production of meat. The focus of this study is on quantitative genetic aspects that determine the potential for improvement in the efficiency of production, the quantity and the quality of meat from Merino sheep.

Merino sheep, a wool breed, are the focus of this study because they make up a large proportion (~97%) of the sheep in Australia as they are used as purebreds for wool and lamb production and often to produce first cross ewes for lamb production (ABARE 2002). Meat production requires the conception and birth of lambs and the Merino is known to have low prolificacy in relation to meat sheep breeds (Purvis 1988). Crossbreeding Merinos with these other breeds is not considered by wool producers due to undesirable fleece characteristics such as high fibre diameter and contamination from pigmented and medullated fibres of the meat breeds (Purvis 1988). However, the reproductive ability both within and between flocks and sheep breeds is one area where large phenotypic variation exists and this may be used to increase the efficiency of production. After birth, the growth of lambs can be manipulated using different nutritional levels. Growth can also be improved and potentially manipulated through selection. Once the lamb has grown, it can be slaughtered at a certain age or weight. Carcase composition is important as it can influence the price received for the carcase. The assessment of carcase composition has three purposes: (i) it assists in assigning carcase value; (ii) it allows carcase sorting for markets; and (iii) it allows transfer of information back to the producer (Stanford *et al.* 1998). Thus, while focussing on issues relevant to the Merino, a specialist wool producing breed, the main areas in which the literature will be reviewed are reproduction, growth, carcase composition and their relationship with wool.

1.2 REPRODUCTION

Reproduction is defined by Webster's new encyclopaedic dictionary (Anon. 1993) as "the act or process … by which plants and animals give rise to offspring". As this suggests, among plants and animals the purpose of reproduction is the perpetuation of the species. However, in the farming environment simple perpetuation is not sufficient, and for economic reasons reproductive performance should be managed (most often increased) to a profitable level. If reproductive rate is improved in the flock or herd, then the overall efficiency of the production system is increased because there will be more 'growing and finishing' animals per dam present in the flock or herd. In addition, there will also be more animals to select from to make genetic improvement. Reproductive rate has high economic value but in sheep genetic improvement programs it is often a small contributor to overall economic gain (Ponzoni and Walkley 1984). This is partly due to the low heritability of reproduction traits and to a lesser extent to their low correlations with other traits in the breeding objective. The low heritability of reproduction traits means that genetic improvement of these traits is possible, but generally with difficulties, and at a slow rate (Purvis 1988). However, for many of these traits there is large variation between breeds, as well as within breeds and flocks (Purvis and Hillard 1997). Therefore, selection differentials can be large, especially if large numbers are screened.

Reproductive rate in the farming system must be clearly defined, as it and its component traits can be interpreted in many ways. For example, the average number of lambs weaned per ewe lifetime is a measure that could be considered as the reproductive rate of a flock. Turner (1969) went further and used two descriptions which may be suitable for different purposes: (i) a measure of a flock's productivity (number of lambs weaned per ewe joined per year), or (ii) a measure of its replacement rate (the number of ewe lambs reaching joining age produced by each ewe in her lifetime). However, the second definition is a lifetime measurement and would therefore slow the rate of genetic improvement considerably. There are many different traits used to measure reproductive rate, some of these have very similar definitions and some have the same definition. Table 1.1 shows seven female reproduction traits and their definitions. Similarities can be seen between some traits, and there are multiple definitions for traits with the same name. The use of the trait and the associated definition depends on the situation being studied. Trait definition is important to consider when estimating genetic parameters as biases may occur depending on the definition, hence large variation in genetic parameter estimates exists in the literature (Tosh and Kemp 1995).

Table 1.1 Seven female reproduction traits and their definitions

Trait name	Definition (unit of measurement)
Weight of lamb weaned	The sum of the weaning weight of lambs 1) per ewe joined (≥ 0 kg)[a] 2) per ewe lambing (≥ 0 kg)[a]
Number of lambs weaned	The sum of the number of lambs weaned 1) per ewe joined (0,1,2…)[a] 2) per ewe lambing (0,1,2…)[a]
Fertility of the ewe	1) The ability of the ewe to conceive (Yes or No) 2) The ability of the ewe to have a lamb (Yes or No)
Litter size or Prolificacy or Fecundity	1) The number of lambs born per ewe joined (contains fertility component) (0,1,2,3…) 2) The number of lambs born per ewe lambing (1,2,3…)
Rearing ability of the ewe	The ability of a ewe to rear all lambs that are born to weaning (measured as a ratio, 0 > 1)

[a] Can be considered per year/season or over a lifetime.

Reproductive rate is often first considered in the female. There are many female traits used to determine a ewe's reproductive rate or ability. However, many of these traits are difficult and expensive to measure. For that reason there has been considerable interest in the use of indirect selection criteria. For example scrotal circumference or testis diameter, are traits that can be taken in males and used to predict reproductive performance, and are less expensive to record and genetically correlated with female reproduction traits.

1.2.1 Reproductive Traits Measured in Females

Most female traits can be described as components of the composite trait number of lambs weaned per ewe joined, or weight of lambs weaned per ewe joined. However, to properly assess reproductive rate both the composite and component traits must be considered.

Composite Traits

Snyman *et al.* (1997) suggested that total weight of lamb weaned per year is the best single measure of a meat producing flock's productivity. Their measure of total weight of lamb weaned was defined as the sum of the weaning weight of all lambs weaned by each ewe in each lambing season adjusted for sex and corrected to 120 days weaning weight. Genetic correlations of weaning weight with lifetime total weight of lambs weaned was 0.75, and with lifetime number of lambs weaned was 0.11 (Snyman *et al.* 1996). This indicates that selection for total weight of lambs weaned would increase the number of lambs as well as the weaning weight of the lambs, which is important when producing sheep for meat. Whereas selecting for number of lambs weaned would increase the number of lambs but would have little effect on the weaning weight of the lambs (Snyman *et al.* 1996). However, Head *et al.* (1995, 1996a) found in a flock selected for lifetime production of kilograms of lamb weaned per ewe, that while there was an increase in kilograms of lamb weaned, or quantity of lamb, the lambs ate more to achieve this and therefore, did not improve the efficiency of production.

The use of composite traits in selection is appealing as they are more representative of the true breeding objective than component traits. Correlated traits offer an alternative way of dealing with composite traits, for example the use of early records as indicators of lifetime production. Lee and Atkins (1996) tested reproductive performance in the first two reproductive cycles with subsequent reproductive performance. They concluded that culling ewes based on the first two years of lambing data would improve the net reproductive rate of the flock. They also indicated that there may be a need to review the selection criteria used to improve reproductive rate. This study reviews the use of scrotal circumference as a selection criterion in relation to female reproduction traits. Historically, litter size has been recommended as the criterion to be used for this purpose (eg. Land *et al.* 1983). However, there are other component traits such as fertility, rearing ability and survival that could also be used.

There is much genetic variation for the composite reproductive traits. Fogarty (1995) did a comprehensive review of parameters estimated for many traits, including those related to reproduction. His review highlights the large variation in parameters estimated for reproductive traits, partly caused by the different definitions of female reproductive traits. Heritability estimates range from 0 to 0.5 for composite traits with a weighted mean of 0.05 for number of lambs weaned and 0.13 for weight of lamb weaned (Table 1.2) (Fogarty 1995, Safari and Fogarty 2003). Since then Safari and Fogarty (2003) have updated this review and heritabilities reported have also been within the range 0 to 0.5. Genetic and phenotypic correlation estimates between the composite traits themselves, component traits range from negative to >1 (although by definition heritabilities must be between zero and one and correlations between negative and positive one). For example, phenotypic and genetic correlations between number of lambs weaned and weight of lambs weaned at the same ewe age were 0.97, 0.98 respectively (Fogarty *et al.* 1985). The weighted means of phenotypic and genetic correlations from Fogarty (1995) are presented in Table 1.2.

Table 1.2 Weighted means of literature estimates of heritabilities (on diagonal), phenotypic correlations (above diagonal) and genetic correlations (below diagonal) (number, standard deviation of estimate) between reproduction traits taken from Fogarty (1995)

	NLW	WLW	OR	LS	RA	SC	BW	WW	YW
NLW	***0.05*** ***(18,0.04)***	0.94 (2, 0.02)					0.06 (1)	0.09 (1)	
WLW	0.93 (2, 0.06)	***0.13*** ***(4,0.12)***							
OR			***0.21*** ***(9,0.20)***	0.18 (1)				0.15 (1)	
LS			1.03 (2, 0.05)	***0.10*** ***(53,0.07)***	-0.16 (2, 0.05)	0.04 (1)	0.07 (1)	0.01 (5, 0.27)	0.09 (1)
RA				-0.19 (2, 0.16)	***0.07*** ***(12,0.08)***		0.04 (1)	0.01 (1)	
SC			0.26 (3, 0.11)	0.06 (2, 0.43)		***0.24*** ***(14,0.16)***		0.40 (4, 0.26)	0.46 (4, 0.18)
BW	0.34 (1)			0.30 (1)	0.16 (1)				
WW	0.34 (1)		-0.13 (1)	-0.10 (6, 0.39)	0.11 (1)	0.53 (4, 0.39)			
YW	0.35 (1)			0.13 (1)		0.70 (4, 0.16)			

Traits: NLW, number of lambs weaned; WLW, weight of lambs weaned; OR, ovulation rate; LS, litter size; RA, rearing ability; SC, scrotal circumference; BW, birth weight; WW, weaning weight; YW, yearling weight.

Component Traits

Composite reproduction traits are conceptually closer to the true breeding objective than components traits. However, component traits may have greater heritabilities than composite traits, and therefore their use as selection criteria may result in greater genetic gain if the correlations among them are favourable. In this section four of the female component reproduction traits that could be used in selection are reviewed.

Ovulation Rate

Ovulation rate can be defined as the number of eggs shed by the ovary at ovulation per oestrus cycle (Turner 1969, Urioste, 1987). Hanrahan (1980, 1982) argued that much of the genetic variation in litter size was due to genetic variation in ovulation rate. Hanrahan (1980) reported the heritability of ovulation rate to be 0.45 in Finnish Landrace and 0.57 in Galway sheep, compared to 0.10 and 0.06 for litter size respectively. He estimated genetic correlations between litter size and ovulation rate between 0.4 and 0.7 and argued that selection for ovulation rate could increase annual genetic gain three fold because of its greater heritability. However, Piper *et al.* (1980) reported that in 14 Merino lines representing the industry, heritability for ovulation rate was as low as for litter size. They concluded that ovulation rate would probably not be useful for predicting ewe reproduction performance and that further research would be required to determine its usefulness in selection. In Fogarty (1995) and Safari and Fogarty (2003) review's, heritability estimates for ovulation rate vary considerably, the range being from 0.05 to 0.50 with a weighted mean of 0.21 (Table 1.2). Davis *et al.* (1998) estimated heritability of ovulation rate to range from 0.03 to 0.16 in three sheep breeds. They concluded that one way to achieve a high reproduction potential within a flock would be to screen ewes for very high litter size and subsequently select for ovulation rate.

Litter Size

Historically, litter size has been one of the main traits used as a selection criterion for improving reproduction rate. This is due to the general agreement that litter size is a major component of total weight of lamb weaned per ewe (Turner 1962, 1969, Hanrahan 1982, Land *et al.* 1983, Bradford 1985, Urioste 1987, de Vries *et al.* 1998). Selection for increased litter size has been shown to increase the quantity of lamb produced. As Turner (1962) pointed out, twins had lighter average weaning weights than single born lambs, but total weight of lamb weaned was higher because of the greater number of lambs. While Snyman *et al.* (1997) agreed with this, they pointed out that in many cases an increase in the number of lambs results in a decrease in the quality of the lamb product. They stated that selection for litter size without considering weaning weight would be "short sighted" and suggested that selection for total weight of lamb weaned would be better to improve lifetime reproductive efficiency. Analla *et al.* (1997b) investigated the optimum selection criteria in the Segurena breed. Their conclusion was that if a producer was supplying the Segurena breed's traditional market, litter size alone as a criterion was suitable. However, for other markets, a selection index including litter size and weaning weight would be more beneficial. This highlights the significance of having a well defined breeding objective and choosing the appropriate selection criteria to achieve it. While improvement in litter size can be achieved, it has a low heritability, although it is generally higher than the heritability of other component traits.

Fogarty (1995) reported heritabilities in the range of 0.0 to 0.4 (with one estimate at 0.6) for litter size and a weighted average mean heritability of 0.10 (Table 1.2), Safari and Fogarty (2003) reported a similar range. Urioste (1987) reported higher estimates of heritability of 0.26 to 0.43 using a threshold model, whereas de Vries *et al.* (1998) estimated low heritabilities in the range of 0.05 to 0.12 for different ages in two sheep breeds. Genetic and phenotypic correlations of litter size with other reproduction traits are generally positive although there have been reports of negative phenotypic and genetic correlations with other reproductive component traits such as lamb survival. Correlations between litter size and composite traits were variable and close to zero between litter size and weight of lamb weaned per ewe joined (Table 1.2). Correlations of litter size with production traits are variable, but generally low to moderate (Fogarty 1995, Safari and Fogarty 2003). The relatively high heritability and positive correlations of litter size with other traits is one of the main reasons for its recommendation for use as a selection criterion.

Lamb Survival and Rearing Ability of the Ewe

Reproductive rate can also be improved in terms of lamb survival or lamb mortality. Lamb mortality is one of the main causes of reproductive and production losses in the farming system (Haughey 1983, Gama *et al.* 1991a,b, Kilgour and Haughey 1993, Cloete and Sholtz 1998). In an average Australian Merino flock it is estimated that one third of lambing potential is lost and is mainly due to lamb mortality (Kleeman *et al.* 1990, Kilgour 1992). The lamb's own ability to survive and its dam's rearing ability or maternal ability contribute to lamb survival (Piper *et al.* 1982). The maternal or rearing ability of the ewe has been reported to be a significant contributor to lamb survival especially in Merino ewes with multiple births (Alexander *et al.* 1982, Stevens *et al.* 1982). Earlier studies have shown that lamb survival has a low heritability (~0.02 – 0.05) and there is little scope for improving lamb survival by direct selection (Piper *et al.* 1982).

The heritable nature of ewe rearing ability has been established in Merinos (Atkins 1980, Donnelly 1982, Piper *et al.* 1982, Haughey 1983). Ewe rearing ability itself is a complex trait and is determined by factors such as milk production, ease of parturition and maternal behaviour. The behaviour of dams has been widely investigated, studies have included observations of behaviour in the field and in relation to human contact. In South Africa, Cloete *et al.* (1998c) observed the levels of separation of ewes and lambs in two Merino lines selected for ewe multiple rearing ability. Their observations indicated that behavioural adaptations had occurred in the high rearing ability line as fewer maiden ewes were separated from their lambs. However, interference from other ewes was more likely in the high line than in the low line. Their conclusion was that some of the observed behavioural differences were due to the selection for multiple rearing ability. Cloete and Scholtz (1998) studied the overall lamb production of the same South African Merino flocks and found that the number of lambs weaned and lamb weaning weights were consistently greater in the high line over five years. They concluded that selection for multiple rearing ability was a viable method of increasing lamb production. Similarly, Kilgour (1998) investigated arena behaviour as a selection criterion for improved rearing ability. Arena behaviour is the measurement of an individual sheep's behaviour (most commonly movement and bleats) within a defined space in the presence of a human being. He determined that behavioural differences occurred between a flock selected for rearing ability and an unselected flock. Kilgour (1998) suggests that arena behaviour is worthy of further investigation as a possible selection criterion as it can be measured in both males and females and can be measured early in life.

Genetic parameters reported in Fogarty's (1995) review for lamb survival both as a trait of the lamb and a trait of the ewe (or rearing ability) were low. Weighted mean estimates for heritabilities of lamb survival and rearing ability were 0.04 and 0.07, respectively (Table 1.2). Genetic and phenotypic correlations between these two traits and other reproductive and production traits were highly variable ranging from strongly negative (-0.73) to 1. Genetic correlations of ewe rearing ability with reports for number of lambs weaned ranging from 0.34 (Fogarty *et al.* 1994) to 1.0 (Brash *et al.* 1994b), with a weighted mean of 0.86 (Fogarty 1995) (Table 1.2). Reports since 1995 agree with the values above (Safari and Fogarty 2003)

1.2.2 Reproductive Traits Measured in Males

As reported, reproduction traits measured in the female often have low heritabilities and low correlations with other production traits. This, combined with the expense and difficulty of measurement and the sex and age limited nature of most reproduction traits, has stimulated the investigation of indirect selection criteria. The low prolificacy of Merinos, coupled with the fact that crossbreeding with more prolific breeds is most often not considered an option due to higher fibre diameters and fleece contamination with pigmented and medullated fibres, make indirect selection criteria especially attractive for Merino flocks (Purvis *et al.* 1988, Purvis 1988). Generally, greater selection intensity is placed on males than on females. Therefore, an indirect trait measured in males may actually prove to be as beneficial in improving genetic gain as direct selection for the female trait and at less cost.

Indirect Selection

Indirect selection can be described as the use of the correlated response in trait D (the 'desired' trait for improvement) when selection is based on trait I (the 'indirect' trait). Indirect selection is useful when trait D is sex limited (e.g. reproduction traits), age limited (e.g. lifetime production traits), or expensive to measure (Walkley and Smith 1980, Haley *et al.* 1987). Indirect selection criteria must be chosen carefully. Their recording should be easy and cost effective, they should be measurable on young animals and on both sexes, and have a strong genetic relationship with the desired trait (Blair *et al.* 1990). For the improvement of a single trait, the relative efficiency of indirect to direct selection when the two are considered as alternatives is (Hill 1985):

$$r_G h_I / h_D \qquad \text{(Equation 1.1)}$$

Where: h_D = square root of heritability of the desired trait

h_I = square root of heritability of the indirect trait

r_G = genetic correlation between the two traits

Assuming: the same selection intensity and generation interval for both traits.

Therefore, the benefits of indirect selection increase when the heritability of the indirect trait and the genetic correlation are high, but decrease as the heritability of the desired trait increases. Candidates for indirect selection need to be thoroughly investigated to determine the most appropriate measurement and to determine their impact on traits other than the desired trait. However, indirect selection has an important contribution to make to overall economic efficiency (Haley *et al.* 1987).

Scrotal Circumference and Testicular Size

The male trait testicular size has been widely considered to be one of the best candidates for use as an indirect selection criterion to improve female reproductive rate in sheep flocks. Land (1973) first suggested testicular size, or more specifically testicular diameter, as a potential criterion for use in selection. Since then, testicular size has been investigated and supported as a criterion in many species including, mice (Islam *et al.* 1976), cattle (Keeton *et al.* 1996), pigs (Wilson *et al.* 1977), and horses (Thompson *et al.* 1979). In contrast to these and many other investigations, with sheep Land *et al.* (1982) found no improvement in female reproductive performance when testicular diameter adjusted for live weight was used as the selection criterion. There are two main differences in the studies carried out on male reproductive traits: (i) whether testicular diameter or scrotal circumference was measured, and (ii) whether the measure was adjusted for live weight or not.

In the majority of studies considering testicular diameter, measurements have been taken using callipers to measure the testis and scrotum. This is followed by an adjustment for skin (scrotum) and in some cases wool thickness was taken into consideration. Some reference is also made to positioning of the ram on angles rather than standing (e.g. Haley *et al.* 1990, Yarney *et al.* 1990, Purvis *et al.* 1991). In studies considering scrotal circumference most commonly a simple tape was used to measure the scrotum at the greatest circumference with the ram in the standing position, hence Matos *et al.* (1992) pointed out that scrotal circumference is easily measured. Notter *et al.* (1981) showed scrotal circumference of rams to be a reliable indicator of testis weight. In the search for indirect selection criteria to improve female reproductive rate, it must be remembered that ultimately the research carried out on these criteria should be applied to, and hopefully widely adopted, in the target industry. Matos and Thomas (1992) carried out a review of testicular size and its various measures. These included testis weight, testicular diameter, scrotal circumference and epididymis weight. They concluded that more research was required before breeding plans including testicular size as a criterion could be used.

Many studies have shown testicular diameter and scrotal circumference to be heritable and correlated with female reproduction traits. Fogarty's (1995) review reports heritabilities ranging from 0.08 to 0.69 for the two traits with the weighted mean being 0.24 (Table 1.2). Safari and Fogarty (2003) report a range from 0.01 to 0.41. Genetic correlations between testicular diameter and scrotal circumference themselves are very high and positive (~0.9), indicating that they may be considered as the same trait. Correlations between the male trait and female reproduction traits vary from negative to high and positive. Correlations between testicular size and scrotal circumference and production traits are generally moderately positive (Table 1.2). Genetic correlations reported by Fogarty (1995) and Safari and Fogarty (2003) between scrotal circumference and yearling weight, clean fleece weight, and fibre diameter at yearling and hogget age were 0.24, 0.15, 0.22 and 0.59 respectively (Brash *et al.* 1994).

1.3 GROWTH AND DEVELOPMENT

In simple terms, a generally accepted aim in the improvement of the efficiency of meat production is the increase of lean tissue deposition and the decrease of body fat (Simm 1987, Cameron and Bracken 1992, Nsoso *et al.* 1999). An understanding of the growth and development processes of the animal is important to achieve that aim. A distinction between growth and development is required for clarity. However, this has still not occurred in the literature despite the call for specific universal definitions since 1974 (De Boer *et al.* 1974, Waldron *et al.* 1992a, Fisher and De Boer 1994). Fisher and De Boer (1994) pointed out that universal definitions would enable easy comparison of research results. Distinction is required between growth and development because the two are related and one is a consequence of the other. They can be measured in both live animals and in the carcase, but they are measured in different units (Nsoso *et al.* 1999). If, as assumed by Nsoso *et al.* (1999), growth is defined as an increase in animal size, and development is a change in shape and body proportion associated with growth, then growth would be measured in weights or linear dimensions (e.g. live weight or carcase length) and development would be measured in indices of shape (e.g. muscularity or proportion of weight). Growth is associated with increases in bone, fat and muscle mass, and therefore causes body and carcase weights to increase. However, the development process has a different effect. Generally, fat weight increases whereas muscle and bone weight decrease relative to carcase weight (McClelland *et al.* 1976, Wood *et al.* 1980).

The objectives of efficient sheep meat production are to increase lean tissue production and to decrease fat at the time of slaughter (Nsoso *et al.* 1999). This is in response to the reality that in many countries financial penalties are imposed on sheep carcases with high intermuscular and subcutaneous fat levels without ignoring minimum fat requirements. Short-term solutions to this would be slaughtering animals at lower weights, not castrating males, and/or manipulating the quality and quantity of feed available (Simm and Dingwell 1989, Simm 1992). However, there are disadvantages to using short-term, non-genetic solutions. Reducing the slaughter weight of animals may actually reduce the production per unit of land and manipulating feed is not a practical option for the extensive production systems of Australia. Feed manipulation has the added disadvantage that timing is important because fat penalties are mainly related to intermuscular fat, which matures early in sheep (Wood *et al.* 1980, Berg and Walters 1983). These 'quick fixes' to avoid or reduce fat penalties would not contribute to the increased efficiency of the production system as a whole.

Genetic improvement may appear slow in comparison to short term solutions, but changes in carcase composition would be permanent and most likely cost effective. Thus, it is a good option for long-term modification of the growth and development processes of a flock (Simm *et al.* 1987, Simm and Dingwell 1989, Simm 1992). To achieve this, development traits such as body composition or proportion of fat and muscle, as well as growth traits, are the criteria needed to estimate the animals' merit for the breeding objective. The success of these traits in achieving the objective depends on their genetic parameters (Wolf *et al.* 1981). As applies to all traits, accurate estimation of these parameters would lead to the most rapid improvement, but over or under estimation would give suboptimal economic gains in the breeding objective (Sheridan 1988, Meyer 1990).

1.3.1 Birth Weight

There is large variation in birth weight between breeds (Cloete *et al.* 1998b), lines (Analla *et al.* 1998) and flocks (Donnelly 1982) of sheep. Birth weight is a trait of potential economic importance (Al-Shorepy and Notter 1998). At birth, excessively large lambs are prone to dystocia problems and excessively small lambs are at risk of hypothermia, respiratory diseases and other infections (Moule 1960, Al-Shorepy and Notter 1998). This suggests an intermediate optimum weight for birth. Lamb survival for meat breeds has been shown to be maximised at birth weights of 5.2 and 5.5 kg by Smith (1977) and Notter and Copenhaver (1980), respectively. However, as is common for sheep, average birth weights in their respective populations were below these optimums being only 4.1 and 3.9 kg. Donnelly (1982) quoted 'ideal' birth weights for Merinos of between 3.5 and 4 kg, but pointed out that in his study the observed birth weights were well above this weight. Seasonal differences also affect birth weight, with autumn born lambs having reduced birth weights compared to spring born lambs (Shelton 1964, Shelton and Houston 1968, Al-Shorepy and Notter 1998).

Heritabilities for birth weight have been reported to range from 0.02 to 0.45, with a weighted mean of 0.13 for wool breeds (Table 1.3) (Fogarty 1995). Al-Shorepy and Notter (1998) reported heritability estimates for spring born lambs to be twice that of autumn born lambs (0.26 and 0.12, respectively). Genetic and phenotypic correlations of birth weight with other weight traits are low to moderate (0.07 to 0.59) with a few exceptions (Table 1.3) (Fogarty 1995, Safari and Fogarty 2003). Genetic and phenotypic correlations with other production traits range from –0.41 to 0.98 (Fogarty 1995, Safari and Fogarty 2003). Genetic correlations reported by Fogarty (1995) and Safari and Fogarty (2003) between birth weight and clean fleece weight and fibre diameter range from –0.08 to 0.43, and –0.15 to 0.30 respectively.

Table 1.3 Weighted means of literature estimates of heritabilities (on diagonal), phenotypic correlations (above diagonal) and genetic correlations (below diagonal) (number, standard deviation of estimate) between weights and fleece traits taken from Fogarty (1995)

	BW	WW	YW	HW	GFW	CFW	FD
BW	***0.13*** ***(6,0.10)***	0.30 (18,0.10)	0.31 (3, 0.08)		0.24 (8, 0.07)	0.25 (5, 0.06)	0.01 (3, 0.08)
WW	0.39 (16,0.31)	***0.33*** ***(9,0.10)***	0.57 (11,0.09)		0.29 (21,0.11)	0.29 (9, 0.07)	0.08 (9, 0.08)
YW	0.32 (3, 0.25)	0.86 (10,0.11)	***0.48*** ***(2,0.20)***		0.38 (7, 0.08)	0.29 (2, 0.01)	0.07 (3, 0.05)
HW				***0.57*** ***(19,0.20)***			
GFW	0.25 (8, 0.30)	0.33 (20,0.23)	0.28 (7, 0.12)			0.88 (19,0.04)	0.28 (18,0.12)
CFW	0.12 (5, 0.28)	0.24 (8, 0.24)	0.09 (2,0.05)		0.84 (20,0.08)		0.27 (15,0.13)
FD	0.17 (3, 0.19)	0.04 (9, 0.30)	-0.11 (3, 0.15)		0.17 (20,0.16)	0.21 (17,0.14)	

Traits: BW, birth weight; WW weaning weight; YW, yearling weight; HW, hogget weight; GFW, greasy fleece weight; CFW, clean fleece weight; FD, fibre diameter.

1.3.2 Weaning Weight

Weaning weight is important in the production system. It is the point at which an animal no longer has its mother's milk as a supply of nutrients and is often the time of sale of the slaughter animal. Weaning weight is important in the consideration of ewe productivity as well as the lambs own productivity. Al-Shorepy and Notter (1996) suggest that correlations of litter size with weaning weight indicate that larger animals may produce larger litters. However, they also suggest that larger animals at weaning may be less fertile, due to the negative correlation between weaning weight and subsequent fertility. Snyman *et al.* (1996) indicate that selection for another ewe reproduction trait, total weight of lamb weaned, would increase weaning weight as outlined in the previous section. Snyman *et al.* (1998c) suggest that the opposite is also true, selection for body weights will improve the total weight of lamb weaned due to high positive correlations between them. In a study by Clarke *et al.* (1997), Romney sheep lines selected for weaning weight or yearling weight were compared to their respective randomly selected control line. They found that the weaning weight selection line was consistently superior to its control for body weight, but was significantly lighter than the yearling weight selection lines. Commonly, in dual purpose and meat breeds of sheep, selection for increased growth rate is based on body size (Clarke *et al.* 1997). So weaning weight has significant implications for both reproductive assessment of the ewe and growth of the lamb.

Fogarty (1995) reported that heritabilities for weaning weight are generally larger than for birth weight, but still range from 0.03 to 0.57, with a weighted mean of 0.33 (Table 1.3). Safari and Fogarty (2003) report a larger range of heritabilities from 0.01 to 0.89. Genetic and phenotypic correlations between weaning weight and other weight traits are moderate to highly positive (0.39 to 0.87). However, correlations with other production traits vary greatly. Genetic correlations for weaning weight and clean fleece weight range from –0.13 (Olesen and Husabo 1994) to 0.53 (Walkley *et al.* 1987), and fibre diameter range from –0.32 (Elliott *et al.* 1979) to 0.53 (Table 1.3). Parameters estimated since 1995, are all generally within the ranges reported by Fogarty (1995) (Clarke *et al.* 1997, Safari and Fogarty 2003).

1.3.3 Maternal Effects

In animal production, individual performance is a result of the individuals' own genetic makeup and the environment in which it is raised. Prior to weaning it is the maternal environment that is one of the most important factors for a young animal (Garrick 1990).

Traits recorded early in the animal's lifetime are most affected by maternal effects (Bradford 1972, Robison 1981). The maternal environment refers to the pre-natal environment provided by the ewe as well as the milking and mothering ability of the dam, where the mothering ability includes the behaviour of the dam towards the offspring. Therefore, the genetic effects on the phenotype of a lamb or calf are made up of half of the direct genes supplied by the dam, or the individuals genotype (direct effect), and the genotype of the dam for milking and mothering ability (maternal effect) (Garrick 1990, Herd 1990, Meyer et al. 1991, Meyer 1992), as well as the obvious environmental effects on both ewe lactation and lamb growth.

It is not clear what the size of maternal effects, and their relationships with direct genetic effects are (Hagger 1998). The nature of the correlation between direct and maternal genetic effects has not been confirmed but are generally negative between direct and maternal genetic effects. For example, Nasholm and Danell (1996) found a small positive correlation when studying daily gain, whereas Notter (1998) suggested that there is relatively strong evidence for a negative relationship between maternal and direct genetic effects for weaning weight. More reliable breed specific estimates of genetic parameters for use in genetic evaluation are required for Australia, especially for multiple trait breeding objectives and if different breeds are included in the model of analysis (Meyer *et al.* 1991). Some of the variation seen may be due to several factors that cause complications in calculating values for traits that are influenced by maternal effects. One of these factors is the nature of the maternal effect itself. Because the dam provides half of the offspring's genes and displays maternal effect, the direct and maternal effects are often confounded, this makes it hard to separate and estimate the correlations between them (Garrick 1990, Meyer 1992). Another factor may be sensitivity to the structure of the data. Gerstmayer (1992) found that the correlation between direct and maternal effects was strongly affected by the population structure, such as low numbers of progeny per dam and a high proportion of dams without a record.

1.3.4 Post-Weaning Weights

Post-weaning weight is used here as a general term referring to weights measured after six months of age (i.e. including yearling and hogget weights) but not adult weights (i.e. post 20 months of age). Weights are currently the most common selection criteria used to improve growth rate. Heritabilities are greater for post-weaning weights than for birth or weaning weights. A study by Clarke *et al.* (1997) on lines selected for weaning or yearling weights showed that selection for yearling weight produced significantly heavier sheep at weaning as well as yearling age. A difference in the patterns of muscle and fat development was noted and a commercial benefit was expected from the yearling weight selection lines if lambs were marketed on a live weight basis. This difference may be due to early maturation of intermuscular fat in sheep (Wood *et al.* 1980, Berg and Walters 1983). Therefore, selection for yearling weight may produce earlier maturing sheep in rclation to their mature weight than if selection were earlier (e.g. for weaning weight). Selection for increased live weight may increase weight at slaughter, but unless live weight selection is coupled with selection for improved carcase characters, it would not improve the carcase characteristics or composition.

The genetic parameters estimated for post-weaning weights support their use as selection criteria for increased carcase weights. Fogarty (1995) reported heritabilities ranging from 0.11 to 0.82, with weighted means for wool breeds of 0.26 for weight at 6 to 9 months, 0.45 for yearling weight and 0.57 for hogget weight (Table 1.3). Weighted means were lower for dual-purpose and meat breeds than for wool breeds. Genetic and phenotypic correlations of the post-weaning weights amongst themselves were high (0.54 to 0.97). Correlations with birth and weaning weights were lower (0.07 – 0.32). Correlations with other production traits were very variable. Genetic correlations reported in Fogarty (1995) between yearling weight and clean fleece weight were 0.08 (Gunawan *et al.* 1985) and 0.15 (Brash *et al.* 1994b), and yearling fibre dimeter was -0.02 (Brash *et al.* 1994b) (Table 1.3). Parameters estimated since 1995 are in agreement with the ranges reported in Fogarty's review (1995) (Clarke *et al.* 1997, 1998, Conington *et al.* 1998, Nicoll *et al.* 1998, Safari and Fogarty 2003).

1.4 CARCASE COMPOSITION

The consumption of lamb has declined noticeably over the past 30 years (Lewis *et al.* 1993). In order to slow and reverse this trend what is produced needs to be what the consumer demands (Stanford *et al.* 1998). In recent years, the Australian lamb industry has set about improving lamb products and lamb image across the industry and in the market place (Hopkins and Fogarty 1998). Reduced fat and increased consistency of product are the main requirements of the modern consumer. Carcase weight and fat depth are the two main specifications for carcases, with some use of conformation by processors and retailers (Hopkins and Fogarty 1998). Lamb producers, wholesalers and retailers are showing increased interest in individual animals rather than placing all emphasis on average weight and fat (Hall *et al.* 1995b). It has been shown that carcase weight of animals of a particular breed and sex is closely associated with carcase composition (Kirton and Barton 1958). To better meet consumer demand, lamb carcases should be evaluated in terms of meat quality attributes (e.g. tenderness and flavour) and carcase composition (e.g. proportion of lean fat and bone). Technology is rapidly changing and there are now many methods of predicting and manipulating carcase composition. For genetic selection purposes, measurement of body composition in young, live animals is preferred enabling animals with superior body composition to be selected as breeding stock as early as possible. However, so that processors can determine the most appropriate market for the meat produced, measurements of carcase composition are required in the carcase itself. So relatives of breeding stock should be evaluated to allow the indirect evaluation of the breeding stock through estimated breeding values.

1.4.1 Measurement in the Live Animal

Subjective measurements

Visual assessment and condition scoring is a quick, inexpensive method of predicting body composition (Kempster 1984) and has been used widely for many years. Nicol and Parratt (1984) suggest that experienced livestock evaluators have been able to use this technique with relatively high accuracy. However, maintaining standards over time and space limit the accuracy and usefulness of subjective live animal measurement (Stanford *et al.* 1998).

Ultrasound measurement

Ultrasound equipment emits high frequency sound waves, which are reflected from the boundaries between tissues of different bioacoustic densities (Stanford *et al.* 1998). Subcutaneous fat depth can be measured using ultrasound scanning. This can be used as a selection tool in a similar manner to eye muscle area or can be used to monitor growth and assist in early selection for target markets. Stanford *et al.* (1995) found that fat depth was a better predictor of saleable meat yield (percentage of carcase that can be sold as meat) than live weight. Heritabilities for fat depth range from 0.01 to 0.61 and genetic correlations between fat depth and growth are generally positive and moderate (Fogarty 1995, Safari and Fogarty 2003). Significant improvements in sheep body composition have been observed after 3-4 years of selection using ultrasound measurements of eye muscle depth and fat depth with live weight (Cameron and Bracken 1992).

Ultrasound equipment can also be used to measure the depth, width and area of the loin muscle (eye muscle). The size of this cut of meat is an indicator of the carcase quality as prime lamb and the yield of lean meat from that carcase (Kenney *et al.* 1995). Although the eye muscle area has stronger genetic correlations with lean meat (Kenney *et al.* 1995), eye muscle depth is easier to measure. Eye muscle width is not so easy to record and its measurement is less accurate. For that reason, eye muscle depth is more frequently used. Kenney (1997) found that it is preferable to measure both depth and width (if eye muscle area is not possible) for use to increase the size of loin or lean meat in selection. However, eye muscle depth may be more important if the shape of the loin is the trait to be manipulated. Kenney (1997) also found that the phenotypic correlation between eye muscle area and eye muscle depth was much greater (0.81) than that between area and width (0.47). Genetic correlations were very high although no standard errors were presented. These estimates were confirmed in Fogarty (1995) and Safari and Fogarty (2003) review's. Heritabilities for eye muscle area, range from 0.08 to 0.45, for eye muscle depth, range from 0.11 to 0.54, and for eye muscle width, range from 0.04 to 0.15 (Fogarty 1995). Weighted means of genetic correlations of eye muscle area and production traits were reported in the range –0.41 to 0.51.

1.4.2 Measurement in the Carcase

Subjective measures

As with live animal body composition, subjective assessment is a quick and inexpensive method of estimating carcase composition. Subjective assessment of fatness or conformation is used for commercial evaluation of lamb carcase composition in many countries including Australia, South Africa, and USA (Jones *et al.* 1992). Carcase fatness and conformation are related. Lamb carcases with good conformation are generally fatter than those with poor conformation (Kempster *et al.* 1981, Stanford *et al.* 1995). Subjective assessment for evaluation of carcases has been more useful when the lambs assessed are from a diverse range (i.e. from different breed types, age or size) (Kirton *et al.* 1992, Tatum *et al.* 1998), compared to assessment of uniform lamb groups (Kempster *et al.* 1981). However, even in these diverse groups subjective measures have only been marginal predictors of carcase composition (Stanford *et al.* 1998).

Carcase Weight

Carcase weight has been shown to be associated with carcase composition for a particular breed and sex (Barton and Kirton 1958). It has also been found to be a superior predictor of carcase fat content (kg) over dressing percentage, as carcase weight is not influenced by variation in gut fill (Barton and Kirton 1958) and is not subject to as many measurement errors as specific gravity (Kirton and Barton 1958). This is supported by Nicoll *et al.* (1998) reporting that Suffolk sired lambs had heavier hot carcase weights and displayed rapid early growth with high fat levels at slaughter. However, carcase weight is not as useful when predicting the proportion or percentage of fat, muscle and bone in the carcase (e.g. Kirton *et al.* 1985, Stanford *et al.* 1998). One of the main reasons for the use of hot carcase weight is the ease and therefore, minimal cost to measure.

There is much variation in heritabilities estimated for carcase weight. For example, 0.17 estimated by Henningsson and Malmfors (1995, cited by Conington *et al.* 1998) and 0.39 (Conington *et al.* 1998). Conington *et al.* (1998) reported genetic correlations for carcase weight, ranging from –0.73 for correlations with pre-slaughter condition score, to unity for correlations with shoulder weight and dissected lean. Phenotypic correlations were slightly less extreme ranging from 0.12 to 0.89. Considering the widely proclaimed use of carcase weight as a predictor of carcase composition (carcase fat content), there are few genetic parameter estimates reported in the literature for carcase weight as a predictor of carcase composition especially for Merinos.

Linear Measures and Grade Rule

Attempts to establish carcase composition using simple, inexpensive and accurate methods using carcase dimensions and fat or muscle depths have occurred for many years (Palsson 1939, Timon and Bichard 1965, Stanford *et al.* 1997). However, no single measurement or group of measures has been identified as optimum for prediction (Stanford *et al.* 1998). Palsson (1939) suggested several carcase measurements including, maximum width and depth of the longissimus muscle, maximum depth of back fat over the rib and longissimus muscle, and carcase length. Kempster (1981) concluded that carcase dimensions are poor individual predictors of carcase composition, but Stanford *et al.* (1997) found that the use of several carcase dimension measurements were useful for the prediction of saleable meat yield and percent of leg primal. However, several carcase measurements (eg depth of the longissimus muscle, fat depth at C and GR sites) would be considered too time consuming for practical use.

Grade rule, or GR, is the total tissue thickness between the carcase surface and the region of the 12th rib, measured 110mm from the carcase midline (Kirton *et al.* 1985, Hopkins and Fogarty 1998, Stanford *et al.* 1998). GR is generally measured in Australia with an optical probe (Hopkins *et al.* 1995a). GR has been shown to explain 40 to 76% of the variation in weight of carcase fat and lean (Jones *et al.* 1992). It has also been shown that using both GR and carcase weight improves the prediction of saleable meat yield (Jones *et al.* 1992, Hopkins *et al.* 1995b). Hopkins and Fogarty (1998) extended this to show that with the inclusion of carcase measured eye muscle area an additional 17% of the variation in saleable meat yield is explained. Generally fat depths measured in the carcase have higher heritabilities than live fat measurements. Heritabilities reported by Fogarty (1995) and Safari and Fogarty (2003) ranged from 0.15 to 0.54 and genetic and phenotypic correlations between live fat records and carcase fat measurements range from 0.39 to 1.0.

1.5 WOOL TRAITS

1.5.1 Reproduction and Wool Traits

It is important to have an indication of the effect of an improvement in productive performance on reproduction traits and vice versa. For the Merino, the impact of reproductive rate improvement on wool traits is important. Correlation estimates between greasy fleece weight and number of lambs weaned are variable and range from –0.85 to 0.87 (Kennedy 1967, Cloete and Heydenrych 1987, Davis 1987). Correlations between clean fleece weight and number of lambs weaned are just as variable ranging from –1.13 to 0.64 (Kennedy 1967, Cloete and Heydenrych 1987, Davis 1987). Fogarty (1995) calculated the weighted means of the correlation between greasy fleece weight and clean fleece weight with number of lambs weaned to be –0.10 and –0.13 respectively (Table 1.4). While the weighted means indicate a negative relationship, the variability of the values reported for Merinos would indicate that correlations between composite reproductive traits and fleece weights needs to be studied further.

Table 1.4 Weighted means of literature estimates of phenotypic and genetic correlations (number, standard deviation of estimates) between reproduction and fleece traits taken from Fogarty (1995)

		NLW	WLW	OR	LS	RA	SC
Phenotypic	**GFW**	-0.10 (5, 0.08)	0.09 (1)	0.11 (1)	0.03 (8, 0.07)	-0.02 (1)	0.12 (1)
	CFW	-0.13 (2, 0.07)		0.10 (1)	-0.01 (2, 0.12)	-0.01 (1)	0.08 (1)
	FD	-0.04 (2, 0.06)		0.01 (1)	-0.04 (2, 0.01)	-0.02 (1)	-0.01 (2, 0.05)
Genetic	**GFW**	-0.16 (5, 0.34)	0.53 (1)	-0.10 (1)	0.01 (8, 0.15)		0.31 (1)
	CFW	-0.10 (2, 0.78)			0.14 (2, 0.08)		0.15 (1)
	FD	0.13 (2, 0.51)			0.08 (2, 0.17)		0.39 (2, 0.26)

Traits: NLW, number of lambs weaned; WLW, weight of lambs weaned; OR, ovulation rate; LS, litter size; RA, rearing ability; SC, scrotal circumference; GFW, greasy fleece weight; CFW, clean fleece weight; FD, fibre diameter.

Weighted means of correlations between fleece weights and component reproductive traits (e.g. litter size) are very low and close to zero (Table 1.4) indicating that there may be no detrimental interactions between reproductive rate and fleece traits. Estimates of genetic correlations between fibre diameter and number of lambs weaned (per ewe joined and per ewe lambing) range from 0.28 to 0.50 in Merinos (Cloete and Heydenrych 1987, Davis 1987). Positive genetic correlations indicate that an increase in reproductive rate will increase fibre diameter which is in contrast to the requirements of a wool producer. However, phenotypic correlations reported are negative but close to zero for both number of lambs weaned and other component reproductive traits (Table 1.4) (Cloete and Heydenrych 1987, Davis 1987, Fogarty 1995, Safari and Fogarty 2003).

Weighted means of correlations reported by Fogarty (1995) between the male reproductive trait scrotal circumference and fleece traits follow the same trend as the female traits (Table 1.4). Fleece weights with scrotal circumference have low correlations both phenotypic and genetic, and fibre diameter with scrotal circumference has negative but close to zero phenotypic correlation and moderate (0.39) genetic correlation.

1.5.2 Growth and Wool Traits

The Australian lamb industry relies predominantly on the Merino to supply ewes for lamb production. Some 40% of the annual slaughter is made up of lambs from Merino ewes, in addition to this crossbred Merino ewes are used to produce second cross lamb (Fogarty *et al.* 2000). The Merino, traditionally considered a wool breed, is providing a large proportion of the genes to the meat sheep of Australia and is actually being used as a dual-purpose breed. Now that this is being acknowledged within the industry and lamb prices have risen relative to wool there is greater interest in the relationship between wool and carcase in the Merino. Growth, measured as weights, has been well correlated with wool traits in the past. However there are few estimates of correlations between wool and carcase traits.

There are many published correlations, both phenotypic and genetic, between wool traits and live weights at various ages. These correlations are generally moderately positive (Table 1.5). This indicates that there is no antagonistic relationship between improving wool characters and increasing the live weight of Merinos. Fogarty (1995) only reports weighted means for correlations of live fat and muscle depth with greasy fleece weight and fibre diameter (Table 1.5). Estimates published since 1995 (Lee *et al.* 2002, Fogarty *et al.* 2003, Greeff *et al.* 2003) are similar to the weighted means (except for correlations between clean fleece weight and eye muscle depth which were low and positive). Estimates between other carcase traits such as pH and colour, which are related to the eating quality of the meat, and fleece traits have been reported by Fogarty *et al.* (2003) and Greeff *et al.* (2003). While the estimates from these two publications do not agree with each other they both indicate that with further investigation some improvement in meat quality of Merinos may be made using selection. Due to the scarcity of estimates between wool and carcase traits further investigation must be carried out on the Merino in the different environments within Australia.

Table 1.5 Weighted means of literature estimates of phenotypic and genetic correlations (number, standard deviation of estimates) between growth traits and fleece traits taken from Fogarty (1995)

		BW	WW	HW	FAT	EMD
Phenotypic	**GFW**	0.24 (8, 0.07)	0.29 (21, 0.11)	0.37 (21, 0.10)	0.15 (3, 0.02)	0.19 (1)
	CFW	0.25 (5, 0.06)	0.29 (9, 0.07)	0.29 (11, 0.09)		
	FD	0.01 (3, 0.08)	0.08 (9, 0.08)	0.13 (9, 0.05)	-0.00 (1)	
Genetic	**GFW**	0.25 (8, 0.30)	0.33 (20, 0.23)	0.21 (22, 0.17)	-0.08 (3, 0.27)	-0.55 (1)
	CFW	0.12 (5, 0.28)	0.24 (8, 0.24)	0.18 (13, 0.15)		
	FD	0.17 (3, 0.19)	0.04 (9, 0.30)	0.10 (11, 0.17)	-0.06 (1)	

Traits: BW, birth weight; WW, weaning weight; HW, hogget weight; FAT, live fat depth; EMD, live eye muscle depth; GFW, greasy fleece weight; CFW, clean fleece weight; FD, fibre diameter.

1.6 SUMMARY

There has been interest in the use of quantitative genetic methods to improve reproduction, growth and carcase composition for over half a century. Improvement of these three aspects of sheep production by genetic means is clearly possible.

Many studies have been carried out to determine how heritable female reproductive traits are and how they interact with other traits. The general conclusion is that female traits are lowly heritable, but while heritabilities are low, they are positive and sufficient variation occurs within these traits to allow for improvements to be made. Reproduction in the female is complex and can be divided into component traits that interact and make up composite traits. Component traits have higher heritabilities than composite traits and historically, the component trait litter size has been recommended and used in selection for improved reproductive rate. Female reproduction traits are expensive and difficult to measure, as well as being sex and age limited. Male reproduction traits have been investigated as alternatives to female traits. The literature suggests that it is possible to use male traits to improve female reproductive ability via indirect selection.

Growth of animals is generally improved or increased by selection for increased weight. Post-weaning weights have higher heritabilities than birth and weaning weights which are complicated by maternal effects. However, knowledge of the interactions of all of these weights is important for the genetic manipulation of growth patterns. At the time of slaughter low levels of fat, large amounts of lean tissue and consistency in relation to quality are desirable. Genetic selection can be used to achieve these requirements if live carcase measurements as well as weights are used for prediction of carcase composition.

The purpose of this study is to estimate genetic parameters for the traits corresponding to reproduction, growth, and wool specifically for Merino sheep. Studies have been carried out on Merinos in the past for wool traits and reproduction individually, but as the Merino is considered mainly as a wool producer there are relatively few estimates for growth and carcase composition for this breed. While further estimating genetic parameters for these trait groups individually, and identifying those that are outstanding for use in breeding objectives, the genetic relationship between wool and reproduction will be further developed and the genetic relationship between wool and growth traits will be investigated.

Chapter 2

General Materials and Methods

In this chapter the environment, sheep, records taken and the statistical procedures used are described in broad terms. Further details specific to each chapter are given within the chapter. Data from two South Australian Research and Development Institute projects were used in this thesis, the Turretfield Resource Flock (TRF) Project, for the reproduction study, and the Selection Demonstration Flock (SDF) Project, for the growth and carcase study. Both were used for associations of these traits with wool traits.

2.1 ANIMALS AND ENVIRONMENT

2.1.1 Turretfield Research Centre

Both of the above mentioned projects were based at the Turretfield Research Centre (TRC), which is located near Rosedale, 55km north east of Adelaide, South Australia. TRC is in the wheat-sheep zone of South Australia, and has an average annual rainfall of 464mm, of predominantly winter (May to September) incidence. At the commencement of the two projects, the TRC comprised 650ha at Rosedale and 420ha at Kingsford. Up to 300ha were cropped annually for pure seed or agronomic trials or as hay or grain crops for sheep feed. The combined carrying capacity of the remaining pasture land was 5000 dry sheep equivalents.

2.1.2 Turretfield Resource Flock

Background

The Turretfield Resource Flock was established in 1988. Ewes were a random selection purchased from four South Australian ("Strong-wool") Merino studs, representing two family groups. The studs were East Bungaree and Anama, which were representative of the Bungaree family group, and Collinsville and Southrose, which were representative of the

Collinsville family group. This created a flock of 2000 ewes ranging from two to six years of age.

Each year approximately 15 rams were purchased from each of the four Merino studs. These were randomly selected from rams that had been performance tested (Anama and Southrosc) or had been assigned various price grades (Collinsville and East Bungaree). The animals used in this project were born over four years (1989 – 1992). There were no like sires across years but there were good genetic linkages across years through dams.

Ram progeny were offspring of 158 sires, with an average of 15 progeny born per sire. In comparison, the ewe progeny were offspring of 150 sires, with an average of 14 progeny (at 16 months) per sire, (Table 2.1). The minor difference between ram and ewe progeny was simply due to the chance effect of some sires leaving only a small number of progeny of one sex.

Table 2.1 The size of the pedigree and overall number of records for each trait analysed in the Turretfield Resource Flock

Trait	Records	Animals	Sires	Dams
Number of lambs weaned	9890	2095	147	1486
Fertility	9890	2095	147	1486
Litter size	8123	2095	147	1486
Rearing ability	8123	2095	147	1486
Scrotal circumference	6702	2353	152	1723
Live weight	10985	4448	152	2443
Fleece traits	53484	4454	160	2440

Management

The management program for the flock reflected (as far as practicable) South Australian stud Merino industry practices. Mating took place over an eight-week period in November and December. Each year, approximately 12 sires (except during 1989, in which it was approximately five sires) from each stud were single sire mated on a within stud basis, to 40 randomly allocated ewes. Lambs were born in April-May and weaned at an average age of 13 weeks in early August. Ram and ewe lambs were managed separately following weaning. All lambs were shorn at about four months of age, soon after weaning. Thereafter, the ram progeny were shorn (six months wool growth) and performance recorded at 10 (February) and 16 (August) months of age, and were sold for slaughter after the 16 month assessment. The ewe progeny were shorn (12 months wool growth) and performance recorded at 16 months of age, and then shorn and performance recorded annually thereafter up to five and a half years of age, when they were discarded from the project. No conscious culling was conducted within the sire groups, therefore any losses were from deaths due to predation or disease only.

Records

For each experimental lamb born, the identity, age of the dam, date of birth, the type of birth and of rearing, and all management details were recorded. The complete list of characters from the TRF project used in this thesis is shown in Table 2.2.

Table 2.2 Traits recorded in the Turretfield Resource Flock and studied in this thesis

	Males				Females			
	Birth	Wean	10 mo.	16 mo.	Birth	Wean	16 mo.	2-5 years
No. of lambs weaned								✓
Fertility								✓
Litter size								✓
Rearing ability								✓
Scrotal circumference		✓	✓	✓				
Live weight	✓	✓	✓	✓	✓	✓	✓	✓
Fibre diameter			✓	✓			✓	✓
Clean fleece weight			✓	✓			✓	✓
Staple length			✓	✓			✓	✓
Staple strength			✓	✓			✓	✓

Wean = weaning, 10 mo = 10 months, 16 mo = 16 months

Measurements

All measurements were taken by a team of South Australian Research and Development Institute employees unless otherwise stated.

Number of lambs weaned (0, 1, and 2) was recorded as the number of lambs weaned per ewe joined per year. There were very few triplet births so they were grouped with twin births to create a multiple birth group.

Fertility (0 or 1) was recorded as whether or not a mated ewe had a lamb.

Litter size (1 or 2) was recorded as the number of lambs born per ewe lambing.

Rearing ability (0 – 1) was considered as a trait of the ewe and was calculated as the proportion of lambs born that were reared to weaning.

Average traits were calculated as the average of the trait over the ewe's reproductive life (four years).

Scrotal circumference (cm) was measured at weaning (5 months), 10 months and 16 months of age with a measuring tape, at the point of maximum diameter along the testicle.

Live weight (kg) was measured shortly after birth, and approximately one month after each shearing (4 months, 10 months (ram progeny only), 16 months and every 12 months following (for ewe progeny)). The live weight was determined using a Ruddweigh® electronic weighing system.

Fibre diameter (μm) was measured by the Turretfield Fleece Measurement Service. A sample from the mid-side fleece sample was measured using a CSIRO developed Fibre Diameter Analyser. The fibre diameter of the samples was measured in a controlled climate of 20 degrees Celsius and 60 per cent humidity.

At each shearing, mid-side fleece samples were taken from the right and the left side of each fleece. The remainder of the fleece, the mid-side fleece samples and the belly were weighed on a weigh pan, and this weight was recorded as the sheep's greasy fleece weight (kg).

Yield (percentage) was measured by the Turretfield Fleece Measurement Service. Approximately 50 grams of the mid-side fleece sample was weighed at room temperature before going into the scourer and then re-weighed after drying and cooling to room temperature. Yield was calculated as the weight of the wool after washing as a percentage of the original greasy wool weight (Equation 2.1).

$$\text{Yield} = (\text{post-wash weight of sample} / \text{pre-wash weight of sample}) \times 100 \qquad \text{(Equation 2.1)}$$

Clean fleece weight (kg) (CFW) was calculated using the above two measurements (Equation 2.2).

$$\text{CFW} = (\text{Greasy Fleece Weight} \times \text{Yield}) / 100 \qquad \text{(Equation 2.2)}$$

Staple length (mm) and Staple strength (Newtons per kilotex N/ktex) were measured by Australian Wool Testing Authority, located in Fremantle using the Automatic Tester for Length and Strength (ATLAS) machine. Fifteen staples from the mid-side fleece sample were used to measure staple length and strength and average values were obtained.

2.1.3 Selection Demonstration Flocks

Background

The Selection Demonstration Flock Project was established in 1996 as a means of illustrating the relative advantages and disadvantages of the alternative breeding strategies available to the sheep industry. Five drops of lambs have been produced at Turretfield Research Centre (1997 – 2002) and a further three drops are expected before the project ends. However, only the 2000 and 2001 drops have been used in this thesis.

Commencing with a first lamb drop born in 1997, four flocks, each comprising 200 ewes were established:

1. Control flock. Selection was at random, 20 sires per year were used to minimise random genetic drift.
2. Selection mainly based on objectively measured performance records (MPR), but with some attention to visually assessed wool and body faults.
3. Selection mainly based on professional classer assessment of wool quantity and quality (PCA), and on the ability of the sheep to thrive and reproduce. Occasional and non-systematic use of objective measurement data.
4. Elite wool flock (EWF). Selection largely based on the technological package that favours sheep having smooth, loose and pliable skin. The approach is commonly known as 'soft rolling skin' (SRS™) or as 'elite wool' and its rationale is given by Elliott (1996) and Watts (1995). It involves a visual and tactile evaluation of the skin, use of objective measurement and matching of sire and ewe characteristics.

These four flocks will be referred to as 'conventional Merinos', to distinguish them from another, more specialised flock, that was established in 2000, namely:

5. The Meat Merino line (Fibre Meat Plus, FM+). The emphasis in this flock was on growth, carcase traits and reproduction, while paying attention to wool quality (fibre diameter

in particular), but only maintaining fleece weight. A total of 190 ewes selected according to an agreed breeding objective emphasising meat related traits (high reproductive rate, growth rate and muscling, and low fibre diameter) were assembled at Turretfield Research Centre. The first artificial insemination (AI) of these ewes took place in January 2000. Four Merino sires were selected according to the breeding objective using Lambplan records and any other performance information available. One Dohne Merino sire was also used. A breeding objective accommodating the following aims has been used when choosing ewe and ram replacements; maintain a high clean fleece weight and approximately 19µm wool, increase reproductive rate, improve: lamb growth rate, carcase quality, and eating quality. The lambs born in 2000 were fully pedigreed and intensely recorded for reproduction, wool and body traits. The lambs have been run in such a way as to enable the comparison with the conventional Merinos in the SA Selection Demonstration Flocks (Ponzoni *et al.* 2000). This will allow the monitoring of progress in reproduction, growth, carcase traits, as well as any changes that could occur in wool traits, and will constitute a direct and highly credible means of benchmarking.

Size and Origin of the SDFs

Each of the conventional Merino flocks (numbers 1 to 4 above) consisted of 200 breeding ewes plus all the corresponding followers. The ewes that formed the basis of these SDFs originated from the TRF described previously. Such ewes were considered to be representative of what was present at the time of beginning the project (1996) in the majority of South Australian Merino flocks.

The FM+ flock (number 5 above) also consisted of about 200 breeding ewes. It was established mainly based on contributions of highly selected ewes by seven participating ram breeders and producers. In addition approximately 23 per cent of ewes were selected from the TRF and SDF projects.

Ram Breeding Policy

The 20 rams initially used in the Control (number 1 above) were purchased in 1993 and 1994 as hoggets for the TRF project, constituting a random selection from the four earlier mentioned South Australian Merino studs (Anama, Collinsville, East Bungaree and Southrose). Twenty new young rams bred within the flock and chosen at random within sire groups were used each year.

SDFs number 2 – 4 (MPR, PCA and EWF) were open to outside sires for the first two matings, which resulted in the 1997 and 1998 lamb drops. From that time onwards, each flock bred its own replacement sires. The FM+ (number 5 above) was open to outside sires for the matings that resulted in the 2000 and 2001 drops.

Sheep Generated to Date

For SDFs 1 – 4, seven rounds of ewe and sire selection have taken place (1996 to 2002). The first drop of lambs was born in June-July 1997, and the sires for the (January) 1999 mating were selected late in 1998 from this drop. The second drop of lambs was born in June-July 1998, and sires for the (January) 2000 mating were selected late in 1999 from this drop. Similarly, the third to sixth drops of lambs were born in June-July 1999 to 2002, and sires for the (January) 2001 to 2003 matings were selected late in 2000 to 2002 from these drops, respectively. Six of the selected sires have been used for mating more than one year, thus providing a genetic link across years.

In the FM+ flock, four rounds of ewe and sire selection have taken place (1999 to 2002). The first two rounds involved the introduction of outside sires, whereas in the third and fourth round a combination of outside and home-bred sires was used. The first drop for this flock was born in June-July 2000, and 3 sires for the (January) 2002 mating were selected from this drop. A second drop for this flock was born in 2001, a third in 2002 and a fourth in 2003. 1791 progeny were offspring of 89 sires, with an average of 18 progeny born per sire (Table 2.3). For the purposes of this study only data from the 2000 and 2001 drops was available.

Table 2.3 The size of the pedigree and overall number of records for each trait analysed in the Selection Demonstration Flocks

Trait	Records	Animals	Sires	Dams
Live weight	15500	1791	89	1052
Fat depth	11796	1791	89	1052
Eye muscle depth	11796	1791	89	1052
Fleece traits	6598	1791	89	1052

Management

Mating occurs for all flocks in January and February. Each year, 20 rams were mated to 10 ewes each in the Control flock and between four and six rams were single sire mated to between 30 and 50 ewes in the other flocks. Lambs were born in June - July and weaned in September - October (at an average of 12 weeks of age). Subsequently rams and ewes were managed separately. All lambs were shorn in October/November and then again as hoggets the following October/November.

The 2000 drop animals were exposed to very high water salinity levels during January 2001. A section of the North Para River, the lambs' water supply, had salt levels up to 8000ppm, which is 3000ppm above what is considered tolerable by lambs (Landcare Notes 1999). Lambs were removed from this area and were grazed on pea stubbles with supplementary feed (0.5kg/head/day of barley/pea mix and 0.5kg of oaten hay/head/day) until the condition of the lambs improved to a satisfactory level. It was believed that this high salt level was the cause of condition loss. However, the same drop in condition occurred at the same time for the 2001 drop with appropriate salt levels, although at 7 months there were less deaths in the 2001 drop (6.5 per cent versus 3.3 per cent).

Records

For each experimental lamb, the identity, age of the dam, date of birth, the type of birth and of rearing, and all management details were recorded. The complete list of characters from this project used in this thesis is shown in Table 2.4.

Table 2.4 Traits recorded in the Selection Demonstration Flocks and studied in this thesis

	Birth	Wean	4 months	5 months	7 months	8 months	10 months	13 months	16 months
Live weight	✓	✓	✓	✓	✓	✓	✓	✓	✓
Fat depth			✓	✓	✓	✓	✓	✓	✓
Muscle depth			✓	✓	✓	✓	✓	✓	✓
Fibre diameter									✓
Clean fleece weight									✓
Staple length									✓
Staple strength									✓

Measurements

All measurements were taken by a team of South Australian Research and Development Institute (SARDI) employees unless stated.

Live weight (kg) was measured within 24 hours of birth, at weaning (average of 12 weeks old) and five measurements approximately every six weeks from an average of 15 weeks of age with two later measurements at yearling and hogget age. All live weights were determined using a Ruddweigh electronic weighing system. Birth and weaning weights were measured by SARDI staff and subsequent measurements were taken by an accredited Lambplan assessor.

Fat and eye muscle depth (mm) was measured using an ultrasound scanner by an accredited Lambplan assessor approximately every six weeks from an average of 15 weeks of age, with two later measurements at yearling and hogget age. Both measurements were taken between the 11th and 12th rib.

Fibre diameter (μm) was measured by Australian Fibre Testing.

One month prior to shearing, a mid-side fleece sample was taken from one side of each sheep. At shearing the fleece and the belly were weighed on a weigh pan, and this weight was recorded as the sheep's greasy fleece weight (kg).

Yield (percentage) was also measured by Australian Fibre Testing.

Clean fleece weight (kg) was calculated using the above two measurements (Equation 2.2).

Staple length (mm) and Staple strength (Newtons per kilotex N/ktex) were measured by Australian Wool Testing Authority.

2.2 DATA EDITING

In all data sets an entire progeny group was discarded if a sire had less than five offspring. In addition, because of low numbers, triplet born lambs were combined with twin born counterparts for analysis. For example, a triplet born lamb that was raised as a twin was combined with twin born lambs raised as twins in the type of birth and rearing class. Similarly, offspring of eight and nine year old dams were combined with those of six year old dams.

2.3 STATISTICAL ANALYSIS AND NOTATION

The models used for each analysis are detailed in the relevant chapter, the general procedure is outlined below. The levels of factors and their abbreviations for each data set and any notation that has been used throughout the thesis is defined below.

A sire model was run initially using PROC MIXED (SAS 1999) to determine significant fixed effects. This model was also used to estimate variance between sire and total phenotypic variance components for each trait, which were then used as starting values for univariate analysis by restricted maximum likelihood procedure within ASReml (Gilmour *et al.* 2002). Multi-variate analyses were then used to estimate genetic parameters determined by fitting a restricted maximum likelihood procedure animal model to the data that included the predetermined fixed effects. For each trait, there were a several parameter estimates calculated from multi-trait analyses. The variance of these different parameter estimates for each trait was determined. The variances indicated that the variation among the estimates from different analyses was small. Confidence intervals calculated from these variances were much smaller than those obtained using the standard errors given by ASReml. This indicates that the parameter values for any given trait were not influenced by the context in which they were in multi-trait analyses. Consequently, the different multi-trait estimates were averaged to represent one multi-trait estimate for the heritabilities and correlations of the traits used in this thesis.

Note that the methods used to estimate the genetic parameters (i.e. heritabilities and genetic correlations) determined only the genetic variation in a particular character that could be attributed to additive genetic differences between individuals. Genetic differences due to dominance deviations or interaction deviations (i.e. epistasis: interaction among two or more non-allelic genes) were ignored, since these sources of genetic variation are difficult to estimate accurately given the family structure of the data. Maternal genetic effects were not able to be estimated due to the lack of depth in the pedigree available.

Throughout this thesis, heritabilities and correlations will be referred to as very low to very high according to the classification in Table 2.5 (adapted from Brown and Turner 1968). All standard errors will be reported at one decimal place more than the corresponding parameter rather than as an indication of accuracy of the measurement.

Table 2.5 Classification of heritability and correlation estimates

Classification	Heritability	Correlations
Very low	< 0.10	0.00 – ±0.19
Low	0.10 – 0.24	±0.20 – ±0.39
Moderate	0.25 – 0.39	±0.40 – ±0.59
High	0.40 – 0.59	±0.60 – ±0.79
Very high	≥ 0.60	≥ ±0.80

2.3.1 Factor Levels

Reproduction Analysis using Turretfield Resource Flock Data

Factors for reproduction and associated fleece analysis are defined as follows:

- Sire of the lamb – 453 levels
  - Year 1. 166 levels
  - Year 2. 134 levels
  - Year 3. 94 levels
  - Year 4. 59 levels
- Year – 4 levels (1989 – 1992)

- Flock of Origin – 4 levels
- Type of birth and rearing (Tobr) – 3 levels (singles raised as singles 11, multiples raised as singles 21, multiples raised as multiples 22)
- Age of dam (Aod) – 4 levels (ewes aged 2 – 5)

Growth Analysis using Selection Demonstration Flock Data

Factors for growth and associated fleece analysis are defined as follows:

- Year – 2 levels (2000 – 2001)
- Flock – 5 levels (Control, MPR, PCA, EWF, FM+)
- Type of birth and rearing (Tobr) – 3 levels (singles raised as singles 11, multiples raised as singles 21, multiples raised as multiples 22)
- Age of dam (Aod) – 4 levels (ewes aged 2 – 6)

2.3.2 Matrix and Vector Notation

Matrix and vector notation used in this thesis is defined as follows:

$x^{n\times 1}$ = a vector "x" of length *n*.

$X^{n\times q}$ = a matrix "X" with *n* rows and *q* columns.

Also, standard statistical notation will be used, so

$$y \sim N\{\mu, \sigma^2\}$$

is interpreted as "y" being normally distributed with mean μ ("mu") and variance σ^2 ("sigma squared").

Where the model fitted is described symbolically interactions between two effects are noted using a colon. For example year by sex interaction symbolically is `year:sex`.

Chapter 3

Genetic Parameters for Reproduction Traits

3.1 INTRODUCTION

Female reproductive efficiency is one important component of the overall productivity of sheep. Much variation exists within and between breeds, flocks, ewes and rams for this complex attribute (Purvis and Hillard 1997). However, the low heritabilities of reproductive traits reported in the literature mean that achieving genetic improvement within a flock is difficult. Number of lambs weaned per ewe joined is a commonly used measure of female reproductive efficiency which has several components (i.e. fertility, litter size and rearing ability). Because of the low heritabilities, and the labour intensive nature of performance recording female reproduction traits, male characters such as scrotal circumference have also been investigated for their possible use as indirect selection criteria.

The suggestion that a genetic relationship exists between male and female reproduction traits is based on the physiological fact that the same hormones are involved in gonadal development and reproductive ability of both sexes (Land *et al.* 1980). Testis size of the male has been suggested as an indicator of female reproductive ability (Land 1973). This hypothesis has been supported by evidence of correlated responses in female or male traits after selection on reproduction traits of the other sex in mice (Islam *et al.* 1976, Eisen and Johnson 1981, Hill *et al.* 1990), pigs (Cunningham *et al.* 1979, Schinckel *et al.* 1983), cattle (Toelle and Robison 1984) and sheep (Land and Carr 1975, Hanrahan and Quirke 1977, Ricordeau *et al.* 1979, Burfening and Tulley 1982, Purvis *et al.* 1988).

As Purvis *et al.* (1988) point out, contradicting results have been found. Hanrahan and Quirke (1977) reported a significant correlated response in testicular diameter from selection on ovulation rate in Finnish Landrace sheep. Whereas Land *et al.* (1982) and Haley *et al.* (1990) found no change in female reproduction when selecting for testicular diameter adjusted for live weight in Finn-Dorset crossbreds. The disagreement between these results may be due to the difference in the definition of the male trait of interest. Definition of reproduction traits is important when attempting to determine the value of a trait as a selection criterion. In order to predict responses in reproductive traits, heritabilities, phenotypic and genetic correlations among these traits and others in the breeding objective must be known. In this chapter, phenotypic and genetic parameter estimates are reported for female and male reproductive traits for South Australian Merino sheep.

3.2 MATERIALS AND METHODS

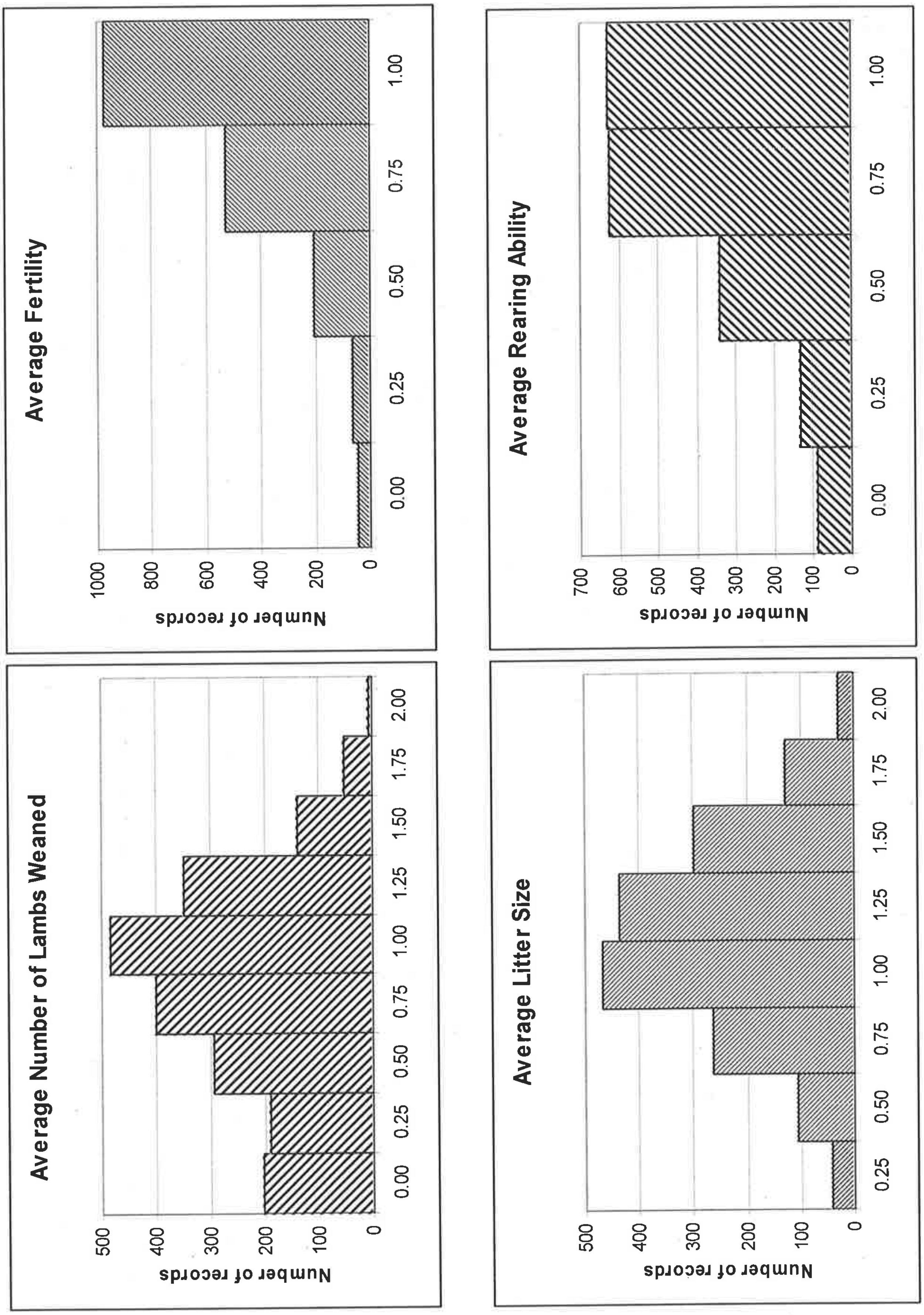
The data are from the Turretfield Merino Resource Flock (Chapter 2.1.2) with the number of records, mean, standard deviation and the range for each of the traits shown in Table 3.1. The distribution of the average female traits is shown in Figure 3.1. Average Female traits are closer to a normal distribution than traits at individual ages.

Table 3.1 Number of records available (n), mean, standard deviation (s.d.), coefficient of variation (CV) and range for ewe reproduction, ram scrotal circumference and live weight

Trait	Abbreviation	n	Mean	s.d.	CV	Range
Number of lambs weaned per ewe joined	**NLW28**	2073	0.59	0.54	0.92	0 – 2
	NLW40	2006	0.87	0.62	0.71	0 – 2
	NLW52	1918	1.02	0.67	0.66	0 – 2
	NLW64	1820	1.07	0.69	0.64	0 – 2
	aNLW	2073	0.90	0.41	0.46	0 – 2
Fertility of the ewe – ewe lambing or not	**Fert28**	2073	0.68	0.47	0.69	0 – 1
	Fert40	2006	0.83	0.37	0.45	0 – 1
	Fert52	1918	0.87	0.34	0.39	0 – 1
	Fert64	1820	0.88	0.33	0.38	0 – 1
	aFert	2073	0.82	0.24	0.29	0 – 1
Litter size – number of lambs born per ewe lambing	**LS28**	1415	1.08	0.28	0.26	1 – 2
	LS40	1671	1.27	0.45	0.35	1 – 2
	LS52	1667	1.43	0.50	0.35	1 – 2
	LS64	1600	1.52	0.50	0.33	1 – 2
	aLS	1770	1.13	0.36	0.32	0.25 – 2
Rearing ability – ratio of lambs reared to lambs born	**RA28**	1415	0.55	0.49	0.89	0 – 1
	RA40	1671	0.70	0.44	0.63	0 – 1
	RA52	1667	0.73	0.41	0.56	0 – 1
	RA64	1600	0.72	0.41	0.57	0 – 1
	aRA	1770	0.69	0.28	0.41	0 – 1
Scrotal circumference (cm)	**SC5**	2336	17.5	3.76	0.21	9.0 – 30.5
	SC10	2202	26.4	3.54	0.13	12.0 – 39.5
	SC16	2164	31.8	2.88	0.09	17.0 – 40.5
Weaning weight (kg)	**WW**	2345	20.9	5.52	0.26	7.0 – 43.9
Live weights (kg)	**WT10**	2209	42.4	7.11	0.17	19.0 – 67.0
	WT16	2170	51.9	7.24	0.14	24.5 – 79.2

Figures after the abbreviation are months of age, aNLW = Average number of lambs weaned over a lifetime, aFert = Average fertility of the ewe, aLS = Average litter size, aRA = Average rearing ability

Figure 3.1. Distributions of average female reproduction traits (per lifetime).



Statistical Analysis

Data were analysed using linear mixed model methodology in ASReml (Gilmour *et al.* 2002). An animal term was fitted allowing optimal analysis of a finite population. All two-way interactions between fixed effects were tested but were non-significant and therefore were not included in the final models.

The final base model can be written as:

$$\mathbf{y} = \mathbf{X\tau} + \mathbf{Z}_1\mathbf{a} + \mathbf{Z}_2\mathbf{s} + \mathbf{e}$$

where

$$\mathbf{y} \sim \mathrm{N}\left(\mathbf{X\tau}, \sigma_a^2\mathbf{Z}_1\mathbf{A}\mathbf{Z}_1' + \sigma_s^2\mathbf{Z}_2\mathbf{Z}_2' + \sigma^2\mathbf{I}_n\right)$$

and

$$\mathbf{e} \sim \mathrm{N}\left(0, \sigma^2\right)$$

where $\mathbf{X}^{n\times t}$ is a design matrix which assigns the effects to animals, $\mathbf{\tau}^{1\times t}$ is the vector of fixed effect means, $\mathbf{Z}_1^{n\times p}$ is the design matrix for the animal effects, $\mathbf{A}$ is the numerator relationship matrix, $\mathbf{Z}_2^{n\times q}$ is the design matrix for the sire of the lamb effects. The vectors $\mathbf{a}$ and $\mathbf{s}$ represent the animal (ewe) and sire of the lamb effects respectively. $\mathbf{e}^{1\times n}$ is the vector of random errors. σ_a^2 is the variance due to the animal (ewe) effect, σ_s^2 is the variance due to the sire of the lamb effect and σ^2 is the residual variance parameter.

The model fitted to the data can also be symbolically written as:

y ~ mean + year (1989-1992) + flock (1-4) + type of birth and rearing (11, 21, 22) + linear regression(age of ewes dam) + animal + sire of the lamb

Terms fitted as random effects in the model are underlined, all other terms are fitted as fixed effects, with levels in brackets. This formed the base model for all analyses. Each variate was tested and the model was modified where necessary. Changes to the base model for each variate are shown in Table 3.2.

Table 3.2 Final models fitted to reproduction traits

Variate	Model fitted	Defined as
Number of lambs weaned	Base model	-
Fertility	Base model	-
Litter size	Base model without Sire of the lamb	-
Rearing ability	Base model	-
Average traits	Base Model without Sire of the lamb	
Scrotal circumference	Base model without Sire of the lamb + Day of birth	Model 1
	Base model without Sire of the lamb + Weight (Weaning, 10, or 16 months as appropriate)	Model 2
	Base model without Sire of the lamb + Day of birth and Weight (Weaning, 10, or 16 months as appropriate)	Model 3

A simple repeatability model was fitted to the female data with a genetic effect, a non-genetic effect and a residual. Fixed effects included were as in the base model. More sophisticated models allowing for different variances and for covariances between age did not show a significant improvement, hence the simpler model assuming equal variance at each age was considered to be sufficient. These analyses were performed using ASReml (Gilmour *et al.* 2002)

Female reproductive traits are generally discrete and are not normally distributed (eg litter size). The assumption of a continuous distribution was considered appropriate for this study using the justification found by Olesen *et al.* (1994). The average reproduction traits were closer to the REML assumption of normal distribution than at individual ages of measurement (Figure 3.1). Analysis of female reproduction traits initially included sire of the lamb as a fixed effect so that the variation due to this effect was removed. However, after comparison of analyses it was decided that sire of the lamb would be better fitted as a random effect for the final analysis. To obtain correlations between scrotal circumference and female reproduction traits data from progeny of the same sire were used in multivariate analysis with no phenotypic covariance estimated.

Heritabilities reported were from univariate analyses. Correlations between different ages of female traits were from multivariate analyses. Correlations between different ages of male reproductive traits, male live weight and between female and male traits were also from multivariate analyses. Heritabilities and correlations are referred to as very low to very high according to the classification in Table 2.5.

3.3 RESULTS

3.3.1 Female Reproduction

Fixed Effects

Analysis of variance tables for female reproduction traits are presented in Table 3.3. Least squares means for fixed effects are presented in Tables A.1 to A.4 (Appendix A). Between year effects were significant for all traits at all ages including average traits. Between year differences increased as age increased. For number of lambs weaned, litter size at older ages (40 – 64 months) and all average traits, except rearing ability, 1991 and 1992 were more productive by 14 to 46 %. For fertility, 1989 and 1990 were always the lowest years.

Flock of origin effects were highly significant at young ages but were not significant for any trait at 64 months of age. Flock effects were significant for all average traits. For number of lambs weaned between flock differences decreased initially but remained the same as age increased. Flock differences in fertility decreased as age increased. Litter size and rearing ability between flock differences increased as age increased. Differences in flock effect were mainly due to Flock 1 consistently having higher reproduction rate (17 % aNLW, 10 % aFert, 12 % aLS, and 14 % aRA) and Flock 3 consistently having lower reproduction rate than flocks 2 and 4.

Type of birth and rearing effects were lowly significant for average number of lambs weaned and average litter size, but were not significant for any other traits at any age. Age of dam was significant for litter size at 40 months of age but was not significant for any other trait at any age.

Table 3.3 Analysis of variance F values for female reproductive traits at 28, 40, 52 and 64 months of age and average over a lifetime

			Number of Lambs Weaned			Fertility			Litter size			Rearing ability		
	Fixed Effect	**Num DF**	**Den DF**	**F value**	**F Sig**	**Den DF**	**F value**	**F Sig**	**Den DF**	**F value**	**F Sig**	**Den DF**	**F value**	**F Sig**
28 Months	Year	3	142	5.28	***	148	11.1	***	158	14.0	**	134	5.00	**
	Flock	3	135	5.60	***	141	6.22	***	155	5.31	**	128	7.48	***
	Tobr	2	2006	1.96	ns	1993	1.30	ns	2031	1.72	ns	2002	1.54	ns
	Age of dam	1	1778	0.00	ns	1845	1.01	ns	1648	0.20	ns	1743	0.01	ns
40 Months	Year	3	129	25.3	***	146	7.03	***	153	52.4	***	127	4.37	**
	Flock	3	87.7	3.67	**	100	3.46	*	153	5.08	**	85	3.40	*
	Tobr	2	1913	0.10	ns	1920	0.02	ns	1954	0.08	ns	1895	0.86	ns
	Age of dam	1	1525	0.03	ns	1696	1.45	ns	1450	4.69	*	1537	0.95	ns
52 Months	Year	3	134	40.5	***	182	12.7	***	156	61.4	***	143	8.40	***
	Flock	3	54.9	2.98	*	72	1.70	ns	153	2.67	*	63	1.49	ns
	Tobr	2	1856	1.99	ns	1839	0.84	ns	1878	1.20	ns	1863	1.75	ns
	Age of dam	1	1293	0.27	ns	1666	0.01	ns	1512	0.01	ns	1445	0.29	ns
64 Months	Year	3	154	8.30	***	171	20.3	***	164	6.39	***	149	13.5	***
	Flock	3	48.0	1.13	ns	53	0.21	ns	163	0.65	ns	42	0.93	ns
	Tobr	2	1688	1.47	ns	1680	1.54	ns	1711	1.51	ns	1668	0.08	ns
	Age of dam	1	1344	0.17	ns	1427	0.65	ns	1463	0.05	ns	1251	0.02	ns
Average	Year	3	159	21.8	***	163	10.5	***	171	33.0	***	156	5.17	**
	Flock	3	156	6.40	***	161	5.27	**	167	4.10	**	154	6.86	***
	Tobr	2	2033	3.12	*	2035	0.67	ns	2038	3.59	*	2031	1.04	ns
	Age of dam	1	1645	0.42	ns	1684	0.45	ns	1774	0.02	ns	1607	1.44	ns

Tobr = type of birth and rearing, Num = numerator, Den = denominator, *** = $P<0.001$, ** = $P<0.01$, * = $P<0.05$, ns = not significant

Genetic Parameters

Phenotypic and genetic variances are presented in Table 3.4. The genetic variance of number of lambs weaned was lower at 40 months of age than the other ages. As ewes aged, the genetic variance of fertility did not change but increased for litter size relative to the mean. The genetic variance of rearing ability fluctuated over different ages. The phenotypic variance in number of lambs weaned and litter size increased as age increased, whereas variance in fertility and rearing ability decreased as age increased relative to the mean. The phenotypic variance of the average traits was lower than the phenotypic variance of individual ages. Variance accounted for by the sire of the lamb did not change for number of lambs weaned, except at 52 months of age when it was close to zero, and generally decreased as age increased for fertility and rearing ability.

Table 3.4 Genetic and phenotypic variances of female reproduction traits at different ages

	Age	NLW	Fert	LS	RA
Genetic Variance	**28**	0.039	0.027	0.047	0.027
	40	0.009	0.010	0.029	0.002
	52	0.018	0.007	0.061	0.014
	64	0.036	0.007	0.087	0.003
	Average	0.028	0.012	0.042	0.012
Sire of the lamb Variance	**28**	0.011	0.012	-[a]	0.009
	40	0.012	0.006	-	0.008
	52	0.001	0.007	-	0.002
	64	0.011	0.005	-	0.004
Phenotypic Variance	**28**	0.287	0.207	0.294	0.235
	40	0.368	0.136	0.362	0.190
	52	0.421	0.110	0.420	0.164
	64	0.445	0.074	0.410	0.145
	Average	0.178	0.069	0.173	0.089

[a] Sire of the lamb not fitted to litter size (Table 3.2)

Heritabilities, phenotypic and genetic correlations for number of lambs weaned, fertility, litter size and rearing ability at different ages are presented in Table 3.5. Generally heritabilities were very low to moderate ranging from 0.02 (± 0.04) to 0.26 (± 0.07) across all traits. The heritability at 28 months of age was highest for all traits, and were lowest at 40 months of age. After 40 months of age, heritabilities generally increased. The heritabilities for litter size were low to moderate, gradually increasing with age, and were greater than all other reproductive traits.

Phenotypic correlations were generally low to moderate between different ages for all traits ranging from 0.13 (± 0.02) to 0.27 (± 0.02) (Table 3.5). In contrast, phenotypic correlations between different ages and average traits, were moderate to high with low standard errors, ranging from 0.58 (± 0.02) to 0.73 (± 0.01). Genetic correlations and their associated standard errors between ages for all traits were generally moderate to very high ranging from 0.45 (± 0.27) to greater than one with very high standard errors (Table 3.5). Genetic correlations between different ages and average traits were high to very high ranging from 0.69 (± 0.14) to 1.0, with moderate standard errors. When genetic correlations were constrained to less than one all correlations converged to 0.99.

Heritabilities for average traits (Table 3.6) were higher than heritabilities at individual ages. Average litter size had the highest heritability. Phenotypic correlations between the different average traits were moderate to high with low standard errors, ranging from 0.59 (± 0.02) to 0.88 (± 0.01), respectively. Genetic correlations between average traits were also moderate to high with moderate standard errors. Average number of lambs weaned was highly correlated with all of its component traits. Although, the genetic correlation was slightly higher with litter size (0.92 ± 0.05) than fertility (0.82 ± 0.08), or rearing ability (0.80 ± 0.07) (Table 3.6).

Table 3.5 Heritabilities (on diagonal), phenotypic (above diagonal) and genetic (below diagonal) correlations (standard error) between ewe reproduction traits

	28 Months	40 Months	52 Months	64 Months	Average
NLW28	**0.14** **(0.046)**	0.21 (0.027)	0.21 (0.026)	0.14 (0.028)	0.59 (0.014)
NLW40	0.97 (0.160)	**0.02** **(0.036)**	0.23 (0.022)	0.20 (0.023)	0.70 (0.014)
NLW52	1.17 (0.260)	1.39 (0.366)	**0.04** **(0.039)**	0.25 (0.023)	0.73 (0.013)
NLW64	1.12 (0.253)	0.90 (0.705)	1.30 (0.349)	**0.08** **(0.047)**	0.71 (0.014)
aNLW	1.05 (0.094)	0.95 (0.018)	0.99 (0.014)	0.99 (0.016)	**0.16** **(0.048)**
Fert28	**0.13** **(0.045)**	0.22 (0.027)	0.21 (0.022)	0.16 (0.023)	0.72 (0.011)
Fert40	1.05 (0.183)	**0.07** **(0.041)**	0.18 (0.022)	0.18 (0.023)	0.71 (0.014)
Fert52	1.65 (0.585)	0.81 (0.491)	**0.06** **(0.040)**	0.26 (0.022)	0.69 (0.015)
Fert64	0.82 (0.333)	0.73 (0.328)	0.79 (0.325)	**0.10** **(0.048)**	0.60 (0.019)
aFert	1.02 (0.060)	0.95 (0.018)	1.01 (0.016)	0.97 (0.027)	**0.18** **(0.049)**
LS28	**0.16** **(0.048)**	0.19 (0.022)	0.20 (0.022)	0.18 (0.024)	0.61 (0.014)
LS40	0.60 (0.274)	**0.08** **(0.041)**	0.17 (0.022)	0.17 (0.024)	0.64 (0.014)
LS52	0.69 (0.196)	0.45 (0.270)	**0.14** **(0.049)**	0.24 (0.023)	0.69 (0.012)
LS64	0.88 (0.164)	0.79 (0.241)	0.79 (0.169)	**0.26** **(0.065)**	0.70 (0.012)
aLS	0.91 (0.078)	0.69 (0.142)	0.86 (0.082)	1.00 (0.049)	**0.23** **(0.057)**
RA28	**0.11** **(0.044)**	0.21 (0.027)	0.19 (0.023)	0.13 (0.023)	0.67 (0.012)
RA40	1.44 (0.450)	**0.01** **(0.034)**	0.23 (0.022)	0.19 (0.023)	0.71 (0.014)
RA52	0.69 (0.301)	ne	**0.08** **(0.044)**	0.24 (0.023)	0.70 (0.014)
RA64	0.93 (0.741)	ne	1.00 (0.592)	**0.02** **(0.041)**	0.58 (0.016)
aRA	1.03 (0.088)	0.97 (0.016)	1.01 (0.015)	0.94 (0.376)	**0.14** **(0.046)**

When estimates >1 were constrained correlations = 0.99, ne = not estimable, Figures after the abbreviation are months of age, prefix a = average over a lifetime, NLW = number of lambs weaned over a lifetime, Fert = fertility of the ewe, LS = litter size, RA = rearing ability

Table 3.6 Heritabilities (on diagonal), phenotypic (above diagonal) and genetic (below diagonal) correlations (standard error) between average female reproduction traits

	aNLW	aFert	aLS	aRA
aNLW	**0.16** **(0.048)**	0.70 (0.011)	0.78 (0.009)	0.88 (0.005)
aFert	0.82 (0.082)	**0.18** **(0.049)**	0.82 (0.008)	0.78 (0.009)
aLS	0.92 (0.048)	0.76 (0.069)	**0.23** **(0.057)**	0.59 (0.015)
aRA	0.80 (0.071)	0.93 (0.056)	0.60 (0.125)	**0.14** **(0.046)**

aNLW = Average number of lambs weaned over a lifetime, aFert = Average fertility of the ewe, aLS = Average litter size, aRA = Average rearing ability

Repeatabilities

The reproduction traits were analysed with a simple repeatability model that allowed for quantification of the heritable as well as the non-genetic variation (Table 3.7). With this model, the heritabilities were approximately half of the heritability of the average traits (Table 3.6) and the repeatabilities ranged from 0.26 to 0.31 (Table 3.7). The phenotypic variances were approximately twice the phenotypic variance of average traits (Table 3.6). This is because the model includes within animal variance as well as between animal variance.

Table 3.7 Heritability, repeatability and phenotypic variance (V_p) for average female traits using repeatability model analysis

	aNLW	aFert	aLS	aRA
Heritability	0.07	0.06	0.08	0.07
Repeatability	0.26	0.31	0.26	0.28
V_p	0.32	0.12	0.33	0.15

aNLW = Average number of lambs weaned over a lifetime, aFert = Average fertility of the ewe, aLS = Average litter size, aRA = Average rearing ability

3.3.2 Male Reproduction

Fixed Effects

Between year effects were significant at all ages of scrotal circumference in all three models except at 16 months of age when live weight was included in the model (Table 3.8). Between year differences were least at older ages and were less when Models 2 or 3 were used (Table A.6, Appendix A). Means from Model 1 (age adjustment only) indicate that 1989 produced the largest scrotal circumferences (47 % SC5, 19 % SC10, 8 % SC16) although this was the opposite for Model 2 (weight adjustment only) (-14 % SC5, -6 % SC10) and 1989 was ranked second when using Model 3 (age and weight adjustment).

Between flock of origin effects were significant for all ages of scrotal circumference for all models except scrotal circumference at 5 months of age using Model 1. Similar to year effects, between flock differences were less when Models 2 or 3 were fitted. However, between flock effects were relatively consistent at all ages (Table A.7, Appendix A).

Type of birth and rearing effects were significant for all ages and models but were smaller at 16 months of age. Differences between birth and rearing types were greater at younger ages and were, again, reduced when adjusted for differences in weight (Models 2 or 3, Table A.8, Appendix A).

The age of the dam was only significant for scrotal circumference at 5 and 16 months of age when using Model 1. The weight covariate was significant whenever included in the model as was age except at 16 months of age when weight and age were in the model.

Table 3.8 Analysis of variance F values for scrotal circumference at 5, 10 and 16 months of age using Models 1, 2 and 3

			Model 1			Model 2			Model 3		
	Fixed Effect	**Num DF**	**Den DF**	**F value**	**F Sig**	**Den DF**	**F value**	**F Sig**	**Den DF**	**F value**	**F Sig**
SC5	Year	3	254	170	***	234	40.1	***	229	38.6	***
	Flock	3	243	2.23	ns	224	8.39	***	220	4.72	**
	Tobr	2	2263	111	***	2267	13.8	***	2267	3.12	*
	Aod	1	2223	5.68	*	2180	1.26	ns	2164	0.88	ns
	Age	1	2165	442	***	-	-	-	2043	93.1	***
	Wt	1	-	-	-	2270	2419	***	2266	1813	***
SC10	Year	3	188	63.2	***	198	22.1	***	199	20.5	***
	Flock	3	182	25.4	***	191	11.4	***	192	11.2	***
	Tobr	2	2137	6.26	**	2138	13.7	***	2137	11.1	***
	Aod	1	1996	0.15	ns	1997	1.63	ns	2000	1.68	ns
	Age	1	1791	126	***	-	-	-	1802	7.43	**
	Wt	1	-	-	-	2137	1330	***	2144	1149	***
SC16	Year	3	194	19.7	***	202	2.25	ns	201	2.18	ns
	Flock	3	187	18.1	***	195	5.97	***	194	5.96	***
	Tobr	2	2100	3.39	*	2101	3.64	*	2099	3.56	*
	Aod	1	1939	6.81	*	1951	2.03	ns	1951	2.02	ns
	Age	1	1731	19.6	***	-	-	-	1754	0.01	ns
	Wt	1	-	-	-	2113	799	***	2112	771	***

Model 1 includes day of birth, Model 2 includes weight and Model 3 includes day of birth and weight as covariates. Tobr = type of birth and rearing, Aod = age of dam, Num = numerator, Den = denominator, *** = P<0.001, ** = P<0.01, * = P<0.05, ns = not significant

Variances

Both phenotypic and genetic variances were reduced when weight (Model 2) or weight and age (Model 3) were included in the model. The variances were also reduced as age increased from 5 to 16 months for all models (Table 3.9). Adjustment for weight accounted for more of the variation in scrotal circumference than age.

Table 3.9 Genetic and phenotypic variances of scrotal circumference at different ages for each model

	Model	SC5	SC10	SC16
Genetic Variance	1	6.01	3.91	2.72
	2	2.78	2.48	2.04
	3	2.51	2.51	2.05
Phenotypic Variance	1	10.20	9.78	7.42
	2	5.78	6.38	5.44
	3	5.52	6.37	5.45

Model 1 includes day of birth, Model 2 includes weight and Model 3 includes day of birth and weight as covariates

Relationship between Scrotal Circumference and Live Weight

Heritabilities, phenotypic and genetic correlations estimated for scrotal circumference and live weight traits at all ages of measurement using Model 1 are presented in Table 3.10. The heritability of scrotal circumference at 5 months of age (0.59 ± 0.07) was greater than at 10 (0.40 ± 0.07) and 16 (0.37 ± 0.06) months. Both phenotypic and genetic correlations for scrotal circumference between different ages were moderate to high, with those between adjacent ages tending to be higher than between 5 and 16 months. The heritabilities of live weights were slightly higher at weaning than later ages but did not differ significantly. The genetic correlation between live weight at 10 and 16 months (0.88 ± 0.03) was higher than those with weaning weight (0.60 ± 0.06, 10 month and 0.64 ± 0.06, 16 month).

Phenotypic correlations between scrotal circumference and live weights ranged from 0.27 (± 0.02) between scrotal circumference at 16 months and weaning weight to 0.70 (± 0.01) between scrotal circumference at 5 months and weaning weight. Phenotypic correlations were greatest between scrotal circumference and live weights at similar ages. Genetic correlations between scrotal circumference and live weights ranged from 0.31 (± 0.10) between scrotal circumference at 16 months and weaning weight to 0.74 (± 0.04) between scrotal circumference at 5 months and weaning weight. As for phenotypic correlations, genetic correlations were greatest between scrotal circumference and live weights at similar ages.

Table 3.10 Heritabilities (on diagonal), phenotypic (above diagonal) and genetic (below diagonal) correlations (standard error) between scrotal circumference and live weight at different ages (Model 1)

	SC5	SC10	SC16	WW	WT10	WT16
SC5	**0.59 (0.065)**	0.50 (0.018)	0.36 (0.021)	0.70 (0.012)	0.57 (0.016)	0.45 (0.019)
SC10	0.60 (0.073)	**0.40 (0.065)**	0.59 (0.015)	0.35 (0.021)	0.60 (0.015)	0.48 (0.018)
SC16	0.49 (0.088)	0.62 (0.079)	**0.37 (0.061)**	0.27 (0.022)	0.44 (0.019)	0.54 (0.016)
WW	0.74 (0.042)	0.38 (0.094)	0.31 (0.102)	**0.39 (0.046)**	0.66 (0.013)	0.57 (0.015)
WT10	0.58 (0.066)	0.60 (0.075)	0.48 (0.094)	0.60 (0.062)	**0.34 (0.048)**	0.79 (0.008)
WT16	0.50 (0.078)	0.56 (0.084)	0.53 (0.086)	0.64 (0.063)	0.88 (0.031)	**0.33 (0.047)**

Figures after the abbreviation are months of age, SC = scrotal circumference, WW = weaning weight, WT = live weight, Model 1 includes day of birth

Genetic Parameters for Scrotal Circumference

Heritabilities, phenotypic and genetic correlations estimated between scrotal circumference at 5, 10 and 16 months of age using the three models are presented in Table 3.11. The heritability of scrotal circumference at 5 months was greater than at older ages. The heritability estimate of scrotal circumference at 5 months was reduced from 0.59 ± 0.07 (Model 1 – age adjustment) to 0.48 ± 0.06 when weight was included (Model 2) and to 0.45 ± 0.06 when both weight and age were included in the model. The estimate of heritability of scrotal circumference at 10 and 16 months of age was not affected by the model used. For both phenotypic and genetic correlations the estimates ranged from moderate to high for Model 1, but ranged from low to moderate for Models 2 and 3. While the different models had a large effect on the variances and phenotypic correlations, there was little difference in the heritabilities (except at 5 months of age) or genetic correlations between scrotal circumference measured at the three ages.

Table 3.11 Heritabilities (on diagonal), phenotypic (above diagonal) and genetic (below diagonal) correlations (standard error) between scrotal circumference at different ages using different models

	Model	SC5	SC10	SC16
SC5	1	**0.59 (0.065)**	0.50 (0.018)	0.36 (0.021)
	2	**0.48 (0.062)**	0.33 (0.021)	0.22 (0.022)
	3	**0.45 (0.061)**	0.33 (0.021)	0.22 (0.022)
SC10	1	0.60 (0.073)	**0.40 (0.065)**	0.59 (0.015)
	2	0.44 (0.095)	**0.39 (0.062)**	0.46 (0.018)
	3	0.46 (0.094)	**0.40 (0.062)**	0.47 (0.018)
SC16	1	0.49 (0.088)	0.62 (0.079)	**0.37 (0.061)**
	2	0.36 (0.102)	0.43 (0.100)	**0.37 (0.060)**
	3	0.43 (0.099)	0.45 (0.098)	**0.38 (0.061)**

Figures after the abbreviation are months of age, Model 1 includes day of birth, Model 2 includes weight and Model 3 includes day of birth and weight as covariates

3.3.3 Male and Female Reproduction

Genetic correlations between scrotal circumference and average female reproduction traits using three models (Table 3.2) are presented in Table 3.12. Genetic correlations between scrotal circumference at different ages and average number of lambs weaned range from very low to moderate. The genetic correlation with scrotal circumference at 5 months was lower (0.12 ± 0.15, Model 3) than correlations with 10 and 16 months of age (0.29 ± 0.16 for both ages, Model 3). The use of weight as a covariate, either alone or with age (Model 2 and 3, respectively) reduced the estimates, but the same trend across ages applied and there was little effect of adjusting for age in addition to weight (Model 2 versus Model 3).

Genetic correlations between scrotal circumference and average fertility ranged from very low to moderate and were highest at 10 months of age (0.26 ± 0.15, Model 3) although standard errors were high. Using models with weight adjustment reduced the correlation at all ages with 10 months of age the highest. Again there was little difference between Models 2 and 3.

Genetic correlations between scrotal circumference and average litter size increased slightly as age of scrotal circumference increased, and were moderate at all ages. Using models with weight adjustment (Model 2 and Model 3) decreased the estimate obtained at all ages, with estimates at 10 and 16 months of age the highest for all models.

Genetic correlations between scrotal circumference and average rearing ability ranged from very low to moderate for Model 1. Models with weight adjustment had little effect on estimates at 5 months of age, reduced the estimates for 10 months of age and reduced the estimates to low and close to zero at 16 months of age.

Average litter size had a greater correlation with scrotal circumference at all ages compared to the other average female reproduction traits. Models with weight adjustment reduced genetic correlation estimates and generally, the estimate from Model 3 (weight and age) was the same as Model 2 (weight) for all ages of scrotal circumference. Standard errors for all genetic correlations were large. Genetic correlations between scrotal circumference and individual ages of all female traits are presented in Appendix A, Tables A.9 to A.12.

Table 3.12 Genetic correlations (standard error) between scrotal circumference and average female traits

	Model	SC5	SC10	SC16
aNLW	1	0.26 (0.139)	0.48 (0.152)	0.51 (0.156)
	2	0.11 (0.151)	0.28 (0.164)	0.26 (0.165)
	3	0.12 (0.152)	0.29 (0.162)	0.29 (0.163)
aFert	1	0.17 (0.136)	0.40 (0.148)	0.29 (0.155)
	2	0.10 (0.144)	0.25 (0.156)	0.07 (0.160)
	3	0.12 (0.144)	0.26 (0.153)	0.09 (0.158)
aLS	1	0.37 (0.117)	0.52 (0.127)	0.53 (0.130)
	2	0.20 (0.129)	0.34 (0.138)	0.32 (0.139)
	3	0.24 (0.129)	0.34 (0.137)	0.34 (0.138)
aRA	1	0.03 (0.153)	0.32 (0.169)	0.22 (0.176)
	2	0.01 (0.159)	0.17 (0.175)	0.01 (0.176)
	3	0.00 (0.159)	0.18 (0.172)	0.03 (0.175)

Figures after the abbreviation are months of age, aNLW = Average number of lambs weaned over a lifetime, aFert = Average fertility of the ewe, aLS = Average litter size, aRA = Average rearing ability, Model 1 includes day of birth, Model 2 includes weight and Model 3 includes day of birth and weight as covariates

3.4 DISCUSSION

3.4.1 Female Reproduction

The low heritability estimates for number of lambs weaned are consistent with those previously reported in the literature for the Merino and other sheep breeds (Fogarty 1995, Safari and Fogarty 2003) (Table 3.5 and Table 3.7). The component traits fertility and rearing ability, followed the same pattern of high heritability at 28 months with lower heritability at older ages, as number of lambs weaned (Table 3.5). Lower heritabilities and genetic correlations with traits measured at 40 months of age may be indicative of a carry over effect from the first lambing. Of the component traits, litter size had the greatest heritability and rearing ability had the lowest. The low to moderate phenotypic correlations among number of lambs weaned records taken at different ages indicate a low to moderate repeatability for this trait. The repeatability model fitted to the data confirmed the low to moderate repeatability indicated by phenotypic correlations for all traits (Table 3.7). Low repeatability would be expected for these traits due to the large environmental influence on them, although repeatabilities from this model were slightly higher than expected (Fogarty 1995). In contrast, the high genetic correlations between records at different ages indicate that records taken at different ages may be considered as essentially the same trait. Low heritabilities, repeatabilities and phenotypic correlations, and high genetic correlations are the consistent with estimates reported in the literature (Fogarty 1995, Safari and Fogarty 2003). The higher heritability for all traits at 28 months of age is encouraging for the use of early selection for reproduction traits.

High genetic correlations between records taken at different ages for the component traits, as for number of lambs weaned, indicates that these expressions can be considered as essentially the same trait. Because it appears that the same or similar genes are controlling the traits at all ages, combining the ages to create an average trait is reasonable. Also, correlations between the average traits and their respective age traits were moderate to high indicating a good representation of the additive genetic component of individual ages by the average. The distribution of average traits (Figure 3.1) also supports the use of average traits as they appear to be more similar to a normal distribution than at individual ages and therefore the model fitted has the correct assumptions. However, there was some difficulty when estimating the genetic correlations between different ages as several were greater than one and required constraint. All genetic correlations had high standard errors and this may be in part attributed to the distribution of the traits.

Number of lambs weaned should be included in the breeding objective because of its direct relationship with income derived from sale of surplus offspring (Ponzoni and Walkley 1984) and the increasing importance of meat relative to wool. The higher heritability at 28 months of age than at older ages indicates that records from the first lambing may be used in a breeding program. The greater heritability for litter size and high positive phenotypic and genetic correlations between all average traits suggests that it may be a useful selection criterion for increasing number of lambs weaned. This is especially so since it can be recorded in early to mid pregnancy using ultrasound, thus avoiding the more laborious lambing records. However, to make genetic progress in any trait, pedigree records are helpful and are essential for traits with low heritability and with current methods these can be easily recorded at the same time as number of lambs born and other birth records.

Genetic correlations between the component traits at different ages and average number of lambs weaned (Table A.5, Appendix A and Table 3.6) give an indication of the variation in one trait accounted for by another, and therefore the different roles each component plays in making up the composite trait. From the data herein, it appeared that rearing ability had a greater influence in the first reproductive year, which decreased with age relative to fertility and litter size. In contrast, litter size had greatest influence at the last reproductive year.

These interactions are reasonable, as it has been suggested that a 'lack of experience' (or the rearing ability) of the maiden ewe in the first year of reproduction reduces lamb survival (Dalton and Rae 1978, McMillan 1983, Alexander 1984). Litter size is itself primarily influenced by ovulation rate (Davis *et al.* 1998) which increases as the ewe ages, peaking at about 3 to 5 years of age (Cahill 1984) which are the later years of this study accounting for the greater influence of litter size in the last reproductive year.

The significance of year and flock effects highlights the importance of adjustment for environmental factors when carrying out genetic studies of grazing animals. Predicted means indicated that between year effects were greater at older ages. This suggests that as a ewe ages, seasonal variation has a greater role in her reproductive ability than at younger ages. The difference between flocks indicates that there are differences between Merino populations within South Australia. Both age of dam and type of birth and rearing were not significant for the female reproductive traits indicating that a ewe's age or whether she has single or multiple lambs does not affect the reproductive performance of her daughters, which is in contrast to the findings of Schoeman *et al.* (2002).

3.4.2 Male Reproduction

Heritabilities estimated herein (Table 3.11) were similar to previous estimates obtained in Merino sheep for testicular diameter (Purvis *et al.* 1988), as are the heritabilities for live weights (Fogarty 1995, Safari and Fogarty 2003). Genetic correlations between scrotal circumferences at different ages (Table 3.11) indicate that considering scrotal circumference as the same trait at very young and older ages would not be appropriate. However, Purvis *et al.* (1991), considering testicular size measurements at monthly intervals between 4 and 12 months of age, reported high correlations and concluded that the same genetic control was operating over testicular size, indicating possible variation in different populations/families of Merinos. Genetic correlations between live weights at different ages indicate that weights at 10 and 16 months of age may be considered to be the same trait, but not in the case of weaning weight (Table 3.10). Both phenotypic and genetic correlations between scrotal circumference and live weights were generally high and positive indicating that there was a strong positive relationship between the two traits at all ages. This relationship has implications for selection and has a significant influence on the definition of scrotal circumference.

It is expected that some of the variation in scrotal circumference is associated with the general growth, or increase in size, of the ram. This is supported by the decreased phenotypic and genetic variances (Table 3.11) at all ages when scrotal circumference was adjusted for either, live weight alone or for live weight as well as age. Also when live weight was included in the definition of scrotal circumference as in Models 2 and 3, heritability estimates were lower at 5 months of age (Table 3.11). For scrotal circumference at 5 months of age, the phenotypic variation was reduced with weight adjustment to a greater extent than at older ages, therefore the heritability at 5 months of age was reduced. The greater changes in variance and lower correlations seen in rams at 5 months of age compared to older ages may be due to the effects of puberty. The occurrence of puberty in ram lambs is difficult to determine, but occurs over a wide range of ages from 84 to 456 days depending on the breed (Dyrmundsson 1973, Foster et al 1978, Haynes and Schanbacher 1983). Onset of puberty is mainly dependent on live weight but also on age, and is reached when the proportion of weight is approximately 40 to 45 percent of adult weight (Courot 1979), again depending on the breed. Purvis *et al.* (1991) also concluded that at 5 months of age testicular size may have had greater environmental influences, specifically maternal effects.

At 10 months of age, phenotypic and genetic variances decreased in similar proportions for all models, therefore the heritabilities at this age were the same or very similar for all models. At 16 months of age, the variances were not reduced as much as at 5 months of age by live weight adjustment and the genetic variance was a greater proportion of the phenotypic variance. Hence, in this case, the heritability of scrotal circumference with live weight adjustment was slightly higher. All genetic and phenotypic correlations were lower when scrotal circumference was adjusted for weight. A change in both the covariance and the variances does not necessarily result in a change in the correlation. However, when a reduction in the variances of two traits is greater than the reduction in the covariance between them, as was the situation here (Table 3.9), the correlation between the two traits is reduced (Table 3.11).

The levels of significance of year of birth and type of birth and rearing effects for all models tested on scrotal circumference reinforces the importance of environmental factors in genetic studies of grazing animals. Predicted means presented in Tables A.6 – A.8 (Appendix A), indicate that the year effect was least at older ages, as differences due to seasonal and other environmental variations tend to be reduced as the animal matures. Similarly, the reduced effect of type of birth and rearing with age (Table A.8, Appendix A) would be due in part to the reduced effect of maternal environment as the animal matures (Garrick 1990). However, the results clearly indicate the need to allow for such effects in genetic evaluation of the traits in question.

In conclusion, selection for live weight may increase scrotal circumference due to the positive correlated response arising from positive genetic correlations between live weight and scrotal circumference. Adjusting scrotal circumference for live weight creates a new trait, scrotal circumference independent of body size. Studies including this one have shown adjustment reduces the heritability and correlations between ages of measurement of this trait. The definition of the trait is important when considering scrotal circumference as a trait for selection because the response in other correlated traits may change. In an experiment in Edinburgh where selection was based upon testicular diameter adjusted for body weight it was shown that the genetic relationship between scrotal circumference and live weight became negative rather than positive as shown in this study (Haley *et al.* 1990). In that same experiment no significant response was found between testicular size and ovulation rate. It was concluded that this may have been due to the adjustment of testicular size for weight (Haley *et al.* 1990, Purvis *et al.* 1988). Adjusting scrotal circumference for age did not have as large an effect as adjustment for live weight, but is required as it contributes to reducing the variation due to different levels of maturity of the animals.

3.4.3 Male and Female Reproduction

Scrotal circumference has been suggested as an indirect selection criterion to improve reproductive rate in Merino flocks (Purvis 1988, Matos and Thomas 1992). In agreement with the literature, heritabilities and repeatabilities estimated in this study were greater for scrotal circumference (Table 3.11) than for the female traits considered (Table 3.5). Variable genetic correlations indicated that it would not be appropriate to consider scrotal circumference as the same trait at young and older ages. Therefore, the relationship between young and older ages of scrotal circumference and female traits should be considered separately.

Genetic correlations between female reproductive component traits and scrotal circumference at 5 months were low and erratic (Table 3.12), but genetic correlations between average female traits and scrotal circumference at 10 and 16 months were large enough (i.e. approx 0.3) to support the notion that scrotal circumference at these ages can be useful selection criteria. Variable correlations for scrotal circumference at 5 months of age may be accounted for due to variation in status of puberty among ram lambs. At weaning, live weight as a proportion of adult weight ranges from 20 to 60 percent (Courot 1979). This indicates that at 5 months of age there will be significant variation in the number of rams that have reached puberty, and therefore large variation in hormonal influences. Correlations reported in the literature are in general agreement with estimates from this study (Fogarty 1995, Safari and Fogarty 2003). Genetic correlation estimates are similar to those between scrotal circumference and ovulation rate reported by Purvis (1985) at 5, 8 and 12 months of age.

Research has been carried out to investigate potential physiological sources of the genetic relationship between male and female reproductive traits. It is known that gonadotrophic hormones control the development of both the testis in males and the ovaries in females. Land (1973, 1974) proposed that because production of gonadotrophic hormones is under the control of autosomal genes, similar endocrinological mechanisms would be operating in both females and males. Studies have been carried out to test this hypothesis. Luteinising hormone (LH) and follicle stimulating hormone (FSH) have been correlated with various reproductive traits (Matos and Thomas 1992) but there have been no conclusive reports. It appears to be generally accepted that a measurement of testis size rather than directly measuring hormone levels is a better choice as selection criteria.

The difference between estimates of variances using the different models again highlights the importance of correct definition of the trait. Hence, the conflicting evidence within the literature regarding significant correlated responses in female reproduction depending on the definition of scrotal circumference. The response to selection for a single trait given by Falconer (1960) is:

$$\mathrm{R}_1 = h_1^2 i \sigma_{P_1} \qquad \text{(Equation 3.1)}$$

where R_1 is the response to selection, h_1^2 is the heritability, i is the selection intensity and σ_{P_1} is the standard deviation.

Assuming a generation interval of one, and using the parameters estimated herein, the direct response to selection for number of lambs weaned would be 0.07 lambs per ewe per generation (Table 3.13).

The correlated response in Trait 2 when selecting for Trait 1 is (Falconer and Mackay 1960):

$$\mathrm{CR}_{2.1} = r_{A_1A_2}\sqrt{h_1^2 h_2^2}\, i_p \sigma_{P_2} \qquad \text{(Equation 3.2)}$$

where $\mathrm{CR}_{2.1}$ is the correlated response, r_{A_1A} is the genetic correlation between Trait 1 and 2, h_1^2 is the heritability of Trait 1, h_2^2 is the heritability of Trait 2, i_p is the selection intensity and σ_{P_2} is the standard deviation of Trait 2. (See Appendix A, section 5 for sample calculation)

Table 3.13 The response to selection for a single trait (R) and the correlated response of Trait 2 when selecting for Trait 1 (CR)[A]

						CR		
						Trait 1		
						LS28	SC10	
Trait 2		h^2	σ_p	r_g	R		**Model 1**	**Model 3**
aNLW		0.16	0.42	-	0.07	0.05	0.05	0.03
LS28		0.16	0.54	0.78	0.09	-	0.02	0.01
SC10	**Model 1**	0.40	3.13	0.48	1.25	0.09	-	-
	Model 3	0.40	2.52	0.29	1.01	0.07	-	-

[A] aNLW = average number of lambs weaned, LS28 = litter size at 28 month of age, SC10 = scrotal circumference at 10 months of age, h^2 = heritability, σ_p = standard deviation, r_g = genetic correlation between aNLW and LS28 or SC10, R = response to selection for a single trait, CR = correlated response, selection intensity of 1.0 was used, Model 1 includes day of birth, Model 3 includes day of birth and weight covariates

So the correlated response for number of lambs weaned when selecting for litter size at 28 months of age would be 0.05 lambs per ewe per generation (Table 3.13), and selecting for scrotal circumference at 10 months of age gives a correlated response of 0.03 lambs per ewe per generation (Table 3.13). These calculations indicate that the use of litter size as a selection criterion would be only slightly less effective as selecting for number of lambs weaned directly, and that there would also be improvement in male reproduction. They also indicate that the use of scrotal circumference without weight adjustment as a selection criterion would give a similar response in the number of lambs weaned compared to litter size. Scrotal circumference was more highly genetically correlated with litter size than the other female traits, which also adds weight to the argument that litter size is the most suitable female component to target for genetic improvement.

3.5 CONCLUSION

This study was in broad agreement with earlier findings that indicate reproductive traits have low to moderate heritabilities, ranging from 0.02 to 0.26 in this study. However, these low values do not mean that genetic improvement in reproduction is impossible, but rather, that it will require an adequately designed selection strategy. For example ewe selection would occur after the first lambing and ram selection after puberty in combination with index selection using both direct and indirect selection criteria such as scrotal circumference and litter size. Accurate reporting of the trait definition and the context in which it is being used is essential for precise use and general application of these traits in selection throughout the Australian sheep industry.

Of the female traits studied litter size would be the trait recommended for use in genetic improvement programs because of its higher heritability than other component traits, especially if pregnancy scanning is already part of the current management practices of the property. If number of lambs weaned was to be used the higher heritability at 28 months of age indicates that it could be included after the ewe's first lambing. The use of scrotal circumference as an indirect selection criterion is again recommended for consideration. However, it should be measured post-puberty and using the ages in this study 10 months would be recommended over 5 months of age. This study suggests that scrotal circumference must be adjusted for age, but to remove variation in ram size the trait should also be adjusted for live weight. However, if scrotal circumference is adjusted for live weight and is used in a selection index then live weight itself must also be included in the index so that live weight is not reduced. The use of a selection index that includes litter size of ewes, or number of lambs weaned at the first lambing, and scrotal circumference of rams, will enable Merino breeders to achieve the greatest level of improvement in reproduction.

Chapter 4

Genetic Relationships Between Fleece And Reproduction Traits

4.1 INTRODUCTION

A considerable amount of selection takes place among Merino sheep well before the expression of ewe reproduction. Most of the emphasis is placed upon wool traits, followed by body traits. With few exceptions, reproductive traits receive a lesser amount of attention (Casey and Hygate 1992). The wool traits that are the main focus of genetic improvement programs include clean fleece weight (CFW), fibre diameter (FD), staple length (SL) and strength (SS). When reproductive rate is part of the breeding objective, information on the genetic correlation between wool and reproductive traits is required for the calculation of relevant selection indices. Furthermore, even when reproduction is not currently in the breeding objective, and where clean fleece weight and fibre diameter are the main traits selected for, knowledge of the relationships between them is important in order to be able to predict correlated responses in reproductive rate so that changes can be made to the breeding objective or selection criteria as required.

In this chapter the phenotypic and genetic correlations between fleece traits and reproduction traits, as described in the previous chapter, are reported. Heritabilities and correlations between fleece traits are also presented. The data set described in Chapter 3, the Turretfield Resource Flocks data, has been used in this chapter for correlations between average reproduction traits; number of lambs weaned, fertility, litter size, rearing ability and scrotal circumference, with fleece traits; clean fleece weight, fibre diameter, staple length and staple strength.

4.2 MATERIALS AND METHODS

The data used are from the Turretfield Merino Resource Flock (Section 2.1.2). The number of records, mean, standard deviation and the range for each trait is presented in Table 4.1. The fleece traits were measured on rams at 10 and 16 months of age, which equates to 6 and 12 months of wool growth, respectively. For ewes, fleece traits were measured from 16 months of age (12 months of wool growth) at 12 monthly intervals up to 5 years of age.

Table 4.1 Number of records available (n), mean, standard deviation (s.d.), coefficient of variation (CV) and range for reproduction and fleece traits

Trait		Age	n	Mean	s.d.	CV	Range
aNLW		-	2073	0.90	0.41	0.46	0 – 2
aFert		-	2073	0.82	0.24	0.29	0 – 1
aLS		-	1770	1.13	0.36	0.32	0.25 – 2
aRA		-	1770	0.69	0.28	0.41	0 – 1
SC (cm)		5	2336	17.5	3.76	0.21	9.0 – 30.5
		10	2202	26.4	3.54	0.13	12.0 – 39.5
		16	2164	31.8	2.88	0.09	17.0 – 40.5
CFW (kg)	Ram	10	2194	2.3	0.55	0.24	0.6 – 4.7
		16	2174	2.9	0.60	0.21	0.9 – 4.9
	Ewe	16	2108	4.4	0.74	0.17	1.4 – 7.3
		28	2015	4.8	0.83	0.17	2.3 – 9.1
		40	1942	5.1	0.87	0.17	1.9 – 8.6
		52	1849	5.0	0.86	0.17	2.4 – 8.1
		64	1176	5.0	0.86	0.17	2.5 – 8.6
FD (µm)	Ram	10	2197	21.3	1.83	0.09	15.3 – 28.5
		16	2174	22.6	2.21	0.10	16.8 – 30.5
	Ewe	16	2108	22.2	1.93	0.09	16.4 – 29.0
		28	2022	24.0	2.03	0.08	18.0 – 31.1
		40	1943	24.8	2.13	0.09	18.5 – 32.6
		52	1851	25.1	2.16	0.09	17.5 – 33.1
		64	1176	25.5	2.39	0.09	19.0 – 33.9
SL (mm)	Ram	10	2140	57.6	5.91	0.10	39.1 – 81.0
		16	2158	65.3	9.31	0.14	35.7 – 97.6
	Ewe	16	2082	115.5	11.84	0.10	62.1 – 159.9
		28	1985	110.3	10.06	0.09	48.8 – 157.4
		40	1934	108.5	10.79	0.10	46.0 – 150.6
		52	1848	107.0	10.86	0.10	68.4 – 144.0
		64	1156	106.4	11.10	0.10	72.0 – 140.8
SS (N/ktex)	Ram	10	2114	42.2	11.80	0.28	3.5 – 85.1
		16	2140	45.4	11.64	0.26	2.7 – 82.0
	Ewe	16	2081	24.6	9.15	0.37	1.6 – 66.3
		28	1985	28.0	10.15	0.36	1.8 – 66.8
		40	1934	30.2	11.73	0.39	1.9 – 73.2
		52	1843	29.3	11.95	0.41	2.6 – 73.5
		64	1154	28.1	12.05	0.43	3.6 – 78.6

Age is in months, aNLW = Average number of lambs weaned over a lifetime, aFert = Average fertility of the ewe, aLS = Average litter size, aRA = Average rearing ability, SC = Scrotal circumference, CFW = Clean fleece weight, FD = Fibre diameter, SL = Staple length, SS = Staple strength

Statistical Analysis

Data were analysed using linear mixed model methodology in ASReml (Gilmour *et al.* 2002). An animal term was fitted allowing optimal analysis of a finite population. All two-way interactions between fixed effects were tested, non-significant interactions were not included in the final models.

The final base model can be written as:

$$\mathbf{y} = \mathbf{X}\boldsymbol{\tau} + \mathbf{Z}_1\mathbf{a} + \mathbf{e}$$

where

$$\mathbf{y} \sim \mathrm{N}\left(\mathbf{X}\boldsymbol{\tau}, \sigma_a^2 \mathbf{Z}_1 \mathbf{A} \mathbf{Z}_1' + \sigma^2 \mathbf{I}_n\right)$$

and

$$\mathbf{e} \sim \mathrm{N}\left(0, \sigma^2\right)$$

where $\mathbf{X}^{n \times t}$ is a design matrix which assigns the effects to animals, $\boldsymbol{\tau}^{1 \times t}$ is the vector of fixed effect means, $\mathbf{Z}_1^{n \times p}$ is the design matrix for the animal effects, $\mathbf{A}$ is the numerator relationship matrix. The vector $\mathbf{a}$ represents the animal effect. $\mathbf{e}^{1 \times n}$ is the vector of random errors. σ_a^2 is the variance due to the animal effect and σ^2 is the residual variance parameter.

This model can also be symbolically written as:

y ~ mean + year (1989-1992) + flock (1-4) +
type of birth and rearing (11, 21, 22) + linear(age of dam) + animal

Terms fitted as random effects in the model are underlined, all other terms are fitted as fixed effects. This formed the base model for all analyses for this data set. Each variate was tested and the model was modified where necessary. Changes to the base model for each variate are shown in Table 4.2.

Table 4.2 Final models fitted to all traits

Variate	Model fitted
Number of lambs weaned	Base model
Fertility	Base model
Litter Size	Base model
Rearing ability	Base model
Scrotal circumference	Base model + Day of birth and Weight (Weaning, 10, or 16 months)
Clean fleece weight	Base model + significant interactions + NLW (at 28, 40, 52, or 64 months only)
Fibre diameter	Base model + significant interactions + NLW (at 28, 40, 52, or 64 months only)
Staple length	Base model + significant interactions + NLW (at 28, 40, 52, or 64 months only)
Staple strength	Base model + significant interactions + NLW (at 28, 40, 52, or 64 months only))

Heritabilities reported were from univariate analyses. Correlations between different ages of female traits were from bivariate analyses but correlations between different ages of male reproductive traits, live weight and between female and male traits were from multivariate analyses. Heritabilities and correlations will be referred to as very low to very high according to the classification in Table 2.5.

Adjustment of fleece traits for Lambing Status

It can be argued that the lambing status of a ewe may have an effect on the ewe's fleece production. Therefore, a preliminary analysis was set up to address whether to adjust adult fleece measurements for lambing status of the ewe. The following models were applied to all of the fleece traits, Model 1 was the same as the base model described above and Model 2 was as Model 1 but included number of lambs weaned at the appropriate age to adjust for the lambing status of the ewe. Number of lambs weaned was used to account for the effects of both carrying a lamb or lambs to term and rearing the lamb/s rather than litter size which would not include the effect of rearing a lamb. For all ages of fleece traits, number of lambs weaned was significant. Genetic variances did not change significantly and the phenotypic variance was reduced slightly (Table B.1 Appendix B). Even though number of lambs weaned was significant, there was little change in the heritability of the trait with or without number of lambs weaned. Due to the reduction in the phenotypic variance, and the lack of change in the heritability of the traits, number of lambs weaned was used in all subsequent analyses of fleece traits for this data set.

RESULTS

4.2.1 Fixed Effects

The significance of fixed effects for fleece traits are presented in Table 4.3 and 4.4. Least squares means are presented in Tables B.2 – B.2 (Appendix B). Between year effects were significant for all ram and ewe traits at all ages. Both rams and ewes had higher clean fleece weight (9 to 32 %) in 1992 than in other years and lower fibre diameter (-5 to -8 %) in 1989. For rams and ewes at 16 months of age, 1989 was also the year for lowest staple length (-14 to -27 %) and strength (-24 to -2 9%), however, for ewes from 40 months of age, 1991 and 1992 were the lowest years for staple length and strength.

Flock effects were significant for rams and ewes at all ages for clean fleece weight, fibre diameter and staple length, but were only significant at 16 months of age for staple strength. Flocks 1 and 4 were consistently lower (approx. -4 to -14 %) than Flocks 2 and 3 for clean fleece weight. Flock 3 had the lowest fibre diameter (approx. -10 %) and staple length (-7 to -10 %) and Flock 2 had the highest across all ages. For staple strength at 16 months of age, Flock 4 had the strongest staple (stronger by approx 10% for rams and 14 % for ewes) and Flock 3 had the weakest.

Type of birth and rearing effects on clean fleece weight were significant for all ages except for ewes at 64 months of age. Single born and raised lambs had the highest clean fleece weight (3 to 9 %) and there was no difference between multiple born and single raised versus multiple born and raised. For fibre diameter, type of birth and rearing was significant at 10 months of age for rams and 16, 28 and 52 months of age for ewes. For rams, single reared lambs had lower fibre diameter than multiple reared lambs by 1 %. For ewes, single born and raised lambs were approximately 2 % finer than twin born and raised animals, lambs born as twins and raised as singles were intermediate between the other two classes. Generally for staple length and strength type of birth and rearing was not significant.

The year by flock interaction was significant for clean fleece weight at three ages, staple length at three ages and staple strength at two ages. For clean fleece weight, the interaction was significant for rams at 10 months of age due to the difference between flocks being greater in 1992 than in other years and no difference between years 1990 and 1991 for any of the flocks. For female fleece weights (16 and 40 months of age), the interaction was due to large differences between the flocks in 1989 compared to other years and little difference between the years 1990 and 1991. The interaction for staple length at 10 months of age was due to smaller differences between the flocks in 1992 than in other years and smaller differences between the years in Flock 1 than other flocks. For the female staple lengths (16 and 28 months of age), the interaction was due to smaller differences between flocks in 1992 than in other years and no differences between 1991 and 1992 for all flocks except Flock 2. The interaction for staple strength at 10 months of age was due to greater differences between flocks in 1990 compared to the other years and greater differences between years for Flock 1 compared to other flocks. For ram staple strength at 16 moths of age, the interaction was due to a greater difference between flocks in 1989 and 1990 compared to other years and a greater difference between years for Flock 3 than other flocks.

Table 4.3 **Analysis of variance F values for clean fleece weight and fibre diameter**

				Clean Fleece Weight			Fibre Diameter		
		Fixed Effect	Num DF	Den DF	F value	F Sig	Den DF	F value	F Sig
Ram	10 Months	Year	3	212	-	-	236	30.2	***
		Flock	3	204	-	-	227	92.3	***
		Tobr	2	1998	12.5	***	2169	8.36	***
		Aod	1	2162	78.7	***	2084	2.41	ns
		Year:Flock	9	218	7.06	***			
	16 Months	Year	3	238	211	***	259	-	-
		Flock	3	228	9.72	***	248	81.6	***
		Tobr	2	2145	28.1	***	2139	2.66	ns
		Aod	1	2061	7.12	**	2090	0.63	ns
		Year:Aod	3				1914	3.32	**
Ewe	16 Months	Year	3	192	-	-	230	30.2	***
		Flock	3	186	-	-	221	76.7	***
		Tobr	2	2067	-	-	2070	11.4	***
		Aod	1	1920	3.39	ns	2043	2.05	ns
		Year:Flock	8	199	2.48	*			
		Year:Tobr	6	228	3.18	**			
		Flock:Tobr	6	228	2.52	*			
	28 Months	Year	3	219	-	-	253	-	-
		Flock	3	213	34.9	***	243	-	-
		Tobr	2	1986	23.6	***	1966	7.92	***
		Aod	1	1910	4.66	*	1968	6.72	**
		NLW	1	1976	65.1	***	1911	5.19	*
		NLW:Year	3	1969	23.8	***	1908	9.14	***
		NLW:Flock	3				1907	3.70	*
	40 Months	Year	3	197	-	-	227	-	-
		Flock	3	190	-	-	217	63.1	***
		Tobr	2	1902	-	-	1903	4.85	**
		Aod	1	1787	4.47	*	1871	2.02	ns
		NLW	1	1898	17.8	***	1869	4.92	*
		NLW:Aod	1	1865	10.9	***			
		NLW:Year	3	1861	4.78	**	1827	4.19	**
		Year:Flock	8	203	4.75	***			
		Flock:Tobr	6	178	2.73	*			
	52 Months	Year	3	213	-	-	242	-	-
		Flock	3	203	-	-	229	56.6	***
		Tobr	2	1813	-	-	1806	7.15	***
		Aod	1	1749	0.09	ns	1796	2.19	ns
		NLW	1	1812	0.00	ns	1788	1.26	ns
		NLW:Year	3	1758	4.89	**	1728	10.8	***
		Flock:Tobr	6	124	2.43	*			
	64 Months	Year	2	137	-	-	137	33.9	***
		Flock	3	137	20.89	***	133	29.7	***
		Tobr	2	1152	4.13	*	1143	4.40	*
		Aod	1	1113	0.03	ns	1139	5.36	*
		NLW	1	1128	8.62	**	1092	46.4	***
		NLW:Year	2	1115	3.30	*	137	33.9	***

^ Tobr = type of birth and rearing, Aod = age of dam, Num = numerator, Den = denominator, *** = P<0.001, ** = P<0.01, * = P<0.05, ns = not significant

Table 4.4 Analysis of variance F values for staple length and staple strength

				Staple Length			Staple Strength		
		Fixed Effect	Num DF	Den DF	F value	F Sig	Den DF	F value	F Sig
Ram	10 Months	Year	3	180	-	-	163	-	-
		Flock	3	174	-	-	158	-	-
		Tobr	2	2105	0.43	ns	2078	0.19	ns
		Aod	1	1856	4.40	*	1657	0.04	ns
		Year:Flock	9	186	2.73	**	172	2.81	**
		Year:Aod	3	2077	2.92	*	2090	2.75	*
	16 Months	Year	3	231	303	***	206	-	-
		Flock	3	222	-	-	197	-	-
		Tobr	2	2128	3.13	*	2104	0.75	ns
		Aod	1	2028	2.73	ns	1953	2.23	ns
		Year:Flock	9				212	2.03	*
		Year:Aod	3				2069	2.67	*
		Flock:Aod	3	2074	3.29	*			
Ewe	16 Months	Year	3	206	-	-	206	44.1	***
		Flock	3	199	-	-	200	6.41	***
		Tobr	2	2048	0.05	ns	2057	-	-
		Aod	1	1974	0.98	ns	1943	2.34	ns
		Year:Flock	8	210	2.76	**			
		Tobr:Aod	2				2050	3.38	*
	28 Months	Year	3	204	-	-	173	-	-
		Flock	3	198	-	-	169	0.54	ns
		Tobr	2	1945	0.85	ns	1959	0.43	ns
		Aod	1	1872	1.77	ns	1811	0.46	ns
		NLW	1	1928	6.24	*	1958	1.90	ns
		Year:Flock	8	210	3.28	**			
		NLW:Year	3	1925	6.98	***	1953	12.4	***
	40 Months	Year	3	203	-	-	170	-	-
		Flock	3	197	31.57	***	164	1.10	ns
		Tobr	2	1903	0.78	ns	1911	3.35	*
		Aod	1	1819	0.12	ns	1714	4.45	*
		NLW	1	1842	0.00	ns	1912	9.29	**
		NLW:Year	3	1848	3.20	*	1873	28.01	***
	52 Months	Year	3	257	32.1	***	165	-	-
		Flock	3	242	23.6	***	157	0.78	ns
		Tobr	2	1807	0.71	ns	1822	2.39	ns
		Aod	1	1800	1.58	ns	1563	0.38	ns
		NLW	1	1788	17.4	***	1826	0.04	ns
		NLW:Year	3				1806	8.86	***
	64 Months	Year	2	131	19.9	***	102	-	-
		Flock	3	129	18.9	***	105	1.11	ns
		Tobr	2	1130	4.70	*	1133	-	-
		Aod	1	1108	3.84	ns	992	1.75	ns
		NLW	1	1092	32.0	***	1130	0.76	ns
		Tobr:Aod	2				1135	3.36	*
		NLW:Year	2				1116	17.9	***

[A] Tobr = type of birth and rearing, Aod = age of dam, Num = numerator, Den = denominator, *** = P<0.001, ** = P<0.01, * = P<0.05, ns = not significant

4.2.2 Variances

Genetic and phenotypic variances of fleece traits are presented in Table 4.5 and 4.6. Genetic and phenotypic variances of all fleece traits increased as age increased, for both rams and ewes.

Table 4.5 Genetic and phenotypic variances of clean fleece weight and fibre diameter at different ages

		Clean Fleece Weight		**Fibre Diameter**	
	Age	**Genetic**	**Phenotypic**	**Genetic**	**Phenotypic**
Ram	**10**	0.061	0.156	1.13	2.35
	16	0.097	0.198	1.72	3.10
Ewe	**16**	0.140	0.364	1.57	2.60
	28	0.237	0.502	2.03	2.86
	40	0.241	0.573	2.04	3.38
	52	0.281	0.573	2.30	3.56
	64	0.315	0.582	2.82	3.95

Age is in months

Table 4.6 Genetic and phenotypic variances of staple length and staple strength at different ages

		Staple Length		**Staple Strength**	
	Age	**Genetic**	**Phenotypic**	**Genetic**	**Phenotypic**
Ram	**10**	9.84	29.0	20.5	102.9
	16	18.2	39.6	44.1	106.8
Ewe	**16**	51.9	99.2	29.7	72.7
	28	46.0	87.0	36.3	94.5
	40	46.5	97.0	37.7	115.2
	52	61.2	93.0	30.1	126.6
	64	63.2	99.6	39.9	128.2

Age is in months

4.2.3 Genetic Parameters for Fleece Traits

Heritabilities of clean fleece weight, staple length and strength for both rams and ewes at 16 months of age were approximately 0.5 (± 0.06) (Table 4.7 and 4.8). The heritability of fibre diameter was slightly higher for both sexes at approximately 0.6 (± 0.06).

Phenotypic correlations among the fleece traits ranged from 0.11 (± 0.02) to 0.37 (± 0.02) for rams (Table 4.7) and 0.09 (± 0.02) to 0.33 (± 0.02) for ewes (Table 4.7) and were similar in each sex except between clean fleece weight and staple strength (ram 0.22, ewe 0.09). Genetic correlations between clean fleece weight and the other traits were about 0.3 among the rams at 16 months of age, but were lower among the ewes. Correlations between fibre diameter and staple length, and fibre diameter and staple strength were similar for both rams and ewes (0.2 and 0.5, respectively). The genetic correlation between staple length and staple strength was low and close to zero in both sexes. Genetic correlations between ram and ewe fleece traits at 16 months of age (Table 4.9) were very high for fibre diameter (0.96 ± 0.05) and staple length (0.92 ± 0.06) and lower for clean fleece weight (0.71 ± 0.09) and staple strength (0.57 ± 0.10).

Table 4.7 **Heritabilities (on diagonal), phenotypic (above diagonal) and genetic (below diagonal) correlations (standard error) between ram fleece traits at 16 months of age (6 months wool growth)**

	CFW	FD	SL	SS
CFW	**0.49** **(0.064)**	0.35 (0.021)	0.37 (0.020)	0.22 (0.022)
FD	0.32 (0.088)	**0.57** **(0.064)**	0.26 (0.022)	0.33 (0.021)
SL	0.36 (0.092)	0.25 (0.094)	**0.46** **(0.063)**	0.11 (0.023)
SS	0.32 (0.098)	0.47 (0.083)	-0.02 (0.109)	**0.45** **(0.062)**

CFW = Clean fleece weight, FD = Fibre diameter, SL = Staple length, SS = Staple strength

Table 4.8 **Heritabilities (on diagonal), phenotypic (above diagonal) and genetic (below diagonal) correlations (standard error) between ewe fleece traits at 16 months of age (12 months wool growth)**

	CFW	FD	SL	SS
CFW	**0.45** **(0.063)**	0.25 (0.023)	0.29 (0.022)	0.09 (0.023)
FD	0.14 (0.101)	**0.60** **(0.069)**	0.33 (0.022)	0.27 (0.022)
SL	0.21 (0.099)	0.21 (0.092)	**0.56** **(0.068)**	0.10 (0.024)
SS	-0.03 (0.115)	0.45 (0.093)	0.06 (0.109)	**0.39** **(0.060)**

CFW = Clean fleece weight, FD = Fibre diameter, SL = Staple length, SS = Staple strength

Table 4.9 **Genetic correlations (standard error) between ram and ewe fleece traits at 16 months of age**

	Ram			
	CFW	**FD**	**SL**	**SS**
Ewe	0.71 (0.085)	0.96 (0.047)	0.92 (0.061)	0.57 (0.101)

CFW = Clean fleece weight, FD = Fibre diameter, SL = Staple length, SS = Staple strength

4.2.4 Correlations between Fleece and Reproduction Traits

Phenotypic correlations between ewe fleece traits at various ages and average reproduction traits of the ewes were generally very low and close to zero (Table 4.10). Phenotypic correlations between clean fleece weight and average female reproduction traits were low (about 0.1), ranging from -0.12 (± 0.03) to 0.22 (± 0.03). Correlations between fibre diameter and average reproduction were also low (about 0.1), with a range of -0.03 (± 0.03) to 0.15 (± 0.04). Correlations between average reproduction traits and staple length and strength were close to zero and ranged from -0.15 (± 0.04) to 0.19 (± 0.03).

Phenotypic correlations between scrotal circumference at 5, 10 and 16 months and clean fleece weight at 10 and 16 months were low ranging from 0.14 (± 0.02) to 0.31 (± 0.02), for rams. Phenotypic correlations between scrotal circumference and fibre diameter (range 0.13 to 0.23) (Table 4.11). Correlations between scrotal circumference and staple length and strength were very low ranging from -0.02 (± 0.02) to 0.18 (± 0.02). There was a tendency for the correlations between traits measured at the same age to be slightly higher than when traits were measured at different ages.

The genetic correlations between average number of lambs weaned and clean fleece weight was close to zero and ranged from -0.15 to 0.13 for clean fleece weight at various ages (Table 4.12). The correlations of average number of lambs weaned and fibre diameter were consistently small and positive and ranged from 0.07 to 0.20. The genetic correlations of average number of lambs weaned and staple length were consistently moderately negative (-0.15 to -0.22), while staple strength was moderately positive (0.3) except for staple strength at 64 months (-0.05). The corresponding genetic correlations of average number of lambs weaned with the wool traits measured in the rams were similar to those in the ewes, with staple strength being slightly higher (0.5).

The genetic correlations of average fertility and average litter size with the wool traits were generally consistent with those found for average number of lambs weaned (Table 4.12). The genetic correlations for average rearing ability and the wool traits were generally similar to those for average number of lambs weaned but were variable for the different ages. All correlation estimates had very high standard errors.

Table 4.10 **Phenotypic correlations (standard error) between average female reproductive traits and fleece traits**

	Age	aNLW	aFert	aLS	aRA
CFW	16	0.06 (0.023)	0.08 (0.023)	0.10 (0.024)	0.03 (0.023)
	28	0.07 (0.031)	0.05 (0.028)	-0.01 (0.029)	-0.12 (0.029)
	40	0.07 (0.032)	0.08 (0.028)	0.12 (0.029)	0.10 (0.029)
	52	0.07 (0.033)	0.11 (0.029)	0.18 (0.028)	0.22 (0.029)
	64	0.06 (0.041)	0.04 (0.037)	0.07 (0.037)	0.08 (0.038)
FD	16	0.09 (0.023)	0.11 (0.023)	0.08 (0.025)	0.08 (0.023)
	28	0.02 (0.031)	0.02 (0.028)	0.01 (0.029)	-0.03 (0.029)
	40	0.03 (0.032)	0.06 (0.029)	0.14 (0.029)	0.13 (0.029)
	52	0.02 (0.033)	0.05 (0.029)	0.12 (0.029)	0.14 (0.030)
	64	0.02 (0.041)	0.04 (0.037)	0.12 (0.036)	0.15 (0.037)
SL	16	0.06 (0.023)	0.06 (0.023)	0.06 (0.025)	0.06 (0.023)
	28	0.00 (0.032)	-0.01 (0.028)	0.00 (0.029)	-0.03 (0.029)
	40	-0.01 (0.032)	0.00 (0.029)	0.07 (0.029)	0.10 (0.030)
	52	0.00 (0.033)	0.01 (0.029)	0.07 (0.029)	0.10 (0.030)
	64	0.00 (0.041)	-0.03 (0.037)	-0.02 (0.037)	0.02 (0.038)
SS	16	0.10 (0.022)	0.10 (0.023)	0.10 (0.024)	0.07 (0.023)
	28	0.02 (0.032)	0.01 (0.028)	-0.01 (0.029)	0.00 (0.029)
	40	0.02 (0.033)	0.03 (0.029)	0.09 (0.029)	0.18 (0.029)
	52	0.02 (0.033)	0.02 (0.029)	0.03 (0.029)	0.19 (0.029)
	64	0.00 (0.042)	-0.06 (0.037)	-0.15 (0.036)	0.04 (0.039)

CFW = Clean fleece weight, FD = Fibre diameter, SL = Staple length, SS = Staple strength, aNLW = Average number of lambs weaned over a lifetime, aFert = Average fertility of the ewe, aLS = Average litter size, aRA = Average rearing ability

Table 4.11 **Phenotypic correlations (standard error) between scrotal circumference and fleece traits for rams**

		SC		
	Age	5	10	16
CFW	10	0.31 (0.022)	0.25 (0.022)	0.14 (0.023)
	16	0.21 (0.023)	0.26 (0.022)	0.30 (0.021)
FD	10	0.17 (0.023)	0.23 (0.022)	0.14 (0.023)
	16	0.13 (0.024)	0.23 (0.022)	0.22 (0.022)
SL	10	0.14 (0.023)	0.18 (0.023)	0.07 (0.023)
	16	0.15 (0.024)	0.16 (0.023)	0.15 (0.023)
SS	10	-0.02 (0.023)	0.01 (0.023)	0.03 (0.023)
	16	0.04 (0.024)	0.06 (0.024)	0.10 (0.023)

CFW = Clean fleece weight, FD = Fibre diameter, SL = Staple length, SS = Staple strength, SC = Scrotal circumference

Table 4.12 Genetic correlations (standard error) between average female reproductive traits and fleece traits

		Age	aNLW		aFert		aLS		aRA	
CFW	Ram	10	-0.02	(0.150)	0.02	(0.141)	0.09	(0.133)	-0.01	(0.157)
		16	0.11	(0.152)	0.15	(0.144)	0.29	(0.132)	0.00	(0.160)
	Ewe	16	-0.15	(0.158)	-0.10	(0.147)	0.09	(0.136)	-0.27	(0.163)
		28	0.07	(0.154)	0.04	(0.146)	0.07	(0.136)	-0.17	(0.160)
		40	0.03	(0.155)	0.08	(0.145)	0.10	(0.137)	0.00	(0.164)
		52	0.13	(0.156)	0.17	(0.145)	0.14	(0.136)	0.13	(0.162)
		64	-0.11	(0.198)	0.04	(0.181)	-0.01	(0.176)	-0.03	(0.201)
FD	Ram	10	0.18	(0.156)	0.14	(0.148)	0.21	(0.137)	0.09	(0.165)
		16	0.12	(0.148)	0.09	(0.140)	0.18	(0.130)	0.05	(0.156)
	Ewe	16	0.19	(0.146)	0.22	(0.134)	0.17	(0.128)	0.16	(0.153)
		28	0.07	(0.144)	0.05	(0.136)	0.05	(0.127)	-0.02	(0.153)
		40	0.20	(0.147)	0.15	(0.138)	0.21	(0.127)	0.23	(0.152)
		52	0.10	(0.149)	0.19	(0.137)	0.19	(0.127)	0.15	(0.154)
		64	0.11	(0.181)	0.22	(0.162)	0.24	(0.154)	0.18	(0.180)
SL	Ram	10	-0.02	(0.175)	0.17	(0.165)	0.01	(0.157)	0.17	(0.182)
		16	-0.10	(0.157)	0.07	(0.149)	0.04	(0.141)	-0.01	(0.165)
	Ewe	16	-0.20	(0.152)	-0.07	(0.143)	-0.14	(0.133)	-0.12	(0.159)
		28	-0.19	(0.152)	-0.05	(0.144)	-0.14	(0.133)	-0.17	(0.162)
		40	-0.22	(0.154)	-0.05	(0.148)	-0.19	(0.140)	-0.06	(0.165)
		52	-0.15	(0.144)	-0.02	(0.136)	-0.08	(0.130)	-0.05	(0.152)
		64	-0.19	(0.190)	-0.05	(0.175)	-0.24	(0.166)	-0.02	(0.194)
SS	Ram	10	0.48	(0.187)	0.41	(0.179)	0.49	(0.170)	0.28	(0.201)
		16	0.49	(0.153)	0.36	(0.148)	0.48	(0.137)	0.37	(0.166)
	Ewe	16	0.34	(0.153)	0.22	(0.148)	0.25	(0.138)	0.31	(0.163)
		28	0.34	(0.169)	0.15	(0.162)	0.33	(0.148)	0.11	(0.183)
		40	0.34	(0.170)	0.26	(0.164)	0.25	(0.151)	0.43	(0.164)
		52	0.31	(0.201)	0.27	(0.191)	0.18	(0.180)	0.48	(0.188)
		64	-0.05	(0.231)	-0.10	(0.211)	-0.37	(0.190)	0.19	(0.233)

CFW = Clean fleece weight, FD = Fibre diameter, SL = Staple length, SS = Staple strength, aNLW = Average number of lambs weaned over a lifetime, aFert = Average fertility of the ewe, aLS = Average litter size, aRA = Average rearing ability

Genetic correlations between scrotal circumference and fleece traits were moderate to very low with high standard errors (Table 4.13). Correlations between scrotal circumference and ram clean fleece weight were low and positive ranging from 0.10 (± 0.11) to 0.37 (± 0.09). Correlations between ewe clean fleece weight and scrotal circumference were generally positive except between scrotal circumference at 16 months of age and ranged from -0.18 (± 0.15) to 0.35 (± 0.10). Generally, correlations decreased slightly as the age of scrotal circumference increased.

Genetic correlations between scrotal circumference and ram fibre diameter were low and positive and were highest for scrotal circumference at 10 months of age. Similarly correlations between ewe fibre diameter and scrotal circumference were low and positive with a range between 0.07 (± 0.10) and 0.30 (± 0.11). Correlations were slightly higher for scrotal circumference at 10 and 16 months of age, and increased slightly as the age of scrotal circumference increased.

Genetic correlations between scrotal circumference and ram staple length were very low and ranged from -0.14 (± 0.13) to 0.12 (± 0.12). Correlations between scrotal circumference and ewe staple length were generally low and negative ranging from -0.31 (± 0.12) to 0.05 (± 0.11).

Genetic correlations between scrotal circumference and ram staple strength were close to zero except between scrotal circumference at 10 months of age and staple strength at the same age which was 0.23 (± 0.15). Correlations between scrotal circumference and ewe staple strength were generally low and negative but ranged from -0.41 (± 0.18) to 0.19 (± 0.12). There was a slight trend for the correlations to become more negative as the age of staple strength increased especially with scrotal circumference at 16 months of age.

Table 4.13 Genetic correlations (standard error) between scrotal circumference and fleece traits

			SC					
		Age	5		10		16	
CFW	Ram	10	0.37	(0.085)	0.29	(0.102)	0.10	(0.110)
		16	0.25	(0.092)	0.32	(0.103)	0.26	(0.105)
	Ewe	16	0.35	(0.097)	0.24	(0.116)	0.09	(0.119)
		28	0.17	(0.101)	0.03	(0.118)	-0.08	(0.119)
		40	0.13	(0.103)	0.02	(0.119)	-0.08	(0.120)
		52	0.07	(0.105)	0.07	(0.121)	-0.09	(0.122)
		64	0.18	(0.131)	-0.10	(0.147)	-0.18	(0.148)
FD	Ram	10	0.09	(0.097)	0.23	(0.108)	0.06	(0.114)
		16	0.09	(0.092)	0.25	(0.101)	0.15	(0.106)
	Ewe	16	0.19	(0.093)	0.28	(0.106)	0.24	(0.108)
		28	0.19	(0.090)	0.23	(0.104)	0.26	(0.105)
		40	0.07	(0.097)	0.09	(0.112)	0.16	(0.112)
		52	0.12	(0.096)	0.17	(0.111)	0.16	(0.112)
		64	0.30	(0.113)	0.24	(0.129)	0.25	(0.131)
SL	Ram	10	0.03	(0.110)	0.12	(0.125)	-0.14	(0.128)
		16	0.10	(0.098)	0.10	(0.114)	0.02	(0.117)
	Ewe	16	0.00	(0.099)	0.05	(0.113)	-0.06	(0.116)
		28	0.01	(0.100)	-0.05	(0.115)	-0.10	(0.117)
		40	-0.12	(0.103)	-0.31	(0.115)	-0.21	(0.120)
		52	-0.14	(0.095)	-0.05	(0.111)	-0.09	(0.112)
		64	0.00	(0.128)	-0.17	(0.143)	-0.19	(0.146)
SS	Ram	10	0.03	(0.128)	0.23	(0.147)	0.01	(0.147)
		16	-0.04	(0.101)	0.00	(0.117)	0.00	(0.118)
	Ewe	16	0.04	(0.108)	0.19	(0.120)	0.06	(0.124)
		28	-0.18	(0.112)	0.04	(0.130)	-0.08	(0.132)
		40	-0.08	(0.121)	-0.06	(0.139)	-0.20	(0.141)
		52	-0.09	(0.138)	0.03	(0.159)	-0.24	(0.159)
		64	-0.20	(0.163)	-0.33	(0.178)	-0.41	(0.180)

CFW = Clean fleece weight, FD = Fibre diameter, SL = Staple length, SS = Staple strength, SC = Scrotal circumference

4.3 DISCUSSION

4.3.1 Fleece Traits

The heritability of, and correlations between fleece traits in Australia and overseas have been well documented (Fogarty 1995, Clarke 2002, Safari and Fogarty 2003). The heritabilities and correlations from this study were similar to those previously reported (Table 4.7 and Table 4.7). Genetic correlations between ram and ewe fleece traits (Table 4.9) were very similar to those calculated by Hill (2001), and Lewer *et al.* (1994). The genetic correlations between ram and ewe traits indicate that ram and ewe data of the same age can be combined and analysed as one trait if required. As reported by Hill (2001), correlations between the same traits at different ages were high indicating that selection for a trait at an early age will result in the expected response at older ages.

The results show that year of birth effects were significant for all fleece traits. This result is supported by Turner and Young (1969) and Hill (2001) who also observed that fleece traits were affected by different years of measurement. Greater fleece weights in 1992 reflect the good seasonal conditions early in that year when the season broke at the end of February leaving abundant autumn feed available. This may also reflect the higher (although not significant) fibre diameter in 1992. Similarly to the results reported for reproduction traits differences between the flocks indicates that there are differences between Merino families in South Australia. Type of birth and rearing effects were significant for clean fleece weight and fibre diameter but not for staple length or strength which is in general agreement with Hill (2001). Least squares means indicated that lambs born as singles had greater fleece weights than lambs born as twins. This implies that the greater fleece weight was due to variation in the pre-natal environment, and considering there were no differences seen in staple length the increase in fleece weight may have been due to a greater number of follicles or fibres produced per unit area of skin. This hypothesis is supported by the greater follicle densities (mean, overall and effective) for single born lambs over multiple born lambs reported by Hill (2001) and supports the theory of follicle competition (greater competition results in fewer follicles with larger developmental capacity) proposed by Moore *et al.* (1989). Another hypothesis for greater fleece weights of singles over twins may simply be due to greater total skin area resulting from higher body weight of single born lambs.

4.3.2 Reproduction and Fleece Traits

A preliminary analysis was carried out for each age of number of lambs weaned recorded to test the effect of reproduction on clean fleece weight and fibre diameter (Appendix E, Ingham and Ponzoni 2002). This analysis considered the effect of adjusting fleece traits for reproductive status, as has been common practice, on the correlations between them by comparing two models, with and without adjustment. The phenotypic variance was more affected by the adjustment than the genetic variance and the adjustment generally reduced the magnitude of the variance. However, there was little change in the heritability of the trait and it was decided that because of this, fleece traits should be adjusted for lambing status rather than possibly over estimating genetic parameters. These preliminary estimates cannot be directly compared with the estimates presented in this chapter as the models used were different. However, correlations from the two analyses were more similar with fibre diameter than with clean fleece weight. The consequence of adjusting for lambing status is that the phenotypic correlations are expected to be zero, which was the case in both studies (Table 4.10 and Appendix E, Table 2, Ingham and Ponzoni 2002).

There is variation in published parameters between fleece and reproduction and their accuracy. Fogarty (1995) cited genetic correlations of 0.07 from Young *et al.* (1963) and 0.70 from Blair (1981) (in Romney sheep) between number of lambs weaned and clean fleece weight and overall 0.41 (0.24) between number of lambs weaned and fibre diameter for Merinos. Estimates from this study (Table 4.12) fit within these ranges and are similar to those reported by Safari and Fogarty (2003). There were no Australian correlation estimates between reproduction and fleece traits reported by Clarke (2002). Generally genetic correlations from this study between female reproduction and clean fleece weight and fibre diameter were low and positive indicating that selection for improvements in fleece traits can be achieved simultaneously with improvement in reproduction rates among Merino flocks. Correlations between reproduction and staple length were low but negative, indicating that selection to increase staple length may slightly reduce the rate of improvement in reproductive rate. However, the low magnitude of the correlations should still allow improvement in both traits. Correlations between staple strength and reproduction traits were slightly higher indicating the possibility of a stronger correlated response in reproductive rate if selection to increase staple strength was used.

Brash *et al.* (1994b) reported genetic correlations between scrotal circumference and clean fleece weight (0.15) and fibre diameter (0.22). Estimates from this study were generally in agreement with these values (Table 4.13). Correlations with staple length and strength were low and negative, no other correlations have been published for these traits. Genetic correlations between the wool traits fibre diameter, staple length and staple strength and scrotal circumference indicate that selection to improve fleece traits will only cause a small response in scrotal circumference. Correlations with clean fleece weight, measured in rams particularly, indicate that there may be a slightly greater correlated increase in scrotal circumference when selecting for clean fleece weight.

Merino Genetic Services, a genetic evaluation service, assumes a genetic correlation of both clean fleece weight and fibre diameter with number of lambs weaned of 0.0 at all ages (Pers. Comm. D. Brown 2003), whereas Rampower, another Australian Merino genetic evaluation service, assumes a value of 0.1 (Pers. Comm. K. Atkins 2003). The analysis carried out between individual ages indicated that the correlations assumed by the genetic evaluation services were in good agreement for fibre diameter but were not for clean fleece weight. The main analysis using average reproduction traits indicated that correlations were in the range 0.0 to 0.2 (Table 4.12), and agreed more closely with the current values used by genetic evaluation services. However, it could be suggested that when creating specific indexes the correlations used may need to be changed depending on the traits being used in the index.

In Chapter 3, litter size was suggested as a candidate for use in genetic improvement programs. The correlations estimated in this chapter support this recommendation. Correlations between average litter size and clean fleece weight were more consistent across ages than fertility, and were similar to correlations between average number of lambs weaned and fleece traits suggesting that it may make a good trait to use in a selection index. Litter size also had mostly positive genetic correlations with fleece traits indicating that selection to improve either reproduction or fleece traits will not adversely affect the other. Similarly for scrotal circumference at 10 months of age, low and mainly positive correlations with fleece traits indicates that scrotal circumference at this age may be safely used as an indirect selection criterion. Correlations between staple length and average litter size were generally small but negative, indicating that there may be a small adverse effect on reproduction if greater staple length was desired. However, correlations at young ages of fleece measurement and for male measurements were low and positive indicating that early selection would possibly give a more desired response.

4.4 CONCLUSION

The results from this study suggest that there are significant non-zero genetic relationships between reproduction and fleece traits. There are very few correlation estimates published in the literature between wool and reproduction traits, and those that are, vary widely. Correlations estimated here were in general agreement with other published estimates from Australian Merinos. While genetic correlations were low overall, they were generally consistent over the different ages of measurement of the wool traits. The standard errors of the correlation estimates mean that they were generally not significantly different from zero, but were favourable for allowing the improvement of both reproduction and fleece characters at the same time using appropriate selection techniques. As has been previously suggested, litter size and scrotal circumference would be recommended as selection criteria for use in an index due to more stable correlations over ages of measurement and slightly higher correlations with fleece traits. The parameters currently used by genetic evaluation services fit within the range of estimates from this study for fibre diameter but not clean fleece weight. Further analysis needs to be carried out on other large data sets to get more estimates from other populations of Merinos to be more confident in applying these values in genetic evaluation programs.

Chapter 5

Genetic Parameters for Growth and Live Carcase Traits

5.1 INTRODUCTION

Traditionally, Merino sheep have been selected mainly for wool traits, with limited attention paid to meat attributes. However, Merino sheep are 'dual purpose' in the sense that they generate income from both the sale of wool and of surplus sheep. Using 1987-88 prices as a basis the corresponding figures in 1999-2000 for wool, lambs and mutton are 65%, 151% and 133%, respectively (ABARE 2000). In many SA Merino flocks and throughout Australia this trend has resulted in an increase in the contribution of lambs and mutton to income, relative to that from wool, and greater emphasis placed (or considered) on sheep meat production, relative to that placed on wool (Ingham and Ponzoni 2001; Safari *et al.* 2001, Clarke 2002; Davidson *et al.* 2002; Fogarty *et al.* 2003).

Genetic parameter estimates are widely available for Merinos for fleece traits and weight traits at birth, weaning and older ages (Ponzoni and Fenton 2000). However, there are few genetic parameter estimates of weight traits between weaning and yearling ages, and fewer estimates of carcase traits at any age. It is important for the further development and proper use of the Merino as a dual-purpose breed, that the gaps in our knowledge of the interactions between weight and carcase traits are filled. This chapter presents genetic parameter estimates for live weight from birth to hogget age (16 months), and for fat and eye muscle depth from four months of age to hogget age.

5.2 MATERIALS AND METHODS

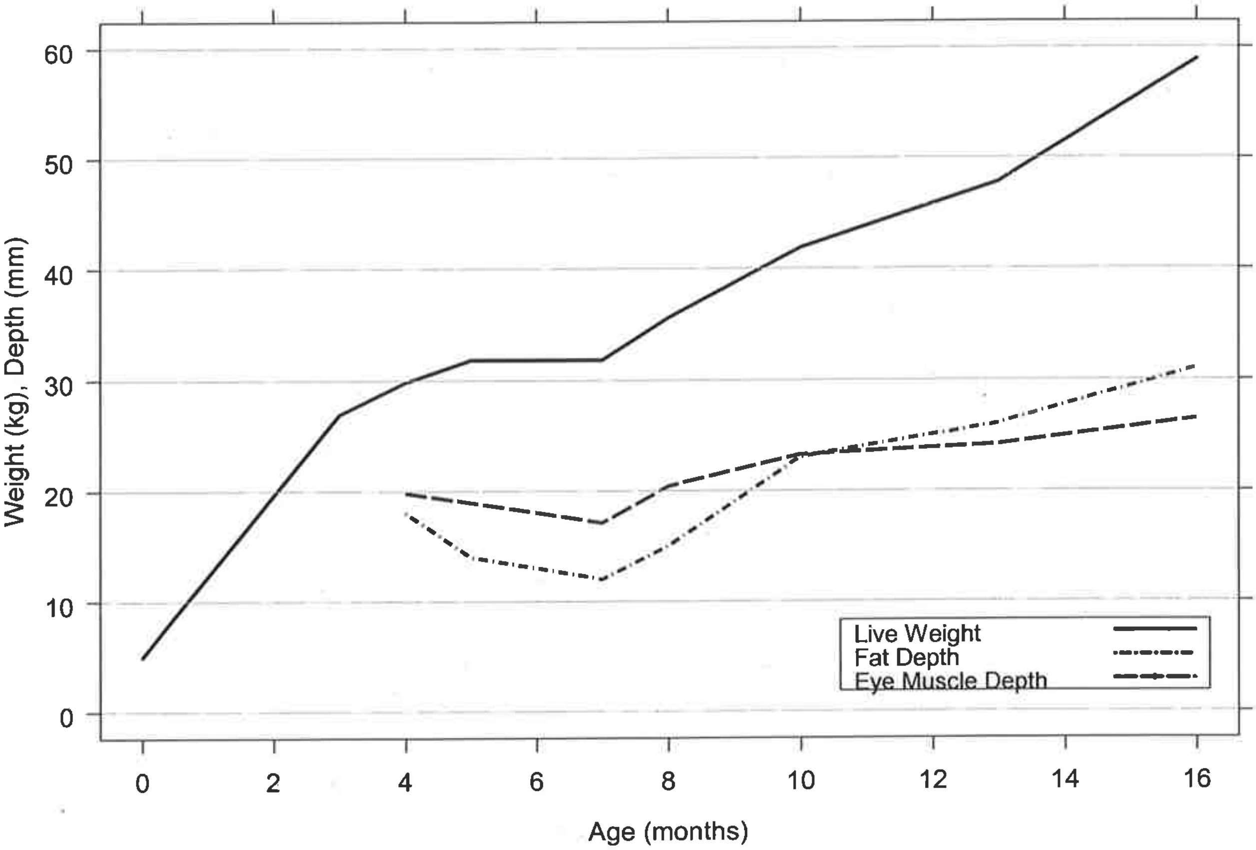
The data used were from the Selection Demonstration Flocks and are described in detail in Chapter 2.1.3. The number of records available, mean, standard deviation and range for each of the traits in Table 5.1. Live weight was measured at birth and weaning, then live weight, fat depth and eye muscle depth were measured at approximately 6 weekly intervals until 10 months of age. Fat and eye muscle depth were measured by ultrasound at the C site.

Table 5.1 Number of records available (n), mean, standard deviation (s.d.), coefficient of variation (CV) and range for live weights, fat depths and eye muscle depths

Trait	Abbreviation	n	Mean	s.d.	CV	Range
Birth weight (kg)	**BW**	1790	5.0	0.91	0.18	1.8 – 8.4
Weaning weight (kg)	**WW**	1789	26.9	5.98	0.22	9.0 – 44.2
Live weight (kg)	**WT4**	1774	29.8	6.33	0.21	9.6 – 48.4
	WT5	1761	31.8	6.23	0.20	13.0 – 50.5
	WT7	1703	31.8	6.02	0.19	13.9 – 54.5
	WT8	1678	35.6	6.56	0.18	14.3 – 58.0
	WT10	1669	41.9	7.19	0.17	20.5 – 67.5
	WT13	1670	47.8	8.79	0.18	24.8 – 74.5
	WT16	1666	58.9	9.03	0.15	31.6 – 88.5
	Weight Gain	1666	0.002	0.09	45	-0.30 – 0.32
Fat depth (mm)	**FAT4**	1769	1.8	0.59	0.33	0.5 – 4.5
	FAT5	1657	1.4	0.48	0.34	0.5 – 3.5
	FAT7	1691	1.2	0.48	0.40	0.5 – 3.5
	FAT8	1674	1.5	0.52	0.35	0.5 – 4.0
	FAT10	1669	2.3	0.56	0.24	1.0 – 4.0
	FAT13	1670	2.6	0.70	0.27	1.0 – 5.0
	FAT16	1666	3.1	0.86	0.28	1.0 – 5.5
	Fat Gain	1666	0.001	0.15	150	-0.57 – 0.40
Eye muscle depth (mm)	**EMD4**	1769	19.8	3.08	0.16	7.0 – 29.0
	EMD5	1657	18.9	2.35	0.12	10.0 – 28.0
	EMD7	1691	17.1	2.91	0.17	8.0 – 25.0
	EMD8	1674	20.4	2.91	0.14	8.0 – 29.0
	EMD10	1669	23.2	2.58	0.11	13.0 – 32.0
	EMD13	1670	24.1	2.42	0.10	16.0 – 37.0
	EMD16	1666	26.4	2.25	0.09	17.0 – 33.0
	Muscle Gain	1666	0.0004	0.10	250	-0.36 – 0.40

Figures after the abbreviation are months of age, Standardised Weight gain (7 – 16 months) units = months^{-1}, Standardised Fat and Muscle gain (7 – 16 months) units = months^{-1}

Figure 5.1 Means of live weight, fat depth (x10) and eye muscle depth



Statistical Analysis

Data were analysed using linear mixed model methodology in ASReml (Gilmour *et al.* 2002). An animal term was fitted allowing optimal analysis of a finite, selected population. All two-way interactions between fixed effects were tested. Where the interactions were non-significant (P>0.05) they were not included in the final models.

The final base model can be written as:

$$\mathbf{y} = \mathbf{X\tau} + \mathbf{Z}_1\mathbf{a} + \mathbf{Z}_2\mathbf{c} + \mathbf{e}$$

where

$$\mathbf{y} \sim \mathrm{N}\left(\mathbf{X\tau}, \sigma_a^2\mathbf{Z}_1\mathbf{A}\mathbf{Z}_1^{'} + \sigma_c^2\mathbf{Z}_2\mathbf{Z}_2^{'} + \sigma^2\mathbf{I}_n\right)$$

and

$$\mathbf{e} \sim \mathrm{N}\left(0, \sigma^2\right)$$

where $\mathbf{X}^{n \times t}$ is a design matrix which assigns the effects to animals, $\boldsymbol{\tau}^{1 \times t}$ is the vector of fixed effect means, $\mathbf{Z}_1^{n \times p}$ is the design matrix for the animal effects, $\mathbf{A}$ is the numerator relationship matrix, $\mathbf{Z}_2^{n \times q}$ is the design matrix for the dam common environmental effects. The vectors $\mathbf{a}$ and $\mathbf{c}$ represent the animal and dam common environmental effects respectively. $\mathbf{e}^{1 \times n}$ is the vector of random errors. σ_a^2 is the variance due to the animal effect, σ_c^2 is the variance due to the dam common environmental effect and σ^2 is the residual variance parameter.

This model can also be symbolically written as:

y ~ mean + year (2000, 2001) + flock (1-5) + type of birth and rearing (11, 21, 22) + linear(age of dam) + linear(day of birth) + <u>animal</u> + <u>dam</u>

Terms fitted as random effects in the model are underlined, all other terms are fitted as fixed effects with levels in parentheses. The dam common environmental component includes both the non-genetic effect of the dam and the direct genetic effect of the dam, or the genetic maternal effect. This will be referred to as the permanent maternal effect. This formed the base model for all analyses. Each variate was tested and the model was modified where necessary. Changes to the base model for each variate are shown in Table 5.2. An ante-dependence model was also tested but was not appropriate for this data.

Table 5.2 Final models fitted to growth traits

Variate	Model fitted	Defined as
Live weight	Base model + significant interactions	-
Fat depth	Base model without <u>dam</u> + significant interactions	Model 1
	Base model without <u>dam</u> + significant interactions + linear(weight) + weight:sex	Model 2
Eye muscle depth	Base model without <u>dam</u> + significant interactions	Model 1
	Base model without <u>dam</u> + significant interactions + linear(weight) + weight:sex	Model 2

A repeatability model was fitted to the female data by using a multivariate analysis. Fixed effects included are shown in Table 5.2. The limitation with repeatability is that it does not allow for differing variances at different ages. However, more sophisticated models did not show a significant improvement, hence the simpler model assuming equal variance at each age was considered to be sufficient. These analyses were also performed using ASReml (Gilmour *et al.* 2002)

A random regression model was fitted to the growth data. This model included the fixed effects as shown in Table 5.2. The random regression model fitted orthogonal polynomials of age at measurement as independent variables. Data from 4 months of age was used to avoid potential problems associated with birth weights; the inclusion of birth weight has been shown to considerably increase the order of polynomial fit required (Meyer 2001). Apiolaza *et al.* (2000) also showed that random regression models may have trouble fitting data containing large scale effects where small variances exist, such as for birth weight. A quadratic model was used for both random effects, the direct genetic and direct permanent environmental effect. For weight the permanent maternal effect was also fitted. Let y_{ij} denote the j^{th} record of animal i at age t_{ij}, then the random regression model was defined as:

$$y_{ij} = F_{ij} + \sum_{m=0}^{2} a_{im}\Phi(t_{ij}) + \sum_{m=0}^{2} p_{im}\Phi(t_{ij}) + \sum_{m=0}^{2} dp_k + \varepsilon_{ij}$$

where:

F_{ij} represents the fixed effects, a_{im} and p_{im} are the m^{th} order random regression coefficients of the direct additive genetic and direct permanent environmental effects, respectively, dp_k is the permanent environmental effect of dam k fitted to live weight only, $\Phi(t_{ij})$ is the m^{th} value of the orthogonal polynomial at age t_{ij}, and ε_{ij} is the residual error.

The standardised difference between measurements of weight, fat and eye muscle depth at 7 and 16 months of age (Equation 5.1) was used to create three new traits, weight gain, fat gain and muscle gain. The difference between 7 and 16 months was used rather than 4 and 16 months because, as can be seen in Figure 5.1, the slope of the growth curve for all three traits was more linear between 7 and 16 months than over the whole time period. The standardised difference of weight, fat depth and eye muscle depth will be referred to as weight gain (WG), fat gain (FG) and muscle gain (MG). Fixed effects were as shown in Table 5.2, but dam was not fitted as a random effect for any of the new traits. Where Model 2 is referred to, fat gain and muscle gain were adjusted for weight gain rather than live weight.

Standardised Difference between measurements at 7 and 16 months:

$$x\textbf{gain}\ (\text{month}^{-1}) = \frac{x16 - x7}{9} \qquad \text{(Equation 5.1)}$$

where 16 and 7 = months of age, 9 = the difference between 7 and 16, x = standardised weight, fat depth or eye muscle depth according to:

$$x = \frac{x_i - \bar{x}}{\sigma} \qquad \text{(Equation 5.2)}$$

where x_i = the *i*th record, $\bar{x}$ = the mean, σ = the standard deviation

Heritabilities reported were from univariate and random regression analyses. Correlations between different ages of the traits and between different traits were from multivariate analyses. Heritabilities and correlations will be referred to as very low to very high according to the classification in Table 2.5.

5.3 RESULTS

5.3.1 Fixed Effects

The significance of fixed effects for live weight, and fat and eye muscle depth using Model 2 are presented in Table 5.3 and Table 5.4, Least squares means are presented in Tables C.1 – C.9 (Appendix C). Between year effects were significant for all traits at all ages except for weight at birth and 4 months of age and fat depth at 7 months of age. The difference between years was greater at older ages for weight, with animals in 2000 at 16 months of age 8 % heavier than animals in 2001. Similarly, for fat depth differences between years was greater at older ages with animals at 16 months of age 39% fatter in 2001 than 2000. Differences between years were greater for eye muscle depth at young ages. Animals had 12% more muscle depth at 4 months of age in 2000 than in 2001.

Flock effects were also significant for all traits at all ages, except at 4 months of age for fat depth (Table C.1). The Measured Performance Recording flock was heavier (6 %) than the other flocks at weaning and 4 months of age. At 5 months of age, the Measured Performance Recording flock and the Fibre meat plus flock were heavier than the other flocks, and the Fibre meat plus flock was heavier (6 to 10 %) than all other flocks from 7 months on. For fat and eye muscle depth, the Control flock was generally fatter (7 to 15 %) and more muscled (3 to 6 %) than the other flocks. For fat depth, the Elite Wool flock was not significantly different from the Control at 5 months of age, and at 8 months of age the Elite Wool flock and the Fibre meat plus flock were not significantly different from the Control. The Fibre meat plus flock was not significantly different to the Control for eye muscle depth at 8 and 10 months of age.

Sex effects were significant for all traits at all ages except fat depth at 7 months of age (Table C.2). Not surprisingly, males were consistently heavier (16 % at 16 months of age) and more muscled (2 % at 16 months of age), but females were fatter (26 % at 16 months of age).

Type of birth and rearing effects were significant for live weight at all ages, with single born and reared animals consistently heavier than twin born and raised animals (Table C.2). Until animals were 10 months of age, single born animals were heavier than twin born by 4 to 17 %, and single raised animals had an advantage of between 2 and 16 % over twin raised animals. From 10 months of age twin born and single raised animals were not significantly different from twin born and raised animals. For fat depth, type of birth and rearing effects were not significant until 8 months of age. Generally twin born and raised animals were fatter (4 to 9 %) than single born and raised, but twin born and single raised were intermediate. Similarly for eye muscle depth, type of birth and rearing effects were not significant until 7 months of age where twin born animals had greater eye muscle depths (1 to 3 %) than single born animals.

The year by flock interaction was significant for all live weight measurements and generally at older ages for fat and eye muscle depth (Table C.3). This interaction was significant due to a re-ranking of the flocks in each year. Year by type of birth and rearing interactions were generally due to a difference in the response of multiples in the different years. Year by sex interactions were due to both sexes responding differently in each of the years.

Table 5.3 **Analysis of variance F values for live weight, fat depth and eye muscle depth adjusted for weight from birth to 4 months of age**

		Live weight		Fat depth		Eye muscle depth	
Age	**Fixed Effect**	**F value**	**F Sig**	**F value**	**F Sig**	**F value**	**F Sig**
Birth	Year	-	-				
	Flock	-	-				
	Sex	129	***				
	Tobr	-	-				
	Aod	89.3	***				
	Age	8.04	**				
	Year:Flock	3.28	*				
	Year:Sex						
	Year:Tobr	4.78	**				
	Sex:Age						
	Tobr:Age	4.63	*				
Weaning	Year	-	-				
	Flock	-	-				
	Sex	-	-				
	Tobr	-	-				
	Aod	23.4	***				
	Age	336	***				
	Year:Flock	14.1	***				
	Year:Sex						
	Year:Tobr	9.24	***				
	Sex:Age	23.4	***				
	Tobr:Age	8.92	***				
4 months	Year	-	-	-	-	-	-
	Flock	-	-	1.38	ns	6.93	***
	Sex	-	-	-	-	-	-
	Tobr	-	-	-	-	-	-
	Aod	24.6	***	0.88	ns	3.74	*
	Age	365	***	0.00	ns	15.4	***
	Weight			528	***	1008	***
	Year:Flock	14.9	***				
	Year:Sex	13.5	***				
	Year:Tobr	6.97	***	18.4	***	4.41	*
	Sex:Age	10.3	**				
	Tobr:Age	6.61	**			3.67	*
	Sex:Weight			87.9	***	13.1	***

Tobr = type of birth and rearing, Aod = age of dam. *** = $P<0.001$, ** = $P<0.01$, * = $P<0.05$, ns = not significant

Table 5.4 **Analysis of variance F values for live weight, fat depth and eye muscle depth adjusted for weight from 5 to 8 months of age**

		Live weight		Fat depth		Eye muscle depth	
Age	**Fixed Effect**	**F value**	**F Sig**	**F value**	**F Sig**	**F value**	**F Sig**
5 months	Year	-	-	-	-	-	-
	Flock	-	-	5.55	***	-	-
	Sex	-	-	-	-	-	-
	Tobr	-	-	-	-	0.42	ns
	Aod	26.9	***	0.30	ns	5.68	*
	Age	224	***	46.5	***	39.6	***
	Weight			176	***	466	***
	Year:Flock	6.89	***			3.13	*
	Year:Sex	10.3	***	15.0	***	15.0	***
	Year:Tobr	4.01	*	3.96	*		
	Sex:Age	9.54	**	12.9	***	15.4	***
	Tobr:Age	3.75	*				
	Sex:Weight			9.91	**	1.68	ns
7 months	Year	-	-	0.53	ns	-	-
	Flock	-	-	4.90	***	-	-
	Sex	-	-	-	-	-	-
	Tobr	45.7	***	2.34	ns	10.5	***
	Aod	13.9	***	0.69	ns	11.3	***
	Age	665	***	0.22	ns	7.06	**
	Weight			304	***	777	***
	Year:Flock	8.06	***	-	-	3.08	*
	Year:Sex						
	Year:Tobr						
	Sex:Age	127	***			75.2	***
	Tobr:Age						
	Sex:Weight			19.1	***	3.46	*
8 months	Year	-	-	-	-	-	-
	Flock	-	-	-	-	-	-
	Sex	-	-	-	-	-	-
	Tobr	40.0	***	13.5	***	13.4	***
	Aod	16.9	***	7.36	**	4.47	*
	Age	244	***	0.00	ns	0.53	ns
	Weight			240	***	833	***
	Year:Flock	4.11	**	2.83	*	3.52	**
	Year:Sex	7.15	**	19.3	***		
	Year:Tobr						
	Sex:Age	7.69	**	20.3	***		
	Tobr:Age						
	Sex:Weight			3.97	*	1.73	ns

Tobr = type of birth and rearing, Aod = age of dam. *** = $P<0.001$, ** = $P<0.01$, * = $P<0.05$, ns = not significant

Table 5.5 **Analysis of variance F values for live weight, fat depth and eye muscle depth adjusted for weight from 10 to 16 months of age**

		Live weight		Fat depth		Eye muscle depth	
Age	**Fixed Effect**	**F value**	**F Sig**	**F value**	**F Sig**	**F value**	**F Sig**
10 months	Year	-	-	-	-	-	-
	Flock	-	-	-	-	4.85	***
	Sex	-	-	-	-	-	-
	Tobr	-	-	17.2	***	14.7	***
	Aod	18.9	***	1.10	ns	2.07	ns
	Age	151	***	0.01	ns	0.19	ns
	Weight			202	***	622	***
	Year:Flock	7.47	***	3.64	**		
	Year:Sex			9.94	**	77.9	***
	Year:Tobr	3.39	*				
	Sex:Age	205	*	8.58	**		
	Tobr:Age	3.26	*				
	Sex:Weight			12.7	***	3.52	*
13 months	Year	-	-	-	-	-	-
	Flock	-	-	-	-	-	-
	Sex	-	-	-	-	-	-
	Tobr	18.3	***	-	-	4.53	*
	Aod	14.5	***	2.73	ns	0.61	ns
	Age	132	***	5.30	*	3.68	*
	Weight			206	***	510	***
	Year:Flock	5.88	***	3.15	*	3.09	*
	Year:Sex	6.51	*			13.7	***
	Year:Tobr			5.93	**		
	Sex:Age	6.04	*				
	Tobr:Age			6.28	**		
	Sex:Weight			35.7	***	16.9	***
16 months	Year	-	-	-	-	-	-
	Flock	-	-	-	-	-	-
	Sex	-	-	-	-	-	-
	Tobr	12.4	***	7.59	***	5.91	**
	Aod	13.6	***	0.93	ns	7.12	**
	Age	187	***	0.00	ns	2.32	ns
	Weight			147	***	374	***
	Year:Flock	5.10	***	3.03	*	4.61	**
	Year:Sex			18.8	***		
	Year:Tobr						
	Sex:Age	3.54	*			12.0	***
	Tobr:Age						
	Sex:Weight			17.8	***	1.90	ns

Tobr = type of birth and rearing, Aod = age of dam. *** = $P<0.001$, ** = $P<0.01$, * = $P<0.05$, ns = not significant

5.3.2 Variances

The phenotypic variance of live weight at different ages increased as age increased (Table 5.6). There were large differences between birth and weaning, and 13 and 16 months of age for weight. Genetic variance also increased with age, but low values were estimated at 4 and 7 months of age. Permanent maternal variance also increased with age.

Phenotypic and genetic variance of unadjusted (Model 1) fat depth was higher at 4 months of age than 5 months of age, but increased as age increased after 5 months of age (Table 5.7). The phenotypic variance of fat depth adjusted for weight (Model 2) was lower than that for unadjusted fat depth but followed the same pattern increasing as age increased. There was very little difference between the genetic variance of the two models fitted, Model 2 estimates were slightly lower. Phenotypic variance of unadjusted eye muscle depth increased to 8 months of age and then decreased. Adjusted eye muscle depth followed a similar pattern although to a lesser extent, and phenotypic variances for adjusted data were much lower. Genetic variances for unadjusted eye muscle depth also increased up to 8 months of age and then decreased. The difference between the two models fitted was not as great as for phenotypic variancc and was greatest at 8 months of age and least at older ages.

Table 5.6 Genetic and phenotypic variances of live weight traits at different ages (months)

Weight Age	Genetic variance	Permanent maternal variance	Phenotypic variance
Birth	0.199	0.253	0.639
Weaning	2.40	2.08	12.09
4	1.77	2.40	14.00
5	4.15	1.12	17.88
7	2.93	2.86	19.15
8	5.49	2.47	23.15
10	4.55	3.07	25.10
13	4.57	3.41	28.43
16	5.80	5.48	39.37
WG	0.0469	-	0.316

WG = Weight gain

Table 5.7 Genetic and phenotypic variances of fat and eye muscle depth at different ages

		Model 1		Model 2	
	Age	**Genetic variance**	**Phenotypic variance**	**Genetic variance**	**Phenotypic variance**
FAT	**4**	0.094	0.217	0.081	0.166
	5	0.032	0.156	0.040	0.136
	7	0.056	0.191	0.047	0.154
	8	0.061	0.217	0.050	0.167
	10	0.067	0.241	0.062	0.202
	13	0.084	0.223	0.077	0.195
	16	0.098	0.245	0.099	0.218
	FG	0.139	0.832	0.0752	0.722
EMD	**4**	1.71	3.97	0.84	2.17
	5	1.37	3.59	0.67	2.12
	7	2.77	6.03	1.58	3.29
	8	2.86	6.27	1.18	3.02
	10	1.85	4.58	1.26	2.67
	13	1.36	3.90	1.02	2.49
	16	1.45	4.12	1.20	2.71
	MG	0.707	0.734	0.0134	0.555

FAT = Fat depth, EMD = Eye muscle depth, Ages are in months, FG = Fat gain, MG = Muscle gain, Model 1 base model, Model 2 includes weight covariate

5.3.3 Heritabilities

Direct heritability for live weights was highest at birth (0.34 ± 0.09) and generally declined with age to 0.18 (± 0.06) at 16 months (Table 5.8, Figure 5.2). The permanent maternal effect (c^2 as a proportion of the phenotypic variance) was higher than direct heritability at birth (0.46 ± 0.03), declined to 0.21 (± 0.03) at weaning, and subsequently stabilised at about 0.15. Immediately after weaning (4 months) direct heritability declined (0.20 ± 0.07), whereas at 5 months, heritability was higher (0.28 ± 0.08) reflecting expression of genes for growth during this period with a corresponding lower maternal environmental heritability. The heritability of weight gain was lower (0.15 ± 0.06) than the heritabilities of weight at individual ages.

Heritability of fat depth generally increased from 0.21 (± 0.06) at 5 months of age to 0.40 (± 0.07) at 16 months of age. The heritability of fat depth was high at 4 months of age (0.43 ± 0.07) (Table 5.8, Figure 5.3). Adjustment for weight slightly increased the heritability estimates for fat. Heritabilities of eye muscle depth were about 0.45 up to 8 months of age and were reduced to 0.35 at 13 and 16 months of age. The heritability increased slightly with age when adjusted for weight. The heritabilities of fat gain and muscle gain were generally significantly lower than the heritabilities at each individual age (fat gain 0.17 ± 0.06, muscle gain 0.10 ± 0.05). Adjustment for weight gain reduced the estimate further (fat gain 0.10 ± 0.05, muscle gain 0.02 ± 0.03).

Table 5.8 Additive heritability (h^2) and permanent maternal effect (c^2) for live weight traits (standard error) for growth traits at different ages

Age	Live weight		Fat depth		Eye muscle depth	
	h^2	c^2	Model 1	Model 2	Model 1	Model 2
Birth	0.34 (0.088)	0.46 (0.029)	-	-	-	-
Weaning	0.26 (0.074)	0.21 (0.034)	-	-	-	-
4	0.20 (0.067)	0.19 (0.034)	0.43 (0.070)	0.49 (0.068)	0.43 (0.076)	0.38 (0.069)
5	0.28 (0.076)	0.12 (0.033)	0.21 (0.064)	0.29 (0.070)	0.38 (0.077)	0.32 (0.069)
7	0.24 (0.072)	0.18 (0.036)	0.29 (0.064)	0.31 (0.065)	0.46 (0.077)	0.48 (0.078)
8	0.26 (0.076)	0.16 (0.035)	0.28 (0.065)	0.30 (0.067)	0.46 (0.078)	0.39 (0.072)
10	0.24 (0.073)	0.15 (0.036)	0.28 (0.066)	0.31 (0.068)	0.40 (0.076)	0.47 (0.077)
13	0.20 (0.068)	0.14 (0.036)	0.38 (0.072)	0.40 (0.074)	0.35 (0.072)	0.41 (0.075)
16	0.18 (0.064)	0.16 (0.036)	0.40 (0.068)	0.45 (0.075)	0.35 (0.077)	0.45 (0.078)
Gain	0.15 (0.057)	-	0.17 (0.059)	0.10 (0.047)	0.10 (0.050)	0.02 (0.033)

Ages are in months, Model 1 base model, Model 2 includes weight covariate

Figure 5.2 Direct heritability and permanent maternal effect of live weight

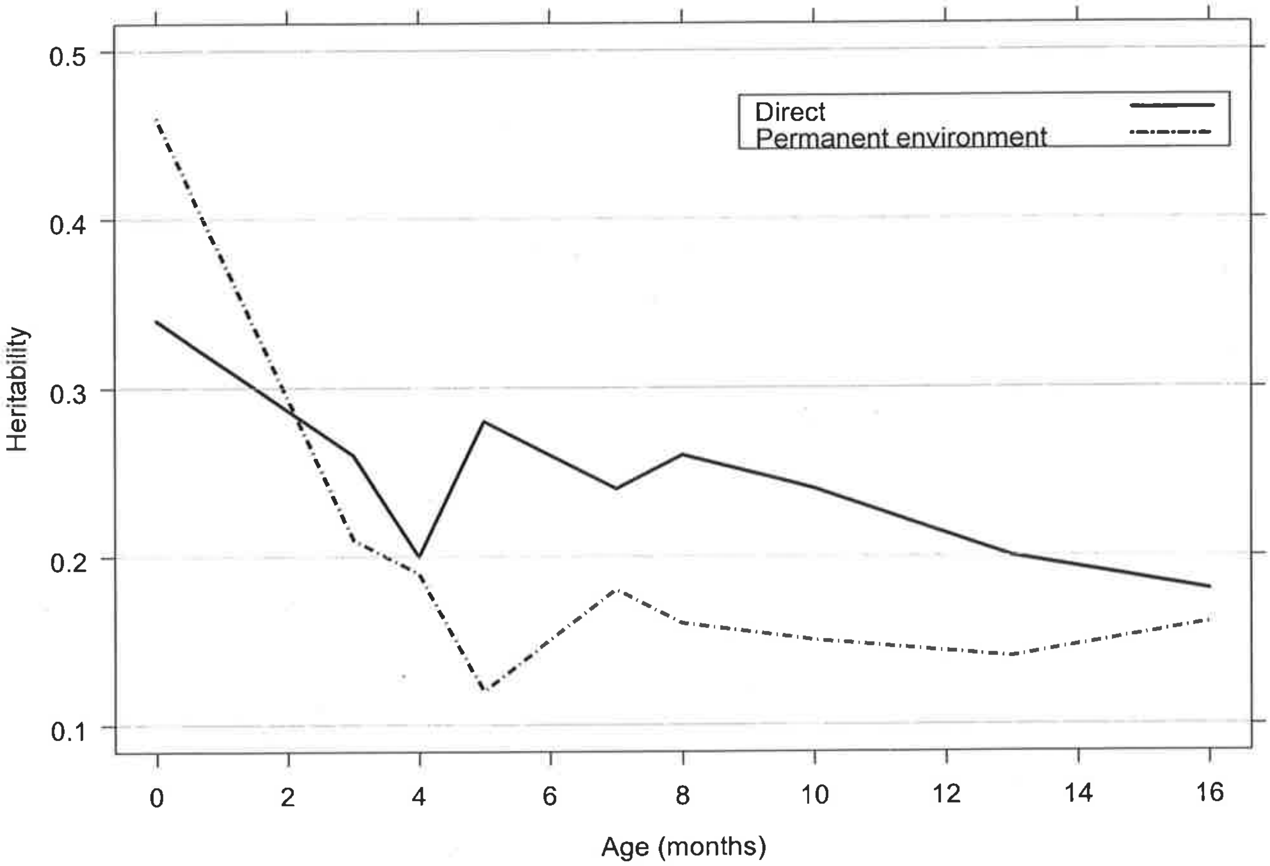


Figure 5.3 Heritability of unadjusted and adjusted fat and eye muscle depth

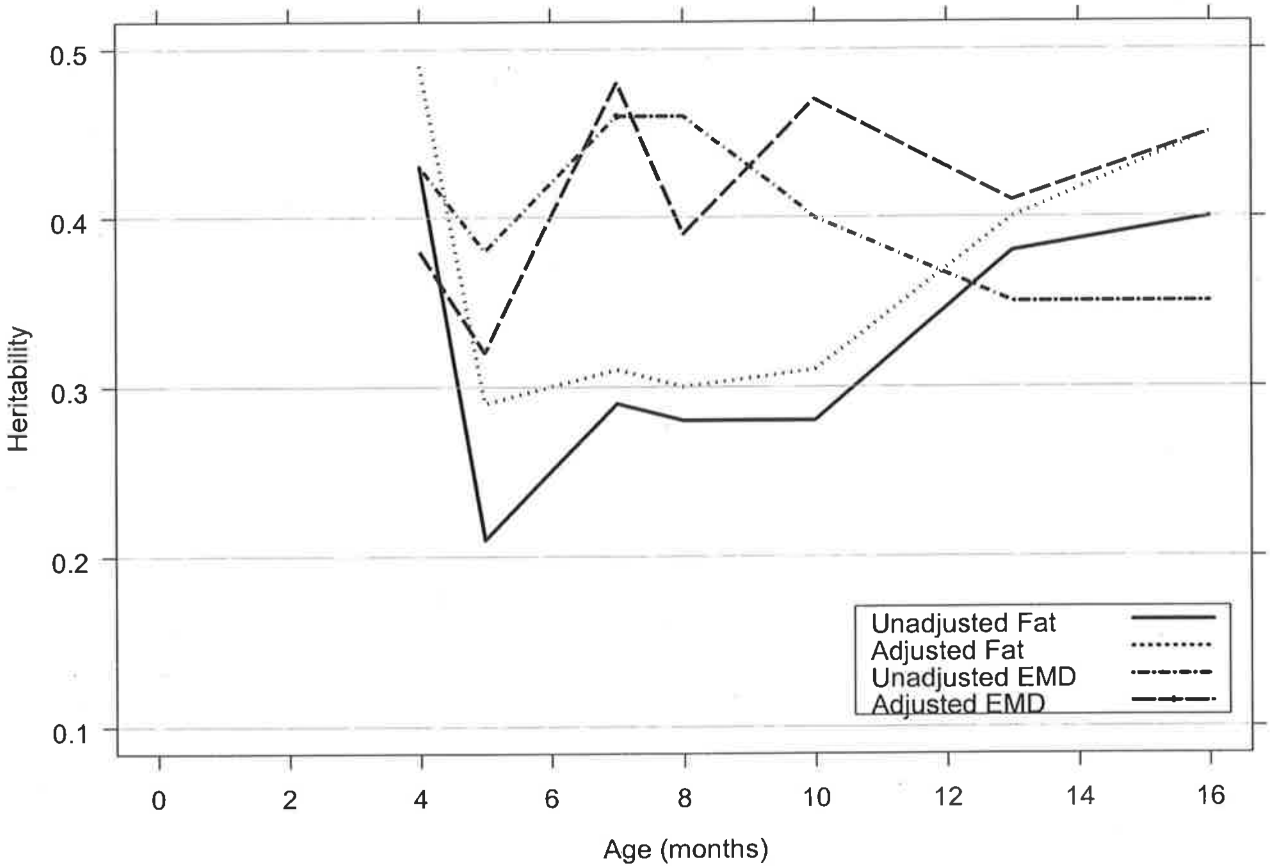
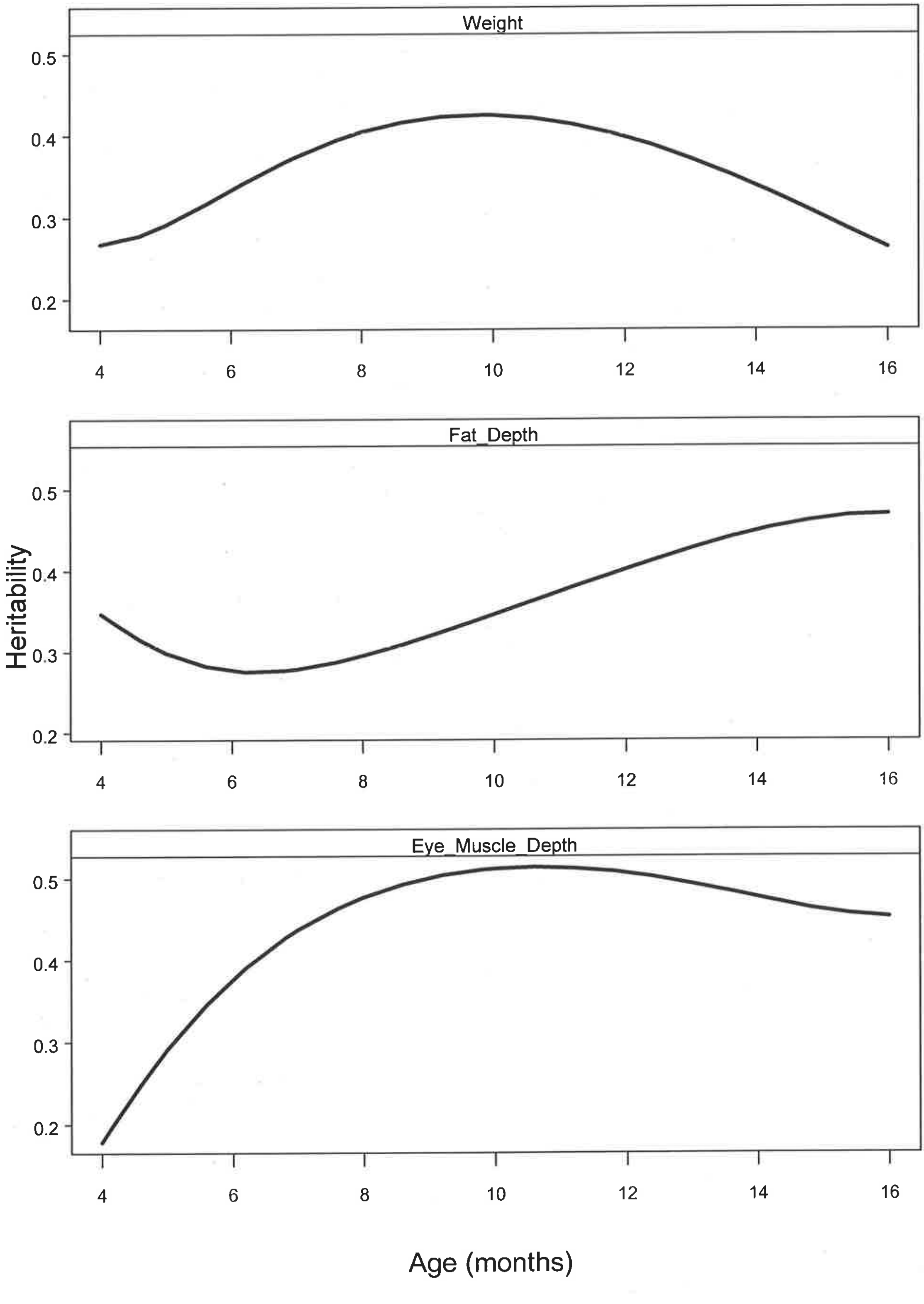


Figure 5.4 Heritability of growth traits using a quadratic random regression model



Heritabilities from random regression analyses for fat and eye muscle depth followed a similar trajectory to those estimated at individual ages (Figure 5.4). The trajectory for live weight was different to the mixed model estimates for the direct effect with heritabilities generally higher from the random regression analysis. The heritability of live weight ranged from 0.26 to 0.42, fat depth ranged from 0.28 to 0.47, and eye muscle depth ranged from 0.18 to 0.51 (Figure 5.4).

5.3.4 Correlations within Growth and Live Carcase Traits

Live Weights

Phenotypic correlations between different ages of live weight increased as the difference between ages decreased i.e. similar ages had greater correlations than different ages (Table 5.9). All correlations were positive and ranged from low (0.24 ± 0.03) to very high (0.88 ± 0.01). Birth weight had the highest correlation with weaning weight (0.37 ± 0.02) and declined to weight at 8 months (0.24 ± 0.27). The phenotypic correlation between weaning weight and other weights were higher and were relatively constant ranging from 0.57 to 0.88. Phenotypic correlations between weight gain and the different ages of live weight were generally negative (range of -0.44 to -0.01) except with weight at 13 and 16 months of age which were positive (0.12 and 0.35).

All genetic correlations between different ages were positive, and over all ages ranged from 0.00 (± 0.22) to 1.00 (± 0.02). Correlations with birth weight were low with high standard errors and ranged from 0.00 (± 0.22) to 0.33 (± 0.19). Genetic correlations among other ages were generally high, ranging from 0.41 (± 0.19) to 0.83 (± 0.08), and decreased as the difference between ages increased. Genetic correlations between weight gain and live weights were generally low to moderate ranging from 0.01 (± 0.16) to 0.51 (± 0.18). The highest was between weight gain and live weight at 8 months, and the lowest were with birth weight and live weight at 16 months.

Fat Depth

Phenotypic correlations between different ages of measurement of fat depth increased as the difference between ages decreased, except at 5 months of age (Table 5.10). Correlations were all low to moderately positive and ranged from 0.27 (± 0.03) to 0.44 (± 0.02). At 5 months of age, phenotypic correlations with older ages changed very little ranging from 0.28 (± 0.03) to

0.30 (± 0.03). Phenotypic correlations between fat gain and fat depths were generally negative and variable. The phenotypic correlations between fat gain and fat depth at 13 and 16 months were positive (0.01 and 0.38)

Genetic correlations were moderate to very highly positive and ranged from 0.57 (± 0.10) to 1.05 (± 0.04) (0.99 when constrained) (Table 5.10). All correlations with fat depth at 8 months of age and older were very high and greater than 0.8. As for phenotypic correlations, genetic correlations between 5 months of age and older ages had a different pattern; correlations increased slightly then were reduced at 13 and 16 months of age. Genetic correlations between fat gain and fat depths were low to moderately positive with the highest at 7 months (0.60 ± 0.14) and the lowest at 13 months (0.06 ± 0.25). Standard errors were very high for all genetic correlations with fat gain.

Eye Muscle Depth

Phenotypic correlations between different ages of eye muscle depth generally increased as the difference between ages decreased (Table 5.11), except for correlations between 5 months of age and all other ages. Correlations between 5 months of age and all other ages changed little ranging from 0.37 (± 0.02) to 0.44 (± 0.02), correlations between other ages were positive and ranged from low (0.33 ± 0.02) to moderate (0.53 ± 0.02). Phenotypic correlations between muscle gain and eye muscle depths at different ages were highly variable ranging from -0.44 (± 0.02) to 0.64 (± 0.02).

Genetic correlations between all ages of eye muscle depth were high to very high and ranged from 0.77 (± 0.09) to 0.99 (±0.04) (Table 5.11). Genetic correlations did not change significantly with age except for correlations with 5 months of age, where they were slightly lower than genetic correlations among other ages. Similarly to phenotypic correlations, genetic correlations between muscle gain and eye muscle depth at different ages were highly variable and ranged from -0.23 (± 0.35) to 0.51 (± 0.26). Standard errors on these correlations were very high.

Table 5.9 **Phenotypic (above diagonal) and genetic (below diagonal) correlations (standard error) between live weight traits at different ages and weight gain (WG)**

	BW	WW	WT4	WT5	WT7	WT8	WT10	WT13	WT16	WG
BW		0.37 (0.024)	0.36 (0.023)	0.30 (0.024)	0.27 (0.026)	0.24 (0.026)	0.27 (0.026)	0.25 (0.026)	0.26 (0.025)	-0.01 (0.029)
WW	0.24 (0.194)		0.87 (0.006)	0.76 (0.011)	0.68 (0.015)	0.64 (0.016)	0.61 (0.017)	0.57 (0.018)	0.58 (0.172)	-0.20 (0.026)
WT4	0.26 (0.225)	0.83 (0.078)		0.81 (0.009)	0.72 (0.013)	0.69 (0.014)	0.64 (0.015)	0.61 (0.016)	0.60 (0.017)	-0.21 (0.026)
WT5	0.33 (0.192)	0.71 (0.115)	0.86 (0.071)		0.78 (0.010)	0.75 (0.012)	0.70 (0.013)	0.68 (0.014)	0.65 (0.015)	-0.22 (0.025)
WT7	0.11 (0.211)	0.41 (0.186)	0.62 (0.152)	0.82 (0.077)		0.86 (0.007)	0.78 (0.010)	0.74 (0.012)	0.69 (0.014)	-0.44 (0.021)
WT8	0.14 (0.208)	0.48 (0.172)	0.69 (0.130)	0.86 (0.068)	1.00 (0.018)		0.85 (0.007)	0.80 (0.009)	0.74 (0.012)	-0.18 (0.026)
WT10	0.08 (0.217)	0.51 (0.173)	0.63 (0.154)	0.77 (0.099)	0.92 (0.052)	0.92 (0.043)		0.86 (0.007)	0.79 (0.010)	-0.04 (0.027)
WT13	0.00 (0.222)	0.50 (0.179)	0.56 (0.176)	0.76 (0.106)	0.93 (0.061)	0.91 (0.058)	0.95 (0.033)		0.88 (0.006)	0.12 (0.026)
WT16	0.29 (0.217)	0.58 (0.172)	0.67 (0.152)	0.80 (0.103)	0.78 (0.111)	0.82 (0.090)	0.83 (0.087)	0.82 (0.087)		0.35 (0.024)
WG	0.01 (0.164)	0.35 (0.181)	0.33 (0.204)	0.39 (0.194)	0.46 (0.176)	0.51 (0.176)	0.36 (0.204)	0.35 (0.213)	0.02 (0.223)	

BW = Birth weight, WW = Weaning weight, WT = Live weight, figures after the abbreviation are months of age

Table 5.10 **Phenotypic (above diagonal) and genetic (below diagonal) correlations (standard error) between adjusted fat depth at different ages and fat gain (FG) (Model 2)**

	FAT4	FAT5	FAT7	FAT8	FAT10	FAT13	FAT16	FG
FAT4		0.38 (0.022)	0.36 (0.023)	0.30 (0.024)	0.31 (0.024)	0.27 (0.025)	0.28 (0.025)	-0.14 (0.026)
FAT5	0.99 (0.058)		0.29 (0.024)	0.30 (0.024)	0.30 (0.024)	0.30 (0.024)	0.28 (0.025)	-0.09 (0.026)
FAT7	0.74 (0.089)	0.73 (0.117)		0.44 (0.021)	0.37 (0.023)	0.29 (0.024)	0.29 (0.024)	-0.80 (0.010)
FAT8	0.82 (0.088)	0.92 (0.090)	0.93 (0.070)		0.41 (0.022)	0.37 (0.023)	0.34 (0.023)	-0.18 (0.025)
FAT10	0.83 (0.072)	0.86 (0.089)	0.85 (0.084)	1.05 (0.039)		0.41 (0.022)	0.37 (0.023)	-0.09 (0.026)
FAT13	0.57 (0.097)	0.74 (0.097)	0.76 (0.103)	0.96 (0.060)	0.97 (0.056)		0.43 (0.022)	0.01 (0.026)
FAT16	0.67 (0.089)	0.70 (0.107)	0.74 (0.103)	0.96 (0.067)	1.00 (0.058)	0.99 (0.043)		0.38 (0.023)
FG	0.21 (0.217)	0.33 (0.281)	0.60 (0.135)	0.16 (0.262)	0.23 (0.261)	0.06 (0.247)	0.11 (0.232)	

FAT = Fat depth, figures after the abbreviation are months of age, Model 2 includes weight covariate

Table 5.11 Phenotypic (above diagonal) and genetic (below diagonal) correlations (standard error) between adjusted eye muscle depth at different ages and muscle gain (MG) (Model 2)

	EMD4	EMD5	EMD7	EMD8	EMD10	EMD13	EMD16	MG
EMD4		0.42 (0.022)	0.36 (0.023)	0.34 (0.024)	0.37 (0.023)	0.35 (0.023)	0.33 (0.024)	0.01 (0.026)
EMD5	0.91 (0.060)		0.44 (0.022)	0.39 (0.023)	0.40 (0.023)	0.38 (0.023)	0.37 (0.023)	-0.01 (0.026)
EMD7	0.89 (0.069)	0.99 (0.041)		0.53 (0.019)	0.49 (0.021)	0.44 (0.022)	0.41 (0.023)	-0.44 (0.021)
EMD8	0.82 (0.079)	0.82 (0.076)	0.97 (0.037)		0.53 (0.019)	0.46 (0.018)	0.41 (0.019)	-0.04 (0.026)
EMD10	0.90 (0.062)	0.85 (0.069)	0.96 (0.045)	0.98 (0.033)		0.50 (0.017)	0.48 (0.018)	0.07 (0.026)
EMD13	0.94 (0.066)	0.77 (0.091)	0.88 (0.062)	0.92 (0.058)	0.92 (0.053)		0.51 (0.019)	0.14 (0.025)
EMD16	0.95 (0.067)	0.80 (0.083)	0.95 (0.045)	0.85 (0.073)	0.99 (0.035)	0.95 (0.045)		0.64 (0.016)
MG	0.26 (0.311)	-0.23 (0.353)	0.20 (0.341)	-0.09 (0.317)	0.42 (0.279)	0.51 (0.259)	0.42 (0.231)	

EMD = Eye muscle depth, figures after the abbreviation are months of age, Model 2 includes weight covariate

5.3.5 Repeatabilities

The growth traits were analysed with the same repeatability model used in Chapter 3 which allowed for quantification of the heritable as well as the repeatable variation. With this model, the heritabilities were much lower (about half for weight and fat depth) than those for individual traits, but were similar to the heritability of gain traits (weight, fat and muscle gain) (Table 5.8). The repeatabilities ranged from 0.46 to 0.59 (Table 5.12) which were similar to the phenotypic correlations estimated within each trait (Table 5.9, Table 5.10 and Table 5.11).

Table 5.12 Heritability, repeatability and phenotypic variance for live weight, fat and eye muscle depth using repeatability model analysis

	Live weight	Fat depth	Eye muscle depth
Heritability	0.10	0.17	0.11
Repeatability	0.48	0.46	0.59
V_p	0.70	0.25	0.33

5.3.6 Correlations between Growth and Live Carcase Traits

Phenotypic Correlations

Phenotypic correlations between live weights and adjusted fat depths ranged from moderate and negative, -0.36 (± 0.03), to moderate and positive, 0.42 (± 0.03) (Table C.12). Phenotypic correlations between fat depth at all ages with birth weight were negative, and were largest (-0.30 ± 0.03) at 10 months of age. Most phenotypic correlations between similar ages and all phenotypic correlations between the same ages were positive. The phenotypic correlation between weight gain and fat gain (0.36 ± 0.02, Table 5.16) was similar, although slightly higher, to phenotypic correlations between live weight and fat depth at the same ages. The correlation did not change when fat gain was adjusted for weight gain (Model 2).

Phenotypic correlations between live weights and adjusted eye muscle depths ranged from low and negative, -0.26 (± 0.03), to high and positive, 0.79 (± 0.01) (Table C.13). Most correlations within this range were very low and close to zero. Phenotypic correlations between live weight and eye muscle depth were higher than phenotypic correlations between live weight and fat depth at the same ages. All phenotypic correlations between eye muscle depth and birth weight were negative, and correlations between similar ages were moderate to highly positive. The phenotypic correlation between weight gain and muscle gain (0.45 ± 0.02, Table 5.16) was similar to phenotypic correlations between live weight and eye muscle depth at the same ages, and did not change with adjustment of muscle gain for weight gain (Model 2).

Phenotypic correlations between adjusted fat and eye muscle depth were all positive and ranged from low (0.14 ± 0.03) to moderate (0.40 ± 0.02) (Table C.14). Correlations between the same age of measurement were the highest (ranging from 0.28 to 0.40) and all others were approximately 0.2 to 0.3. The phenotypic correlation between fat gain and muscle gain (0.32 ± 0.02, Table 5.16) was similar, although slightly lower than the phenotypic correlations between fat depth and eye muscle depth at the same ages. This value decreased to 0.19 (± 0.02) when both traits were adjusted for weight gain (Model 2).

Genetic Correlations

Genetic correlations between live weight and adjusted fat depth at different ages ranged from -0.86 (± 0.06) to 0.52 (± 0.16), with the majority of estimates low and negative (Table 5.13).

Genetic correlations between birth weight and fat depth were highly negative. Genetic correlations between traits measured at the same age were positive. The correlations at early ages for both traits (weaning, 4 and 5 months) were low, and between 7 months onwards for fat depth and weaning, 4 and 5 months for weight correlations were moderate and negative. Similarly, correlations between young ages of fat depth (4 to 10 months of age) and older ages of live weight (7 to 16 months of age) were negative. Genetic correlations between all ages of fat depth and live weight at 16 months of age were negative and from 4 to 10 months of age were moderate.

Correlations between live weight and adjusted eye muscle depth at different ages ranged from -0.66 (± 0.12) to 0.72 (± 0.07), with most estimates low or very low and positive (Table 5.14). Genetic correlations between birth weight and eye muscle depth were highly negative. Genetic correlations between traits measured at the same age were generally positive, and were higher than the correlations between fat depth and weight at the same ages. Generally the genetic correlations were low to moderate. Genetic correlations between all ages of eye muscle depth and live weight at 16 months of age were low and negative.

Table 5.13 Genetic correlations (standard error) between live weight and adjusted fat depth (Model 2)

	BW	**WW**	**WT4**	**WT5**	**WT7**	**WT8**	**WT10**	**WT13**	**WT16**
FAT4	-0.74 (0.094)	-0.06 (0.158)	0.10 (0.184)	-0.19 (0.165)	-0.38 (0.164)	-0.35 (0.152)	-0.48 (0.158)	-0.50 (0.165)	-0.79 (0.170)
FAT5	-0.57 (0.147)	-0.16 (0.191)	0.14 (0.224)	0.06 (0.196)	-0.21 (0.216)	-0.15 (0.202)	-0.38 (0.207)	-0.31 (0.218)	-0.59 (0.225)
FAT7	-0.58 (0.112)	-0.55 (0.122)	-0.48 (0.148)	-0.43 (0.139)	0.15 (0.193)	0.18 (0.187)	-0.36 (0.175)	-0.33 (0.187)	-0.58 (0.182)
FAT8	-0.81 (0.079)	-0.56 (0.115)	-0.55 (0.137)	-0.49 (0.134)	0.06 (0.210)	0.21 (0.197)	-0.48 (0.168)	-0.46 (0.183)	-0.44 (0.201)
FAT10	-0.86 (0.060)	-0.37 (0.133)	-0.34 (0.170)	-0.27 (0.156)	-0.38 (0.160)	-0.28 (0.167)	0.17 (0.193)	0.24 (0.199)	-0.45 (0.172)
FAT13	-0.74 (0.080)	-0.57 (0.115)	-0.47 (0.154)	-0.21 (0.159)	-0.12 (0.183)	-0.00 (0.185)	0.45 (0.159)	0.52 (0.155)	-0.06 (0.196)
FAT16	-0.63 (0.106)	-0.29 (0.140)	-0.39 (0.126)	-0.34 (0.122)	-0.27 (0.160)	-0.16 (0.165)	-0.19 (0.175)	-0.24 (0.183)	-0.06 (0.203)

BW = Birth weight, WW = Weaning weight, WT = Live weight, FAT = Fat depth, figures after the abbreviation are months of age, Model 2 includes weight covariate.

Table 5.14 Genetic correlations (standard error) between live weight and adjusted eye muscle depth (Model 2)

	BW	WW	WT4	WT5	WT7	WT8	WT10	WT13	WT16
EMD4	-0.66 (0.122)	0.36 (0.138)	0.72 (0.073)	0.61 (0.087)	0.18 (0.171)	0.07 (0.175)	-0.18 (0.188)	-0.19 (0.197)	-0.46 (0.195)
EMD5	-0.41 (0.160)	0.29 (0.150)	0.58 (0.109)	0.57 (0.101)	0.30 (0.145)	0.25 (0.148)	0.13 (0.190)	0.19 (0.193)	-0.28 (0.213)
EMD7	-0.55 (0.114)	0.01 (0.157)	0.02 (0.155)	0.03 (0.173)	0.31 (0.135)	0.26 (0.136)	0.16 (0.177)	0.14 (0.185)	-0.24 (0.203)
EMD8	-0.57 (0.111)	-0.11 (0.171)	0.03 (0.198)	0.09 (0.165)	0.31 (0.187)	0.32 (0.166)	0.12 (0.173)	0.09 (0.184)	-0.20 (0.197)
EMD10	-0.10 (0.126)	-0.08 (0.170)	0.05 (0.193)	0.07 (0.161)	0.25 (0.180)	0.26 (0.169)	-0.04 (0.177)	-0.08 (0.188)	-0.22 (0.199)
EMD13	-0.52 (0.122)	-0.11 (0.170)	-0.08 (0.199)	0.09 (0.163)	0.22 (0.190)	0.21 (0.181)	0.31 (0.170)	0.32 (0.176)	-0.11 (0.207)
EMD16	-0.57 (0.117)	-0.06 (0.172)	0.05 (0.195)	0.11 (0.166)	0.15 (0.196)	0.18 (0.186)	0.12 (0.188)	0.12 (0.199)	-0.27 (0.200)

BW = Birth weight, WW = Weaning weight, WT = Live weight, EMD = Eye muscle depth, figures after the abbreviation are months of age, Model 2 includes weight covariate.

All genetic correlations between adjusted fat and eye muscle depth were positive and ranged from low (0.34 ± 0.13) to high (0.79 ± 0.08) (Table 5.15). Generally correlations increased as the difference between ages decreased. Genetic correlations between the traits at the same ages were high to very high and positive. Genetic correlations with eye muscle depth at 7 months of age were slightly higher than at other ages at approximately 0.7. Generally, genetic correlations between these traits were 0.5 or greater across all ages, except correlations between fat depth at 5 months of age and eye muscle depth at 10, 13 and 16 months of age which were approximately 0.4. The genetic correlation between fat gain and muscle gain was very high (0.85 ± 0.16, Table 5.16), and generally higher than correlations between individual ages of fat depth and eye muscle depth. When fat gain and muscle gain were adjusted for weight gain (Model 2), the genetic correlation decreased to 0.48, but had a standard error of 0.43.

The genetic correlation between weight gain and fat gain was 0.74 (± 0.15) (Table 5.16) which was significantly higher than estimates between live weight and fat depth at individual ages. Adjusting fat gain for weight gain (Model 2) increased this estimate slightly (0.87 ± 0.14). The genetic correlation between weight gain and muscle gain was also significantly higher than correlations between live weight and eye muscle depth at individual ages. However, when muscle gain was adjusted for weight (Model 2) gain, there was no change in the correlation.

Table 5.15 Genetic correlations (standard error) between adjusted fat depth and adjusted eye muscle depth (Model 2)

	EMD4	EMD5	EMD7	EMD8	EMD10	EMD13	EMD16
FAT4	0.79 (0.076)	0.66 (0.096)	0.66 (0.087)	0.49 (0.105)	0.51 (0.100)	0.43 (0.112)	0.54 (0.105)
FAT5	0.62 (0.129)	0.59 (0.118)	0.58 (0.116)	0.52 (0.124)	0.49 (0.125)	0.38 (0.136)	0.37 (0.142)
FAT7	0.61 (0.124)	0.63 (0.120)	0.76 (0.084)	0.56 (0.118)	0.67 (0.105)	0.51 (0.125)	0.73 (0.104)
FAT8	0.62 (0.130)	0.46 (0.140)	0.72 (0.095)	0.56 (0.117)	0.67 (0.107)	0.63 (0.117)	0.69 (0.115)
FAT10	0.68 (0.121)	0.55 (0.124)	0.72 (0.094)	0.56 (0.111)	0.52 (0.110)	0.60 (0.114)	0.72 (0.101)
FAT13	0.46 (0.131)	0.50 (0.125)	0.69 (0.095)	0.53 (0.115)	0.52 (0.112)	0.66 (0.100)	0.66 (0.104)
FAT16	0.60 (0.112)	0.34 (0.130)	0.58 (0.105)	0.49 (0.119)	0.59 (0.107)	0.65 (0.100)	0.78 (0.080)

FAT = Fat depth, EMD = Eye muscle depth, figures after the abbreviation are months of age, Model 2 includes weight covariate

Table 5.16 Genetic (below diagonal) and phenotypic (above diagonal) correlations for weight gain, fat gain and muscle gain

	Model 1			Model 2		
	WG	**FG**	**MG**	**WG**	**FG**	**MG**
WG		0.36 (0.022)	0.45 (0.020)		0.37 (0.029)	0.45 (0.027)
FG	0.74 (0.153)		0.32 (0.023)	0.87 (0.138)		0.19 (0.024)
MG	0.89 (0.133)	0.85 (0.160)		0.89 (0.131)	0.48 (0.425)	

WG = weight gain, FG = fat gain, MG = muscle gain, Model 1 = base model, Model 2 = base model + weight gain adjustment

5.4 DISCUSSION

5.4.1 Relationships within Growth and Live Carcase Traits

Heritabilities

As expected, the permanent maternal effect, which also includes the maternal genetic heritability, in weight was very high at birth and decreased as the age of the lamb increased to 5 months of age. The permanent maternal effect was higher in this study than maternal heritabilities in other reports at older ages for Merino (Mortimer and Atkins 1995, Vaez Torshizi *et al.* 1995) (Figure 5.2). However, this is not unexpected as the permanent maternal variance as a proportion of the phenotypic variance is greater in this study as it is not the maternal component alone. Direct heritability also decreased with age. Figure 5.2 indicates that from birth to 4 months of age environmental effects were large, and at 4 months of age, the direct heritability was very low. This drop in the direct heritability may be due to early post-weaning environmental effects. From 5 months of age, the direct heritability declined, and the permanent maternal heritability was greatly reduced, but was relatively constant at approximately 0.15. This suggests that the influences of temporary environmental effects such as milk and other random non-genetic effects are reduced following weaning and the remaining portion of the permanent maternal component as defined here would then be maternal genetic effects. The higher heritability at 5 months of age may also reflect the expression of genes for growth, and some compensation for the growth set back experienced at weaning.

Birth weight heritabilities were higher in this study than estimates reported for Merinos by Fogarty (1995) and were higher than the majority of estimates by Safari and Fogarty (2003). However, they fitted within the range reported by Fogarty (1995) for dual purpose breeds and were within the range reported by Clarke (2002). Birth weight heritabilities were similar to those reported by Lewer *et al.* (1994) and Wuliji *et al.* (2001) for the Merino. Weaning weight heritability estimates were within the range for Merinos and dual purpose sheep reported by Fogarty (1995), were similar to Vaez Torshizi *et al.* (1995) estimates, but were larger than heritabilities reported by Cloete *et al.* (2001b), and were lower than those reported by Greeff & Karlsson (1998) and Ponzoni & Fenton (2000). Post weaning estimates were similar to dual purpose sheep estimates reported by Fogarty (1995), where there were no heritability estimates reported for Merinos. Yearling weight heritability was the same as Vaez

Torshizi *et al.* (1995), but lower than estimates reported by Clarke (2002). Live weight heritabilities at 13 months and hogget age were lower than all others reported.

In general the trends for the direct genetic heritability and the permanent maternal effect were as expected, however, the direct heritability especially at older ages was lower than expected. This may be explained by the structure of the data not allowing the model fitted to separate the variance components accurately especially the permanent maternal effect. Safari (2005 unpublished) has found that the variance is not separated into its components appropriately if the data structure is not sufficient or appropriate. Because there were only two years of data available in this study there were insufficient numbers of dams with lambs in both years to completely separate the maternal effects from the direct and residual.

The heritabilities of fat and eye muscle depth at 4 months of age (Figure 5.3) were very high. While maternal effects were not significant for this data, in other flocks of sheep small maternal effects have been reported as significant up to yearling age (Clarke *et al.* 2003). The heritability of fat depth tended to increase with age irrespective of the model fitted, whereas the heritability of unadjusted eye muscle depth tended to decrease slightly with age. Adjusting fat depth for weight increased the heritability slightly but did not have much effect, whereas estimates after adjusting eye muscle depth for weight tended to be higher at older ages than the unadjusted estimates (Figure 5.3). The similar trend for unadjusted and adjusted fat depth is supported by the values summarised in Fogarty (1995).

Heritabilities for fat depth at hogget age have been reported by Davidson *et al.* (2002) at 0.28 and by Clarke *et al.* (2003) and Greeff *et al.* (2003) at 0.19, which are lower than the estimate from this study (0.40 – 0.45, Table 5.8). Clarke *et al.* (2003) also reported a yearling heritability of 0.19 which was also lower than the estimate from this study. However, there are no other reported heritabilities for fat depth at other ages and the estimates from this study fit within the range reported by Fogarty (1995) for dual purpose sheep. Similarly for eye muscle depth, heritabilities from this study were higher than those reported by Davidson *et al.* (2002) (hogget 0.23), Clarke *et al.* (2003) (yearling 0.27, hogget 0.26) and Greeff *et al.* (2003) (hogget 0.24), but fit within the range and were similar to the weighted mean (0.31) reported by Fogarty (1995). These differences in Merinos across Australia indicate that there may be genotype by environment interactions influencing the Australian sheep flock that need to be investigated. The heritabilities of gain traits were lower than heritabilities of the traits at individual ages, especially for fat and eye muscle depth (Table 5.8). This indicates that selection for increased weight gain, fat deposition or muscle growth in Merinos would be slower than selection for a direct increase in the relevant trait at a certain age.

Heritability estimates for live weight from the random regression analysis (Figure 5.4) were considerably higher than estimates from the mixed models analysis at individual ages. The random regression estimates were closer to those reported by Safari and Fogarty (2003) up to 12 months of age however, the estimates from 14-16 months of age were still slightly lower than expected. The decreasing trend of heritability of live weight at older ages is in contrast to other studies but seems to be real for these particular flocks of Merino sheep. In contrast the heritabilities from random regression for fat and eye muscle depth follow a similar pattern to the mixed model estimates. Estimates for eye muscle depth from random regression have a greater range compared to the mixed model estimates but have a similar trajectory. The inability to separate direct and maternal genetic effects and direct and maternal environmental effects due to the lack of depth in the data seems to be affecting the estimates of live weight considerably. Several studies have shown that the direct heritability is inflated when maternal effects were not accounted for (Maniatis and Pollot 2002, Vaez Torshizi *et al.* 1996 and Nasholm and Danell 1996). In this study the estimates are inflated when maternal effects were not included in the model but were overly reduced when some maternal component was removed.

Correlations

Phenotypic correlations between live weights behaved as expected and were similar to those reported in Chapter 3 (Table 3.11). The phenotypic correlations were also similar to estimates reported by Ponzoni *et al.* (1995) and Vaez Torshizi *et al.* (1995) for birth and weaning weight but were slightly higher for older ages. Weaning and yearling estimates were similar to Greeff & Karlsson (1998), and estimates for yearling and hoggets were similar to Brash *et al.* (1997).

Genetic correlations between live weights were very low between birth weight and older ages which were lower than Vaez Torshizi *et al.* (1995) or other reports, except between birth weight and 16 months of age. The estimates in this study also do not agree with previously published estimates between weaning weight and older ages of measurement. All published genetic correlation estimates of weight at yearling and hogget age are high and similar to the estimates reported here. There are few estimates of post weaning correlations in the literature but these estimates show a similar trend to older ages. Genetic correlations between weight gain and individual ages of live weight were generally moderate to high, with the exceptions at birth and 16 months of age (Table 5.9). This indicates that when selecting for live weight there is also a positive response in weight gain, so that selection for weight at early ages may increase the growth rate of the animal.

Correlation estimates between fat depth measurements from this study (Table 5.10) were higher than estimates from dual-purpose sheep reported by McEwan (1991). These estimates were similar to post weaning and yearling estimates for Coopworth sheep reported by Beatson (1987), but were again higher than estimates with hogget age. Fogarty (1995) reports 0.6 as a weighted average of genetic correlations between fat depth measurement at different ages and 0.4 as a weighted average for phenotypic correlations. Genetic correlations estimated herein were higher than the weighted average but phenotypic correlations were similar. Fogarty (1995) also reports little difference between weight adjusted and unadjusted models for correlations of fat and eye muscle depth. No correlation estimates are reported in the literature for Merinos for either fat or eye muscle depth measurement at different ages. Genetic correlations between eye muscle depth measurements at different ages were particularly high with a small range indicating that this trait is controlled by the same set of genes from weaning to maturity. Genetic correlations between fat gain and individual ages of fat depth were generally low (Table 5.10). These correlations indicate that selection for fat depth will not increase the rate of gain of fat as quickly compared to weight gain. The genetic correlations between muscle gain and individual ages of eye muscle depth were variable with large standard errors (Table 5.11) indicating that this may not be a reliable trait option.

Fat and eye muscle depth decreased dramatically at 5 and 7 months of age (Figure 5.1), which has implications for the accuracy of the measurements at those ages, especially for fat depth (Fogarty *et al.* 2003). The lower heritabilities of both fat and eye muscle depth at 5 months of age was due to lower genetic variance at 5 months of age as a proportion of the total variance which indicates that there may be greater environmental influences and measurement inaccuracy at this age. Figure 5.1 also shows that while fat and muscle dropped, live weight did not. Therefore, the animals were still growing but may have been using fat and muscle reserves to do so. Genetic correlations between 5 and 7 months of age were also reduced compared to other ages, indicating again that there may be a greater environmental influence between 5 and 7 months than at older ages. Between the ages of 7 to 10 months of age there was a period of increased growth (Figure 5.1) in both fat and eye muscle depth of lambs. This may be attributed to compensatory growth after the considerable drop in fat and eye muscle between 5 and 7 months of age.

5.4.2 Correlations between Growth and Live Carcase Traits

Genetic correlations with birth weight were very high and negative for both weight adjusted fat and eye muscle depth (Table 5.13 and Table 5.14), and while an optimum birth weight should be selected for, this study indicates that selection for increased birth weight will decrease subcutaneous fat and reduce eye muscle depth. Therefore, increases in birth weight may have been due to increased development (or size) in organs and or bone, hence improvement to the optimum in lamb survival. However, genetic correlations between unadjusted eye muscle depth and birth weight were low and close to zero (Appendix C, Table C.15) indicating that there may be no detrimental effect of selection for increased birth weight. Genetic correlations between fat depth and live weights were generally high and negative (Table 5.13) which may explain in part why Merinos selected for higher live weights are generally lean unless managed correctly.

The only other correlation estimates published between weight and ultrasound measured traits for Merinos (Clarke *et al.* 2003) are similar, but are generally lower than estimates herein. Estimates of genetic correlations at hogget age from Clarke *et al.* (2003) were; weight and fat depth 0.12, weight and eye muscle depth -0.12, fat and eye muscle depth 0.61. The mainly positive genetic correlations between eye muscle depth and live weight indicate that increases in live weight may result in improvements in muscle depth. However, the correlations are small and selection for growth and an increase in eye muscle depth rather than improving overall carcase conformation may not be particularly beneficial in the Merino. Further work on carcase traits in Merinos will show genetic relationships of carcase conformation and if selection can be used to improve it. Genetic correlations between live weights and these ultrasound measured traits also suggest that the C site may not be the best site for measuring carcase composition in the Merino. The advantage of the C site is ease of measurement and is a better option than no measurement at all. However, further carcase studies may elucidate another option in the live animal that will give a better prediction of carcase composition.

There are contrasting reports of positive or negative genetic correlations between fat depth and eye muscle depth in the literature. However, the majority of estimates reported for live measures are positive. Safari and Fogarty (2003) only report one negative estimate between live measures of fat and eye muscle depth from Conington *et al.* (1995) at -0.21, in Scottish Blackface sheep. In contrast to that estimate, Roden *et al.* (2003) report a positive genetic correlation for Scottish Blackface sheep of 0.25. Generally, genetic correlations reported between carcase measures of fat depth and eye muscle depth are negative. The estimates also vary in magnitude, with a range of positive values reported by Safari and Fogarty (2003) of 0.05 to 0.61, which are from a range of breeds including Poll Dorset, Welsh Mountain, Suffolk and Merino sheep. The genetic correlations from this study generally fit within this range (Table 5.15). Positive genetic correlations between fat depth and eye muscle depth indicate that selection to increase one would also increase the other. However, Simm *et al.* (2002) have shown that despite a positive correlation between fat and eye muscle depth, Suffolk sheep have been successfully selected for decreased carcase fat weight and increased carcase lean weight using ultrasound fat depth and eye muscle depth as selection criteria.

5.5 CONCLUSION

Estimates from this data set were generally similar to previously published estimates. However, genetic correlations were slightly different. Heritabilities of live weights at different ages ranged from 0.18 to 0.34, fat depth 0.29 to 0.49 and eye muscle depth 0.32 to 0.48. Genetic correlations between ages within each trait were generally high and above 0.7. Genetic correlations between traits were generally encouraging for improvements in these traits in Merinos.

Selection has been used to improve or increase live weight in Merinos for decades, but only in recent years has there been a greater interest in other aspects of the carcase. The heritabilities of fat and eye muscle depth estimated in this study indicate that these traits may be used in a selection index to improve carcase attributes in Merinos as has already been practiced in meat breeds of sheep. The correlations estimated indicate that if the traits are selected for at the same or very similar age, improvement may be made in all three traits, but the timing of selection will be important to ensure the desired outcome is achieved. How these improvements are applied to the Merino depends on the target market requirements and how significant the income from meat is for the producer. Market specifications tend to penalise over fat lambs, therefore reductions in fat depth would be beneficial. However, the Merino is already a lean animal compared to traditional meat breeds, so reducing fat would not be desirable. Ultimately the decision to select for either increased or decreased fat depth would depend on the market specifications and the producers breeding objective.

Using the results herein as a guide, recommendations for time of measurement of these traits for use in a breeding program would be, for early selection, measure live weight at weaning and fat and eye muscle depth between weaning and 4 months of age. However, the accuracy of measurement of fat and eye muscle depth must be considered and when the animals are very young the accuracy of measurement will be lower than at older ages due to size and immaturity. Alternatively, or for a second stage of selection, 8 to 10 months of age is recommended for all three traits.

Chapter 6

Genetic Relationships Between Fleece, Growth And Live Carcase Traits

6.1 INTRODUCTION

Merinos have traditionally been selected for wool. Recent trends in wool and lamb prices, have increased the proportion of producer's income derived from lamb, and therefore a greater emphasis has been placed on growth and carcase attributes (Clarke *et al.* 2002; Davidson *et al.* 2002; Ingham and Ponzoni 2001; Safari *et al.* 2001). Parameter estimates are widely available for fleece traits and weight traits at birth, weaning and older ages (Safari and Fogarty 2003, Ponzoni and Fenton 2000). However, there are few genetic parameter estimates of weight traits between weaning and yearling ages, or carcase traits at any age, and even fewer estimates between these traits and fleece traits for Merinos. It is important for the further development and proper use of the Merino as a dual-purpose breed that the gaps in our knowledge of the correlations between fleece, weight and carcase traits be filled.

In this chapter the phenotypic and genetic correlations between fleece traits and growth traits as described in previous chapters are reported. Heritabilities and correlations between fleece traits are also presented. The data set from Chapter 5, the Selection Demonstration Flocks data, has been used in this chapter to estimate correlations between growth traits; live weight, scanned fat and eye muscle depth, and fleece traits.

6.2 MATERIALS AND METHODS

The data used were from the Selection Demonstration Flocks and are described in detail in Chapter 2.1.3. The number of records available, mean, standard deviation and range for each of the traits is presented in Table 6.1. Live weight was measured at birth and weaning, then live weight, fat depth and eye muscle depth were measured at approximately 6 weekly intervals until 10 months of age. Fat and eye muscle depth were measured by ultrasound at the C site. Fleece traits were measured at 16 months of age with 12 months of wool growth.

Table 6.1 Number of records available (n), mean, standard deviation (s.d.), coefficient of variation (CV) and range for live weights, live carcase and fleece traits

Trait	Abbreviation	n	Mean	s.d.	CV	Range
Birth weight (kg)	**BW**	1790	5.0	0.91	0.18	1.8 – 8.4
Weaning weight (kg)	**WW**	1789	26.9	5.98	0.22	9.0 – 44.2
Live weight (kg)	**WT4**	1774	29.8	6.33	0.21	9.6 – 48.4
	WT5	1761	31.8	6.23	0.20	13.0 – 50.5
	WT7	1703	31.8	6.02	0.19	13.9 – 54.5
	WT8	1678	35.6	6.56	0.18	14.3 – 58.0
	WT10	1669	41.9	7.19	0.17	20.5 – 67.5
	WT13	1670	47.8	8.79	0.18	24.8 – 74.5
	WT16	1666	58.9	9.03	0.15	31.6 – 88.5
	Weight Gain	1666	0.002	0.09	45	-0.30 – 0.32
Fat depth (mm)	**FAT4**	1769	1.8	0.59	0.33	0.5 – 4.5
	FAT5	1657	1.4	0.48	0.34	0.5 – 3.5
	FAT7	1691	1.2	0.48	0.40	0.5 – 3.5
	FAT8	1674	1.5	0.52	0.35	0.5 – 4.0
	FAT10	1669	2.3	0.56	0.24	1.0 – 4.0
	FAT13	1670	2.6	0.70	0.27	1.0 – 5.0
	FAT16	1666	3.1	0.86	0.28	1.0 – 5.5
	Fat Gain	1666	0.001	0.15	150	-0.57 – 0.40
Eye muscle depth (mm)	**EMD4**	1769	19.8	3.08	0.16	7.0 – 29.0
	EMD5	1657	18.9	2.35	0.12	10.0 – 28.0
	EMD7	1691	17.1	2.91	0.17	8.0 – 25.0
	EMD8	1674	20.4	2.91	0.14	8.0 – 29.0
	EMD10	1669	23.2	2.58	0.11	13.0 – 32.0
	EMD13	1670	24.1	2.42	0.10	16.0 – 37.0
	EMD16	1666	26.4	2.25	0.09	17.0 – 33.0
	Muscle Gain	1666	0.0004	0.10	250	-0.36 – 0.40
Clean fleece weight (kg)	**CFW16**	1644	4.8	0.9	0.19	2.2 – 7.7
Fibre diameter (µm)	**FD16**	1654	20.0	1.7	0.09	15.4 – 26.7
Staple length (mm)	**SL16**	1650	89.1	9.4	0.11	56.7 – 124.7
Staple strength (N/ktex)	**SS16**	1650	33.0	11.1	0.34	4.6 – 78.7

Figures after the abbreviation are months of age, Standardised Weight gain (7 – 16 months) units = months^{-1}, Standardised Fat and Muscle gain (7 – 16 months) units = months^{-1}

Statistical Analysis

Data were analysed using linear mixed model methodology in ASReml (Gilmour *et al.* 2002). An animal term was fitted allowing optimal analysis of a finite, selected population. All two-way interactions between fixed effects were tested. Where the interactions were non-significant ($P>0.05$) they were not included in the final models.

The final base model can be written as:

$$\mathbf{y} = \mathbf{X}\boldsymbol{\tau} + \mathbf{Z}_1\mathbf{a} + \mathbf{Z}_2\mathbf{c} + \mathbf{e}$$

where

$$\mathbf{y} \sim \mathrm{N}\left(\mathbf{X}\boldsymbol{\tau}, \sigma_a^2\mathbf{Z}_1\mathbf{A}\mathbf{Z}_1' + \sigma_c^2\mathbf{Z}_2\mathbf{Z}_2' + \sigma^2\mathbf{I}_n\right)$$

and

$$\mathbf{e} \sim \mathrm{N}\left(0, \sigma^2\right)$$

where $\mathbf{X}^{n\times t}$ is a design matrix which assigns the effects to animals, $\boldsymbol{\tau}^{1\times t}$ is the vector of fixed effect means, $\mathbf{Z}_1^{n\times p}$ is the design matrix for the animal effects, $\mathbf{A}$ is the numerator relationship matrix, $\mathbf{Z}_2^{n\times q}$ is the design matrix for the dam common environmental effects. The vectors $\mathbf{a}$ and $\mathbf{c}$ represent the animal and dam common environmental effects respectively. $\mathbf{e}^{1\times n}$ is the vector of random errors. σ_a^2 is the variance due to the animal effect, σ_c^2 is the variance due to the dam common environmental effect and σ^2 is the residual variance parameter.

This model can also be symbolically written as:

y ~ mean + year (2000, 2001) + flock (1-5) + type of birth and rearing (11, 21, 22) + linear(age of dam) + animal + dam

Terms fitted as random effects in the model are underlined, all other terms are fitted as fixed effects. The dam common environmental component includes both the non-genetic effect of the dam and the direct genetic effect of the dam, or the genetic maternal effect. This will be referred to as the permanent maternal effect. This formed the base model for all analyses. Each variate was tested and the model was modified where necessary. Changes to the base model for each variate are shown in Table 6.2.

The calculation of gain traits is described in detail in Chapter 5. Heritabilities reported were from univariate analyses. Correlations between different ages of the traits and between different traits were from multivariate analyses. Heritabilities and correlations will be referred to as very low to very high according to the classification in Table 2.5.

Table 6.2 Final models fitted to all traits

Variate	Model fitted	Defined as
Live weight	Base model + significant interactions	-
Fat depth	Base model without dam + significant interactions	Model 1
	Base model without dam + significant interactions + linear(weight) + weight:sex	Model 2
Eye muscle depth	Base model without dam + significant interactions	Model 1
	Base model without dam + significant interactions + linear(weight) + weight:sex	Model 2
Clean fleece weight	Base model without dam + significant interactions	-
Fibre diameter	Base model without dam + significant interactions	-
Staple length	Base model without dam + significant interactions	-
Staple strength	Base model without dam + significant interactions	-

6.3 RESULTS

6.3.1 Fixed Effects

The significance of fixed effects for fleece traits are presented in Table 6.3. Least squares means are presented in Tables D.1 – D.4 (Appendix D). The main effect of year was significant for clean fleece weight and fibre diameter but was not significant for staple length or strength. The year 2000 produced a heavier clean fleece and in 2001 the fleece was finer.

Between flock effects were significant for all traits. The Measured Performance Records flock and Elite Wool flock produced heavier fleeces than the Control and Professional Classer Assessment flocks but were not different from the Fibre Meat Plus flock. Similarly, the Measured Performance Records and Fibre Meat Plus flocks produced the finest fleeces but were not different from the Elite Wool flock, and the control had a significantly higher fibre diameter than any other flock. The Professional Classer Assessment flock had the lowest staple length and the Measured Performance Records flock had the lowest staple strength.

The main effect of sex was only significant for clean fleece weight where males had a 10 % heavier fleece weight than females.

Type of birth and rearing was significant for clean fleece weight and fibre diameter. Single born lambs had a heavier fleece than multiple born lambs (4 %) and multiple raised lambs had a greater fibre diameter than single raised lambs (2 %).

Year × sex interaction was significant for all traits (Table D.2, Appendix D). For clean fleece weight this was due to a greater difference between males and females in 2000 (14 %) than in 2001 (4 %) and a greater difference between males (16 %) in each year than females (6 %). For fibre diameter the interaction was due to a smaller difference between females in each year (3 %) than males (7 %). Females in 2000 had a significantly longer staple length than males and females in 2001, and for staple strength the interaction was due to a significantly greater difference between females in each year (17 %) compared to that of the males (1 %). Flock × sex interaction was significant for clean fleece weight and was due to a smaller difference between males and females in the Professional Classer Assessment flock (4 %) than in the other flocks (10 to 14 %) (Table D.3, Appendix D).

The three way interaction of year × flock × sex was significant for clean fleece weight (Table D.4, Appendix D). There were no differences between the sexes in 2001, and there were no differences between the years for females in the Measured Performance Recording and Fibre Meat Plus flocks. The males in the Elite Wool flock and the Control had heavier fleeces than males in the PCA in the year 2000. Males in 2001 from the MPR and EWF flocks had heavier fleeces than males in the Control. Females in the PCA and EWF had heavier fleeces than females in the FM+ in the year 2000. Females in the MPR in 2001 had heavier fleeces than females in the Control and FM+ flocks.

Table 6.3 **Analysis of variance F values for fleece traits at 16 months of age**

	Fixed Effect	Num DF	Den DF	F value	F Sig
CFW	Year	1	356	-	-
	Flock	4	158	-	-
	Sex	1	1509	-	-
	Tobr	2	1582	17.1	***
	Aod	1	1438	29.5	***
	Age	1	672	73.4	***
	Year:Sex	1	1538	43.9	***
	Flock:Sex	4	1506	7.20	***
	Year:Flock	4	299	3.52	**
	Flock:Aod	4	1449	5.06	***
	Year:Flock:Sex	4	1535	2.69	*
FD	Year	1	483	-	-
	Flock	4	183	37.9	***
	Sex	1	1484	-	-
	Tobr	2	1610	7.50	***
	Aod	1	1433	0.25	ns
	Age	1	908	7.31	**
	Year:Sex	1	1525	29.1	***
SL	Year	1	326	-	-
	Flock	4	146	1.58	ns
	Sex	1	1526	-	-
	Tobr	2	1602	2.57	ns
	Aod	1	1453	0.52	ns
	Age	1	673	38.3	***
	Year:Sex	1	1555	11.8	***
SS	Year	1	144	-	-
	Flock	4	79.1	4.13	**
	Sex	1	1598	-	-
	Tobr	2	1592	0.34	ns
	Aod	1	1495	1.10	ns
	Age	1	294	2.28	ns
	Year:Sex	1	1611	32.8	***
	Sex:Aod	1	1595	5.14	*

CFW = Clean fleece weight, FD = Fibre diameter, SL = Staple length, SS = Staple strength, Tobr = type of birth and rearing, Aod = age of dam, Num = numerator, Den = denominator, *** = $P<0.001$, ** = $P<0.01$, * = $P<0.05$, ns = not significant

6.3.2 Variances and Genetic Parameters between Fleece Traits

The genetic and phenotypic variances of clean fleece weight for the Selection Demonstration Flocks data (Table 6.4) were higher than the variances estimated separately for rams and ewes in the Turretfield Resource Flocks (Chapter 4, Table 4.5). For fibre diameter, the variances were more similar to the ewe estimates in the previous chapter and were lower than the ram estimates (Table 4.5). Variances of staple length, in this data set were intermediate between the ram and ewe estimates from the Turretfield Resource Flocks (Table 4.6). For staple strength, the genetic variance was similar to the previous ewe estimate and lower than the ram estimate, but the phenotypic variance was similar to the Turretfield Resource Flock rams estimate and higher than the ewes estimate (Table 4.6).

Heritabilities from the Selection Demonstration Flocks (Table 6.5) were slightly higher with higher standard errors than those estimated from the Turretfield Resource Flocks (Chapter 4, Tables 4.7 and 4.8) except for staple strength. Phenotypic correlations ranged from very low and negative (-0.12 ± 0.03) to low and positive (0.30 ± 0.03). All genetic correlations were similar to Turretfield Resource Flock estimates (Table 4.7 and 4.8) except between clean fleece weight and staple strength (-0.28 versus -0.03 for ewes and 0.32 for rams). Genetic correlations had higher standard errors for this data set than the Turretfield Resource Flocks data set.

Table 6.4 Genetic and phenotypic variances of fleece traits

	Genetic variance	Phenotypic variance
CFW	0.251	0.451
FD	1.47	2.17
SL	44.7	84.3
SS	20.8	114.1

CFW = Clean fleece weight, FD = Fibre diameter, SL = Staple length, SS = Staple strength

Table 6.5 Heritabilities (on diagonal), phenotypic (above diagonal) and genetic (below diagonal) correlations (standard error) between fleece traits at 16 months of age

	CFW	FD	SL	SS
CFW	**0.55** **(0.076)**	0.15 (0.029)	0.29 (0.026)	0.00 (0.027)
FD	-0.06 (0.113)	**0.68** **(0.080)**	0.27 (0.027)	0.30 (0.025)
SL	0.33 (0.107)	0.37 (0.103)	**0.53** **(0.079)**	-0.12 (0.026)
SS	-0.28 (0.157)	0.58 (0.125)	0.02 (0.166)	**0.20** **(0.056)**

CFW = Clean fleece weight, FD = Fibre diameter, SL = Staple length, SS = Staple strength

6.3.3 Correlations between Fleece, Growth and Live Carcase Traits

Phenotypic correlations

Phenotypic correlations between live weights and clean fleece weight ranged from 0.27 (± 0.03) to 0.43 (± 0.02) and increased slightly as age increased (Table D.7, Appendix D). Correlations with fibre diameter were lower and ranged from -0.07 (± 0.03) to 0.23 (± 0.03) as were correlations with staple length (range 0.01 ± 0.03 to 0.26 ± 0.03) and correlations with staple strength were lower again and ranged from -0.02 (± 0.03) to 0.17 (± 0.03). Generally correlations were lower at birth and increased as age increased.

Phenotypic correlations between weight adjusted fat depth and clean fleece weight were very low and negative (-0.07 to -0.15) whereas correlations between fat depth and the other fleece traits were very low but positive (Table D.7, Appendix D). Correlations with fibre diameter had the greatest range (0.05 to 0.17) and correlations between fat depth and staple length and strength ranged from -0.02 (± 0.03) to 0.13 (± 0.03). Phenotypic correlations between unadjusted fat depth and fleece traits were slightly higher than correlations with adjusted fat depth especially for clean fleece weight (Table D.5, Appendix D).

Phenotypic correlations between weight adjusted eye muscle depth and clean fleece weight were very low, close to zero and negative (-0.02 to -0.06) (Table D.7, Appendix D). Correlations with the other traits were all very low and positive. Correlations with fibre diameter increased from 0.05 (± 0.03) at birth to 0.18 (± 0.03) at 7 months of age. Correlations with staple length and strength ranged from 0.01 (± 0.03) to 0.13 (± 0.03). Phenotypic correlations between unadjusted eye muscle depth and fleece traits were higher than correlations with adjusted eye muscle depth especially for clean fleece weight (Table D.5, Appendix D).

Phenotypic correlations between weight gain and fleece traits were very low (Table 6.6). The correlation between weight gain and clean fleece weight (0.09 ± 0.03) was much lower than correlations between individual ages. Phenotypic correlations between the other fleece traits and weight gain were similar to estimates between fleece traits and weight at early stages of life (i.e. birth, weaning and 4 months of age). Phenotypic correlations between fat gain and fleece traits did not change significantly when fat gain was adjusted for weight gain (Model 1 vs Model 2) and were very low and negative (Table 6.6). The phenotypic correlations between fat gain and clean fleece weight (Model 1 -0.04 ± 0.03, Model 2 -0.06 ± 0.03) were similar to correlations between fat depth at individual ages and clean fleece weight. Phenotypic correlations between the other fleece traits and fat gain were very low and negative in contrast to the low and positive correlations between individual ages of fat depth and fleece traits. As for fat gain, phenotypic correlations between muscle gain and fleece traits from the two models fitted were not different (Table 6.6). Phenotypic correlations between muscle gain and clean fleece weight were positive, whereas correlations between individual ages of eye muscle depth with clean fleece weight were negative. Phenotypic correlations between the other fleece traits and muscle gain were similar to phenotypic correlations between the respective fleece traits and eye muscle depth at 4 to 5 months of age.

Table 6.6 Phenotypic correlations (standard error) between fleece traits and gain traits

	Weight Gain	**Fat Gain**		**Muscle Gain**	
		Model 1	**Model 2**	**Model 1**	**Model 2**
CFW	0.09 (0.027)	-0.04 (0.027)	-0.06 (0.033)	0.07 (0.027)	0.09 (0.046)
FD	0.03 (0.027)	-0.09 (0.027)	-0.10 (0.032)	0.02 (0.027)	0.06 (0.045)
SL	-0.01 (0.027)	-0.09 (0.026)	-0.11 (0.032)	0.00 (0.026)	-0.01 (0.034)
SS	0.00 (0.026)	-0.07 (0.026)	-0.08 (0.033)	0.00 (0.026)	-0.01 (0.029)

CFW = Clean fleece weight, FD = Fibre diameter, SL = Staple length, SS = Staple strength, Model 1 base model, Model 2 includes weight covariate

Genetic correlations

Genetic correlations between live weight and clean fleece weight ranged from -0.28 (± 0.22) to 0.24 (± 0.17) with high standard errors (Table 6.7). Genetic correlations at birth, weaning and 16 months of age were positive, but all others were negative and were lowest at 7 months of age. Correlations with fibre diameter were low and negative, ranging from -0.36 (± 0.22) to 0.00 (± 0.22) with the lowest point at 4 months and zero at 8 months of age. Correlations with staple length were very low to moderate ranging from -0.04 (± 0.24) to 0.44 (± 0.18) and tended to increase as age increased up to 8 months of age. Correlations with staple strength ranged from very low to moderate. The lowest correlation was at 16 months of age (-0.03 ± 0.28) and the highest was at 4 months of age (0.44 ± 0.26).

Genetic correlations between weight adjusted fat depth and clean fleece weight were low to moderate and negative, ranging from -0.48 (± 0.12) to -0.22 (± 0.12) (Table 6.7). Correlations with fibre diameter were positive (except one estimate) and ranged from 0.12 (± 0.11) to 0.43 (± 0.13). Correlations with staple length ranged from -0.10 (± 0.15) to 0.24 (± 0.14) and correlations with staple strength ranged from -0.10 (± 0.16) to 0.32 (± 0.17). Generally correlations increased in magnitude to 7 or 8 months of age and then, except for correlations with clean fleece weight, decreased slightly. Standard errors were lower than those for correlations between live weight and fleece traits. Genetic correlations between unadjusted fat depth and fleece traits were slightly lower in magnitude with higher standard errors for clean fleece weight, but were the same for the other fleece traits (Table D.6, Appendix D).

Genetic correlations between weight adjusted eye muscle depth and clean fleece weight were low and negative, ranging from -0.39 (± 0.12) to -0.26 (± 0.12) (Table 6.7). Correlations with fibre diameter were very low, except at 7 months of age, and ranged from -0.01 (± 0.14) to 0.33 (± 0.11). Correlations with staple length were very low and positive, ranging from 0.00 (± 0.14) to 0.20 (± 0.13). Correlations with staple strength ranged from -0.11 (± 0.19) to 0.22 (± 0.16). There was no trend with age, correlations were relatively constant and standard errors were lower than those for correlations between live weight and fleece traits. Genetic correlations between unadjusted eye muscle depth and fleece traits were slightly lower in magnitude for clean fleece weight and fibre diameter with higher standard errors, but were slightly higher for staple length and strength with higher standard errors (Table D.6, Appendix D).

Genetic correlations between weight gain and fleece traits ranged from high and positive (0.61 ± 0.18) to low and negative (-0.31 ± 0.22, Table 6.8). These genetic correlations were in contrast to genetic correlations between individual ages of weight and fleece traits, except the correlation with fibre diameter. Genetic correlations between fat gain and the fleece traits, clean fleece weight and staple length, changed from positive to negative when fat gain was adjusted for weight gain (Model 2). Standard errors of the genetic correlations between fleece traits and fat gain were lower when Model 2 was fitted. All genetic correlations between fat gain adjusted for weight gain and fleece traits were negative, and ranged from -0.31 and -0.21. Using estimates from Model 2, genetic correlations were similar to correlations between individual ages of measurement of fat depth and clean fleece weight, but were different for all the other fleece traits. Genetic correlations between muscle gain and fleece traits ranged from low and negative (-0.21 ± 0.24) to low and positive (0.27 ± 0.25, Table 6.8). The correlations between muscle gain and clean fleece weight and fibre diameter swapped sign, from positive to negative and negative to positive, respectively, when comparing Model 1 to Model 2 (weight gain adjusted). Comparing the correlations of muscle gain from Model 2, with individual ages of measurement of eye muscle depth and fleece traits, correlations of muscle gain were similar between fibre diameter, of the same sign but lower in magnitude between clean fleece weight, and of the reverse sign (negative) and closer to zero between staple length and staple strength.

Table 6.7 **Genetic correlations (standard error) between fleece traits (16 months of age) and weight adjusted growth traits at different ages (Model 2)**

	Age	Birth	Weaning	4	5	7	8	10	13	16
WT	CFW	0.24 (0.166)	0.06 (0.199)	-0.12 (0.238)	-0.25 (0.200)	-0.28 (0.224)	-0.17 (0.218)	-0.17 (0.212)	-0.19 (0.222)	0.14 (0.208)
	FD	-0.27 (0.173)	-0.10 (0.206)	-0.29 (0.232)	-0.10 (0.204)	-0.04 (0.225)	0.00 (0.217)	-0.08 (0.223)	-0.21 (0.222)	-0.36 (0.221)
	SL	0.07 (0.185)	0.14 (0.204)	-0.04 (0.238)	0.25 (0.190)	0.42 (0.190)	0.44 (0.177)	0.30 (0.196)	0.39 (0.199)	0.26 (0.220)
	SS	0.16 (0.223)	0.20 (0.244)	0.44 (0.260)	0.33 (0.225)	0.08 (0.266)	0.14 (0.250)	0.31 (0.235)	0.14 (0.262)	-0.03 (0.279)
FAT	CFW			-0.26 (0.103)	-0.48 (0.119)	-0.46 (0.131)	-0.36 (0.136)	-0.22 (0.123)	-0.36 (0.114)	-0.29 (0.116)
	FD			0.12 (0.112)	-0.09 (0.141)	0.30 (0.134)	0.43 (0.128)	0.43 (0.122)	0.22 (0.127)	0.33 (0.124)
	SL			-0.03 (0.119)	-0.10 (0.150)	-0.03 (0.144)	0.24 (0.140)	0.18 (0.137)	0.24 (0.130)	0.18 (0.128)
	SS			-0.10 (0.156)	0.00 (0.190)	0.31 (0.169)	0.32 (0.171)	0.21 (0.173)	0.11 (0.173)	0.18 (0.173)
EMD	CFW			-0.36 (0.120)	-0.39 (0.124)	-0.29 (0.118)	-0.38 (0.123)	-0.38 (0.120)	-0.33 (0.122)	-0.26 (0.124)
	FD			-0.01 (0.136)	0.11 (0.135)	0.33 (0.114)	0.10 (0.125)	0.10 (0.122)	0.10 (0.123)	0.20 (0.121)
	SL			0.08 (0.138)	0.00 (0.139)	0.20 (0.125)	0.19 (0.124)	0.12 (0.125)	0.20 (0.128)	0.13 (0.130)
	SS			-0.11 (0.187)	0.12 (0.173)	0.13 (0.163)	0.22 (0.159)	0.17 (0.160)	0.17 (0.163)	0.14 (0.168)

CFW = Clean fleece weight, FD = Fibre diameter, SL = Staple length, SS = Staple strength, WT = Live weight, FAT = Fat depth, EMD = Eye muscle depth, Ages are in months

Table 6.8 **Genetic correlations (standard error) between fleece traits and gain traits**

	Weight Gain	Fat Gain		Muscle Gain	
		Model 1	Model 2	Model 1	Model 2
CFW	0.61 (0.177)	0.40 (0.203)	-0.23 (0.083)	0.27 (0.252)	-0.03 (0.182)
FD	-0.12 (0.177)	-0.20 (0.173)	-0.31 (0.098)	-0.21 (0.240)	0.20 (0.196)
SL	-0.12 (0.184)	0.15 (0.195)	-0.28 (0.083)	0.06 (0.249)	-0.02 (0.149)
SS	-0.31 (0.223)	-0.32 (0.218)	-0.21 (0.094)	-0.11 (0.300)	-0.06 (0.150)

CFW = Clean fleece weight, FD = Fibre diameter, SL = Staple length, SS = Staple strength, Model 1 base model, Model 2 includes weight covariate

6.4 DISCUSSION

6.4.1 Fleece Traits

The heritability of and correlations between fleece traits in Australia and overseas have been well documented (Fogarty 1995, Clarke 2002, Safari and Fogarty 2003). The heritabilities and correlations from this study are similar to those previously reported (Table 6.5). The high genetic correlations between ram and ewe traits estimated in Chapter 4 (Table 4.9) indicates that, as expected, the same genes are controlling fleece traits in both sexes as well as at all ages. Thus, combining ram and ewe data where the measurements are the same, as was done in this chapter, is appropriate. Heritabilities estimated from the Selection Demonstration Flocks data (Table 6.5) were slightly higher than from the Turretfield Resource Flocks except for staple strength which was lower. This demonstrates that genetic parameter estimates within the Merino are generally robust for fleece traits. Correlation estimates in the two data sets were similar, except between clean fleece weight and fibre diameter. In the Turretfield Resource Flocks these correlations were undesirably positive (0.32 and 0.14, Table 4.7 and 4.8), but in the Selection Demonstration Flocks the correlation was slightly negative (-0.06, Table 6.5). These differences probably reflect the intense selection within the Selection Demonstration Flocks for increased fleece weight and decreased fibre diameter, although there were significant standard errors with all the estimates and it would be expected that the REML estimates would have accounted for the effect of selection.

6.4.2 Relationships between Fleece, Growth and Live Carcase Traits

Genetic correlations between live weight traits and clean fleece weight were low and negative, except for correlations with birth and weaning weight (Table 6.7). Genetic correlations were lower than the range reported by Safari and Fogarty (2003) of -0.09 to 0.58. Other correlations between weight traits and fleece traits fit within the ranges reported by Safari and Fogarty (2003), although there is considerable variation in estimates reported. Clarke (2002) reported a lack of estimates between early ages of live weight and fleece traits in Australian Merino sheep. The only reported estimates between 3 months of age (weaning weight) and fleece traits from Australian Merinos were published by Lewer *et al.* (1994) and Greeff and Karlsson (1998), both of which were on Western Australian Merinos. Genetic correlations in this study were lower for clean fleece weight, although were not different with consideration of the standard error, higher for staple length, of the reverse sign and slightly higher for staple strength and more similar for fibre diameter (although reverse sign) than those reported by Lewer *et al.* (1994) and Greeff and Karlsson (1998).

There are few estimates for Merinos between fleece and carcase traits. Due to the increased importance of income from meat Merino breeders and producers are now more interested in the relationships between these traits (Safari *et al.* 2001). Considering Merinos contribute over half the genes of all slaughter lambs in Australia (Fogarty *et al.* 2003) it is remarkable that the crossbred lamb industry has not placed greater pressure on Merino breeders to improve carcase qualities other than weight in the Merino prior to now. Following the Australian lamb industry investing in research and development through levies introduced in 1985, genetic improvement has been shown to improve the profitability of sheep enterprises. This has been a contributing factor to the increased interest lamb and wool producers have placed on genetic improvement and the desire to know about relationships between different trait groups (Banks 2003).

Genetic correlations between clean fleece weight and fat depth were similar to other recent Australian Merino estimates (Table 6.7). Lee *et al.* (2002) studied live measurement of fat depth at the C site in the CSIRO Merino bloodlines and Greeff *et al.* (2003) studied carcase fat at the C site using the Katanning Merino resource flocks. Correlations with fibre diameter from this study were generally higher than the estimate of 0.04 (± 0.24) reported by Greeff *et al.* (2003) and were lower with lower standard errors than the 1.14 (± 0.50) reported by Lee *et al.* (2002). Correlations with staple strength were similar to the 0.21 (± 0.21) reported by Greeff *et al.* (2003). Fogarty *et al.* (2003) measured fat depth at the C site in the carcase of animals from the QPLU$ Merino selection lines. Correlations between this study and those reported by Fogarty *et al.* (2003) were similar for clean fleece weight but were higher with fibre diameter. This higher estimate for carcase measured fat depth may be due to, or indicative of, the accuracy of measurement which is a significant issue for live measurement of fat depth in Merinos due to their natural leanness. There were no published estimates between fat depth and staple length. It should also be noted that for all of the published parameters quoted and the parameters from this study there were very high standard errors reported. This suggests that larger data sets are required to obtain more accurate estimates fo the genetic correlations between growth and fleece traits.

Genetic correlations between clean fleece weight and eye muscle depth from this study were all negative (Table 6.7), whereas previously reported correlations have all been positive for either live animal measurement or carcase measurement (Fogarty *et al.* 2003, Greeff *et al.* 2003). Correlations with fibre diameter were however, similar to those from Fogarty *et al.* (2003) and Greeff *et al.* (2003), which were 0.05 (± 0.18, carcase measurement) and 0.10 (± 0.25, live measurement), respectively. As for fat depth, correlations between eye muscle depth and staple strength were similar to the correlation of 0.19 (± 0.24) reported by Greeff *et al.* (2003) and there were no previously published correlations with staple length.

Historically, Merino breeding programs have focussed on improving fleece traits, with clean fleece weight and fibre diameter the main traits used for selection. Fogarty *et al.* (2000) have shown that Merinos are leaner than meat breed crosses and the correlations estimated in this study indicate a possible explanation for this. After so many years of selection for greater clean fleece weight and lower fibre diameter, it is probable that the correlated response from the negative genetic correlations with fat depth (and positive with eye muscle depth), has contributed to the Merino's lean and slightly less muscled carcase compared to breeds selected for dual-purpose use or meat production. However, within the Merino breed there is still much genetic variation for growth and carcase related traits (Fogarty *et al.* 2000, Greeff *et al.* 2003) and the vast majority of genetic correlations previously reported, as well as the correlations from this study, were low. This means that, like reproduction traits, growth and carcase traits can be improved in the Merino using the appropriate selection methods without causing a significant loss in wool quantity or quality (Fogarty *et al.* 2003, Greeff *et al.* 2003).

6.5 CONCLUSION

This study suggests that there are favourable genetic relationships between growth and live carcase traits and fleece traits. The results from this study are some of the first estimates of the genetic relationship that exists between fleece traits and weight and fleece traits and live carcase traits in the Merino. However, those that have been published were in agreement with the parameters estimated here, except for correlations between eye muscle depth and clean fleece weight which were in complete contrast (negative) with high standard errors. Genetic correlations were low but were favourable for genetic improvement of growth traits in Merinos without significant loss in fleece quantity or quality. Accuracy of measurement of ultrasound fat depth needs to be considered, especially in lean Merinos. However, as discussed in the previous chapter, early measurement of fat and eye muscle depth (weaning to 4 months of age) appears to give a good indication of older growth and have moderate to high correlations with fleece traits. The use of two stage selection would be beneficial for optimum improvement of these traits. A second stage of measurement at 7 to 8 months of age is supported by moderate to high correlations with fleece traits.

The parameters currently used by genetic evaluation services fit within the range of estimates from this study, but may require some updating as more information becomes available and as Merino breeders place greater emphasis on growth and carcase traits. Ongoing research is required to get more and better information on the relationships between meat and wool traits. This is currently being undertaken through support from the Sheep CRC and MLA for the recording of carcase information within the Katanning Demonstration Flocks in WA, the SDF in SA and the Trangie QPLU$ flocks in NSW, and live scanning measurements in the Merino Validation Project. The similarity between some estimates reported for meat breeds of sheep and these estimates in Merinos indicates that existing indexes may be able to be used without much alteration for growth or carcase improvement in Merinos. The main alteration suggested would be to the significance placed on reducing fatness depending on the target market, as Merinos are generally already lean.

Chapter 7

General Discussion

The Merino is used as a dual-purpose sheep, and the Merino's contribution to the sheep meat produced in Australia is considerable. The current trend within the Australian sheep flock is for greater meat production due to the current price received for meat relative to wool (ABARE 2002). However, in the past the Merino has been primarily used for wool production and has had little emphasis placed on its carcase. The aim of this study was to determine if there are genetic relationships between traits important to the dual-purpose use of Merino sheep. To do this, genetic parameters for reproduction, growth, live carcase and fleece traits were estimated. These parameters showed that genetic relationships do exist and were, with few exceptions, favourable for simultaneous improvement of all traits.

Correlations among female reproduction traits were all high to very high (Table 7.1). This indicates that the component traits are good indicators of the composite trait number of lambs weaned, and that there is some underlying effect common to all reproductive traits. One possibility is the hormonal control of each trait. It has been argued that much of the variation in litter size is due to ovulation rate (Hanrahan 1980, 1982; Davis *et al.* 1998) and it is no surprise that the hormonal control of ovulation rate and fertility are related. However, the link between rearing ability and the other reproductive traits is not so obvious. Rearing ability itself is a complex trait, so it is possible that hormonal control of such contributors to rearing ability such as milk production may be linked.

Genetic correlations between different ages of measurement of fat and eye muscle depth were all high to very high (Tables 5.10 and 5.11) and generally did not change over age. This indicates that fat and eye muscle depth are controlled by the same genes at all ages up to 16 months so these measures can be considered as genetically the same trait. Genetic correlations between different ages of weight measurement indicated that only after puberty (or about 5 months of age) could weight be considered the same trait (Table 5.9). Genetic correlations between these three traits at the same ages (i.e. WT4, FAT4 and EMD4) indicated that the genetic relationship between weight and eye muscle depth was higher than between weight and fat depth, although the relationship between fat and eye muscle depth was moderate to high. However, the accuracy of correlations with fat especially at younger ages may have been reduced due to the leanness of the animals reducing the variation at younger ages. To determine the true relationship with fat depth in Merinos, further study with animals fed high energy rations should be considered. If fat and eye muscle depth are considered components of weight, the genetic correlations indicate that eye muscle depth explains a greater proportion of the variation in weight at young ages than older ages, and a greater proportion than fat which explains a constantly low proportion of weight variation at all ages. However the genetic correlations between fat and eye muscle depth did not change with age. Very high genetic correlations among weight, fat and muscle gains (Table 7.1) indicate that weight gain was genetically the same as fat and muscle gain. However, the correlation between fat and muscle gain (0.48) does not indicate that these are the same trait. This is reasonable if fat and muscle gain are considered as components of weight gain as both are contributing to weight gain, but are not necessarily contributing to each other and may actually be operating at different stages of development. However, the correlation between fat and muscle gain was moderate and positive indicating that increases in one will increase the other.

Table 7.1 **A summary of heritabilities (on diagonal), phenotypic (above diagonal) and genetic (below diagonal) correlations between reproduction traits, weights, weight adjusted growth traits and fleece traits**

	aNLW	aFert	aLS	aRA	SC10	WT4	FAT4	EMD4	WT16	FAT16	EMD16	Wt gain	Fat gain	EMD gain	CFW16	FD16	SL16	SS16
aNLW	***0.16***	0.70	0.78	0.88	ne	•	•	•	•	•	•	•	•	•	0.06	0.09	0.06	0.10
aFert	0.82	***0.18***	0.82	0.78	ne	•	•	•	•	•	•	•	•	•	0.08	0.11	0.06	0.10
aLS	0.92	0.76	***0.23***	0.59	ne	•	•	•	•	•	•	•	•	•	0.10	0.08	0.06	0.10
aRA	0.80	0.93	0.60	***0.14***	ne	•	•	•	•	•	•	•	•	•	0.03	0.08	0.06	0.07
SC10	0.29	0.26	0.34	0.18	***0.40***	0.35	•	•	0.48	•	•	•	•	•	0.26	0.23	0.16	0.06
WT4	•	•	•	•	0.38	***0.20***	0.35	0.72	0.60	-0.15	-0.06	-0.21	-	-	0.30	0.03	0.11	0.01
FAT4	•	•	•	•	•	0.10	***0.49***	0.40	-0.14	0.28	0.21	-	-0.14	-	-0.11	0.05	-0.02	0.05
EMD4	•	•	•	•	•	0.72	0.79	***0.38***	-0.06	0.17	0.33	-	-	0.01	-0.06	0.05	0.05	0.01
WT16	•	•	•	•	0.56	0.67	-0.79	-0.46	***0.18***	0.13	0.58	0.35	-	-	0.43	0.22	0.21	0.11
FAT16	•	•	•	•	•	-0.39	0.67	0.60	-0.06	***0.45***	0.33	-	0.38	-	-0.11	0.13	0.05	0.07
EMD16	•	•	•	•	•	0.05	0.54	0.95	-0.27	0.78	***0.45***	-	-	0.64	-0.06	0.12	0.11	0.04
Wt gain	•	•	•	•	•	0.33	-	-	0.02	-	-	***0.15***	0.37	0.45	0.09	0.03	-0.01	0.00
Fat gain	•	•	•	•	•	-	0.21	-	-	0.11	-	0.87	***0.10***	0.19	-0.06	-0.10	-0.11	-0.08
EMD gain	•	•	•	•	•	-	-	0.26	-	-	0.42	0.89	0.48	***0.02***	0.09	0.06	-0.01	-0.01
CFW16	-0.15	-0.10	0.09	-0.27	0.24	-0.12	-0.26	-0.36	0.14	-0.29	-0.26	0.61	-0.23	-0.03	***0.55***	0.15	0.29	0.00
FD16	0.19	0.22	0.17	0.16	0.28	-0.29	0.12	-0.01	-0.36	0.33	0.20	-0.12	-0.31	0.20	-0.06	***0.68***	0.27	0.30
SL16	-0.20	-0.07	-0.14	-0.12	0.05	-0.04	-0.03	0.08	0.26	0.18	0.13	-0.12	-0.28	-0.02	0.33	0.37	***0.53***	-0.12
SS16	0.34	0.22	0.25	0.31	0.19	0.44	-0.10	-0.11	-0.03	0.18	0.14	-0.31	-0.21	-0.06	-0.28	0.58	0.02	***0.20***

Values from tables 3.6, 3.10, 3.12, 4.10, 4.11, 4.12, 4.13, 5.8, 5.9, 5.10, 5.11, 5.13, 5.14, 5.15, 5.16, 6.5, 6.6, 6.7, C.12, C.13, C.14, (C.15), D.7. ne = not estimable, • = not able to be estimated, - = not estimated. Figures after the trait are months of age. All correlations from multivariate analysis. All FAT and EMD traits adjusted for WT.
Correlations colour coded: ☐ = very low, 🟦 = low, 🟦 = moderate, ⬛ = high, ⬛ = very high, 🟩 = heritability

Clean fleece weight and live weight (at 4 months of age), fat and eye muscle depth were negatively correlated, but fleece weight and live weight gain were positively correlated (Table 7.1). It would be expected that protein directed to wool production would not be available for growth, but as described by Adams and Cronje (2003), the metabolic relationships are not simple. Adams *et al.* (2000) reported different protein synthesis rates in skin were associated with similar differences in muscle protein synthesis and therefore whole body protein synthesis rate. However, most of the additional protein is degraded, and increased protein degradation rate may result in decreased muscle deposition (Oddy *et al.* 1995). Reduction in fat depth may also be due to a reduction in the energy available because of the change in protein synthesis and degradation (Harris *et al.* 1992 cited by Adams and Cronje 2003). These metabolic responses to increased fleece weight are also related to changes in fibre diameter (Adams and Cronje 2003). Many studies have reported positive genetic correlations between fibre diameter and live weight although these correlations are generally very low. In this study genetic correlations were negative or zero for all ages (Table 6.7). Genetic correlations between fibre diameter and eye muscle depth were all very low indicating very little gene interaction between these traits. Genetic correlations with fat depth were positive and low to moderate but were quite variable. The correlated response of growth traits when selecting for either clean fleece weight or fibre diameter were low except for the response of weight when selecting for lower fibre diameter. However, the correlated response of live weight, fat or muscle gain were zero when selecting for either clean fleece weight or fibre diameter. Adams and Cronje (2003) concluded that there was little effect of fleece weight or diameter on live weight and growth, the values estimated in this study add support to this conclusion.

Genetic correlations between clean fleece weight and reproduction traits were low or very low (Table 7.1). The genetic correlations with scrotal circumference indicate that selection for scrotal circumference to improve reproductive rates may have a small increase in both fleece weight and fibre diameter. This is supported by the correlated response of scrotal circumference when selecting for either fleece weight or reduced fibre diameter shown in Table 7.2. All genetic correlations between fibre diameter and reproduction traits were positive which is undesirable (Table 7.1). However, the correlations were low and the correlated responses for female reproductive traits when selecting for clean fleece weight or fibre diameter were very low (Table 7.2). It has been reported that Merinos with fine wool have reduced reproductive ability (Mortimer *et al.* 1985). Adams and Cronje (2003) suggested that the hormone prolactin may contribute to this reduction in reproduction due to its role in both maternal behaviour and the wool follicle cycle, although this has not been studied in Merino sheep. There is an obvious lack of information on the biological relationships between fleece and reproduction traits which considering the complexity of both trait types is not surprising.

Table 7.2 Correlated responses per generation in Trait 2 from selection for Trait 1, clean fleece weight (CFW) or reduced fibre diameter (FD) and parameters used

			Trait 1			
			r_g		CR	
Trait 2	h^2	σ_p	**CFW**	**FD**	**CFW**	**FD**
aNLW	0.16	0.42	-0.15	0.19	-0.02	-0.03
aLS	0.23	0.42	0.09	0.17	0.01	-0.03
SC10	0.40	2.52	0.24	0.28	0.28	-0.37
WT4	0.20	3.74	-0.12	-0.29	-0.15	0.40
FAT4	0.49	0.41	-0.26	0.12	-0.06	-0.03
EMD4	0.38	1.47	-0.36	-0.01	-0.24	0.01
WT16	0.18	6.27	0.14	-0.36	0.28	0.79
FAT16	0.45	0.47	-0.29	0.33	-0.07	-0.09
EMD16	0.45	1.65	-0.26	0.20	-0.21	-0.18
Wt gain	0.15	0.06	0.61	-0.12	0.01	0.00
Fat gain	0.10	0.10	-0.23	-0.31	-0.01	0.01
EMD gain	0.02	0.08	-0.03	0.20	0.00	0.00

h2 = heritability, σ_p = phenotypic standard deviation, r_g = genetic correlation between Trait 1 and Trait 2, CR = correlated response, a selection intensity of 1.0 was used, see Equation 3.2, aNLW = Average number of lambs weaned over a lifetime, aLS = Average litter size, SC10 = scrotal circumference at 10 months of age, WT = live weight at 4 and 16 months of age, FAT = Fat depth at 4 and 16 months of age, EMD = Eye muscle depth at 4 and 16 months of age

Genetic correlations between staple length, growth and reproduction were generally very low and it would appear from this study that there is little genetic interaction between these traits. Genetic correlations with staple strength ranged from low to moderate across all traits which is not surprising considering the low heritability of staple strength (Table 7.1). Correlations for staple strength with growth traits suggest that there is a higher genetic relationship with live weight at younger than older ages. The biological relationship of growth and staple strength is also related to the previous discussion of protein synthesis and degradation. Adams *et al.* (2000) found that animals selected for greater staple strength exhibited less change in rate of protein synthesis in both skin and muscle than animals selected for reduced staple strength at various levels of nutrition. This resulted in higher protein turnover at low intake for strong staple strength animals. Adams *et al.* (2000) stated that when sheep have a strong body demand for growth, differences between the genotypes in wool growth were not observed. The conclusion from much of the research so far shows that selection for fleece traits affects protein metabolism in not only the skin but muscle as well.

There are few estimates of genetic parameters for carcase traits in Merinos specifically, because they have traditionally been considered a wool breed. Now that there is more interest in the Merinos contribution to lamb and meat production, and the ever present requirement for increased or improved production rates, accurate parameter estimates are required for use in increasingly complex breeding indexes and evaluation of animals. Ultrasound measurements of fat depth and eye muscle depth have been successfully used to improve carcase composition in the traditional meat breeds for some time. Estimates from this study indicate that this may also be achieved in the Merino. However, because the Merino is a lean animal (low subcutaneous fat), the accuracy of measurement of fat and eye muscle depth may not be as great as for meat breeds. This also has implications for the timing of measurement. Genetic correlations from this study indicate that early selection for growth traits would not be detrimental to fleece traits and is highly correlated with later measurements. However, if the animal is too lean then a reliable measurement cannot be taken, which is a concern with Merinos at 3 – 4 months of age unless fed well. With further investigation into carcase traits in Merinos other more accurate predictions of carcase composition in the live animal may be found.

If the breeding objective aims to increase the reproductive rate or number of lambs weaned, then estimates from this study suggest that litter size, at the first lambing or earlier with ultrasound measurement, and scrotal circumference measured at 10 months of age, should be used as selection criteria. If the breeding objective aims to increase growth rate, it has been recommended that live weight at weaning (or 3 – 4 months of age) should be used as the selection criteria, with possibly another measurement at 10 months of age or older. Improvement of carcase traits in the Merino can be achieved using live ultrasound scan measurements of subcutaneous fat depth and eye muscle depth as selection criteria. It is recommended that these scanned traits be measured at the same time as live weights, 4 and 10 months of age. All of these traits have a genetic relationship to fleece traits. Generally, the genetic correlations were favourable for improvement of all traits. However, those that were not favourable were generally low to moderate, so with the use of a multiple trait selection index improvements can still be made.

A consideration for producers using Merinos is the difference between the nutritional and management requirements of wool producing sheep and dual-purpose sheep. As a dual-purpose sheep the Merino plays different roles, one is as the wool producing mother of a crossbred lamb, and another is as a wool and meat producing lamb. These two roles have different management and nutrition requirements. Merino lambs generally have little fat cover, but also are generally not fed in the same way that crossbred lambs need to be to have rapid growth and meet market specifications. If a producer is considering using the Merino to produce meat and wool, both products will have to achieve certain market requirements and the management of the sheep will have to change accordingly. If Merinos were fed for meat production, they would not be as lean as those fed for wool production, which will change the emphasis that is required in a selection index on fat depth, and may overcome concerns of accuracy of ultrasound fat depth measurement.

The trend toward greater lamb and meat production in the sheep industry has implications for the genetic evaluation services operating within Australia. While the parameters currently used by these services generally fit within the range of genetic parameters estimated in this study, there were some differences and the requirements of the Merino breeder are changing. Scrotal circumference and ultrasound fat and muscle depth measurements are already included in the list of traits offered for analysis by the genetic evaluation services. Genetic parameters were similar to estimates reported for meat breeds of sheep and existing indexes may be appropriate for use to improve growth and carcase characters in the Merino. However, as discussed current management practices increase the leanness of the Merino compared to meat breeds and may require a different index depending on the level of meat production the breeder or producer is aiming for. As further studies are carried out to confirm the parameters for growth and carcase in the Merino, genetic evaluation services will have to update their information and possibly offer selection indices specific for meat producing Merinos.

This study reported some of the few estimates available between fleece and reproduction and fleece and growth traits. The limitation of this study was the lack of estimates of genetic correlations between reproduction, growth and live carcase traits. This work was not possible within the time frame of this study due to the structure of the data from the two projects (TRF and SDF). Ewes transferred from the TRF to the SDF were subject to a confidentiality agreement and were allocated new tag numbers. There was insufficient time available to find and use the information required to convert these tag numbers into a useable form. At the end of the Selection Demonstration Flocks project reproduction data will be able to be correlated with the growth data which was also collected on the 2002 drop. Additional to this study, these two data sets are being combined with other data from around Australia in a Sheep Industry CRC project to estimate and evaluate genetic parameters (pers. comm. Alex Safari 2003). Time constraints also did not allow for testing of combinations of growth and reproduction traits into different traditional wool selection indices.

Other research is ongoing around Australia to get more and better information on the relationships between fleece and meat type traits. Carcase evaluation of Merinos is being carried out though support from the Australian Sheep Industry CRC and Meat and Livestock Australia. Animals from the Selection Demonstration Flocks, and other populations of Merinos, namely, the Katanning Demonstration Flocks in Western Australia and the Trangie QPLU$ flocks in New South Wales are being used for this carcase evaluation. The measurements from these flocks will enable the comparison of ultrasound measurements and carcase measurements, as well as providing a better understanding of the carcase of the Merino. Within the Merino Validation Project, supported by Meat and Livestock Australia, large numbers of records from commercial flocks all over Australia of reproduction, growth and live carcase are being taken. This project will also provide further estimates of correlations between these traits.

It is concluded that there is considerable variation in the South Australian Merino population for reproduction, growth and live carcase traits. For the South Australian Merino breeder this means that there are significant gains to be made both genetically and financially. While there were some low genetic correlations that were in unfavourable directions, this study has not identified any major genetic antagonisms between potential gain in wool, meat and reproduction traits.

Appendix A

A.1 LEAST SQUARES MEANS FOR FEMALE REPRODUCTION TRAITS

All means adjusted to single born, single raised, ewe lambs, from 3 year old dams.

Table A.1 Least squares means (standard error) for number of lambs weaned at 28, 40, 52 and 64 months of age and lifetime average for each year of birth and flock of origin[A]

		NLW28	NLW40	NLW52	NLW64	aNLW
Year	1989	0.46 (0.066)^{a}	0.82 (0.071)^{a}	0.60 (0.078)^{a}	0.98 (0.085)^{a}	0.70 (0.051)^{a}
	1990	0.68 (0.057)^{b}	0.69 (0.064)^{b}	0.89 (0.068)^{b}	1.14 (0.074)^{b}	0.83 (0.044)^{b}
	1991	0.65 (0.060)^{b}	0.87 (0.065)^{a}	1.13 (0.071)^{c}	1.18 (0.079)^{b}	0.94 (0.046)^{c}
	1992	0.64 (0.056)^{b}	1.07 (0.062)^{c}	1.13 (0.068)^{c}	1.30 (0.077)^{c}	0.98 (0.043)^{c}
Flock	1	0.70 (0.058)^{a}	0.95 (0.064)^{a}	0.99 (0.070)^{a}	1.21 (0.081)	0.93 (0.045)^{a}
	2	0.58 (0.059)^{b}	0.87 (0.066)^{b}	0.97 (0.071)^{a}	1.17 (0.082)	0.87 (0.045)^{a}
	3	0.50 (0.064)^{b}	0.77 (0.072)^{b}	0.85 (0.075)^{b}	1.06 (0.090)	0.77 (0.048)^{b}
	4	0.64 (0.057)^{a}	0.86 (0.064)^{b}	0.93 (0.069)^{ab}	1.16 (0.080)	0.87 (0.044)^{a}

[A] Within a cell means with no superscript or with a common superscript do not differ significantly ($P > 0.05$) from each other.

Table A.2 Least squares means (standard error) for Fertility at 28, 40, 52 and 64 months of age for each year of birth and flock of origin[A]

		Fert28	Fert40	Fert52	Fert64	aFert
Year	1989	0.48 (0.056)^{a}	0.86 (0.045)^{a}	0.67 (0.042)^{a}	0.85 (0.035)^{a}	0.72 (0.032)^{a}
	1990	0.73 (0.049)^{b}	0.75 (0.040)^{b}	0.83 (0.036)^{b}	0.83 (0.031)^{a}	0.78 (0.027)^{b}
	1991	0.73 (0.052)^{b}	0.87 (0.040)^{a}	0.87 (0.037)^{b}	0.84 (0.033)^{a}	0.84 (0.028)^{c}
	1992	0.74 (0.048)^{b}	0.87 (0.039)^{a}	0.87 (0.036)^{b}	0.97 (0.032)^{b}	0.84 (0.027)^{c}
Flock	1	0.76 (0.050)^{a}	0.89 (0.040)^{a}	0.84 (0.039)	0.88 (0.036)	0.84 (0.028)^{a}
	2	0.62 (0.051)^{b}	0.81 (0.041)^{b}	0.78 (0.039)	0.86 (0.036)	0.77 (0.028)^{bc}
	3	0.60 (0.056)^{b}	0.81 (0.045)^{b}	0.79 (0.045)	0.86 (0.041)	0.76 (0.030)^{b}
	4	0.71 (0.049)^{a}	0.82 (0.040)^{b}	0.83 (0.039)	0.88 (0.036)	0.81 (0.027)^{ac}

[A] Within a cell means with no superscript or with a common superscript do not differ significantly ($P > 0.05$) from each other.

Table A.3 Least squares means (standard error) for Litter size at 28, 40, 52 and 64 months of age for each year of birth and flock of origin^{A}

		LS28	LS40	LS52	LS64	aLS
Year	**1989**	0.52 (0.066)^{a}	1.09 (0.070)^{a}	0.82 (0.081)^{a}	1.19 (0.086)^{a}	0.90 (0.052)^{a}
	1990	0.84 (0.056)^{b}	0.89 (0.062)^{b}	1.11 (0.096)^{b}	1.35 (0.072)^{b}	1.03 (0.044)^{b}
	1991	0.82 (0.059)^{b}	1.10 (0.065)^{a}	1.53 (0.073)^{c}	1.42 (0.076)^{bc}	1.21 (0.046)^{c}
	1992	0.81 (0.055)^{b}	1.38 (0.061)^{c}	1.46 (0.069)^{c}	1.48 (0.072)^{c}	1.25 (0.043)^{c}
Flock	**1**	0.83 (0.057)^{a}	1.20 (0.063)^{a}	1.27 (0.071)^{a}	1.35 (0.075)	1.15 (0.045)^{a}
	2	0.73 (0.058)^{bc}	1.13 (0.064)^{a}	1.29 (0.072)^{a}	1.40 (0.076)	1.12 (0.046)^{a}
	3	0.65 (0.062)^{b}	1.02 (0.067)^{b}	1.14 (0.077)^{b}	1.31 (0.081)	1.01 (0.049)^{b}
	4	0.78 (0.056)^{ac}	1.11 (0.062)^{a}	1.22 (0.070)^{ab}	1.37 (0.073)	1.11 (0.044)^{ab}

^{A} Within a cell means with no superscript or with a common superscript do not differ significantly ($P > 0.05$) from each other.

Table A.4 Least squares means (standard error) for Rearing ability at 28, 40, 52 and 64 months of age for each year of birth and flock of origin^{A}

		RA28	RA40	RA52	RA64	aRA
Year	**1989**	0.43 (0.059)^{a}	0.64 (0.051)^{ab}	0.52 (0.050)^{a}	0.73 (0.047)^{a}	0.57 (0.036)^{a}
	1990	0.61 (0.051)^{b}	0.57 (0.046)^{a}	0.70 (0.043)^{b}	0.72 (0.042)^{a}	0.64 (0.031)^{b}
	1991	0.59 (0.054)^{b}	0.69 (0.047)^{b}	0.68 (0.045)^{b}	0.70 (0.045)^{a}	0.66 (0.032)^{b}
	1992	0.58 (0.050)^{b}	0.67 (0.045)^{b}	0.70 (0.043)^{b}	0.86 (0.043)^{b}	0.67 (0.030)^{b}
Flock	**1**	0.64 (0.052)^{a}	0.71 (0.046)^{a}	0.68 (0.045)	0.79 (0.046)	0.69 (0.031)^{a}
	2	0.50 (0.053)^{b}	0.62 (0.047)^{b}	0.63 (0.045)	0.75 (0.047)	0.61 (0.032)^{bc}
	3	0.46 (0.058)^{b}	0.60 (0.052)^{b}	0.62 (0.049)	0.72 (0.051)	0.59 (0.034)^{b}
	4	0.59 (0.051)^{a}	0.63 (0.046)^{b}	0.66 (0.044)	0.76 (0.046)	0.65 (0.031)^{ac}

^{A} Within a cell means with no superscript or with a common superscript do not differ significantly ($P > 0.05$) from each other.

A.2 GENETIC PARAMETERS BETWEEN REPRODUCTIVE COMPONENT TRAITS AND AVERAGE NUMBER OF LAMBS WEANED

Table A.5 Phenotypic and genetic correlations (standard error) between component traits at different ages and average number of lambs weaned

	Phenotypic correlations			Genetic correlations		
Age	Fert	LS	RA	Fert	LS	RA
28	0.48 (0.019)	0.49 (0.019)	0.54 (0.017)	0.71 (0.161)	0.78 (0.145)	0.92 (0.127)
40	0.46 (0.019)	0.48 (0.019)	0.55 (0.016)	0.78 (0.254)	0.78 (0.254)	0.66 (0.333)
52	0.47 (0.019)	0.51 (0.018)	0.57 (0.016)	0.81 (0.139)	0.81 (0.139)	0.54 (0.203)
64	0.37 (0.021)	0.47 (0.019)	0.56 (0.016)	0.93 (0.106)	0.93 (0.106)	0.52 (0.362)

A.3 LEAST SQUARES MEANS FOR SCROTAL CIRCUMFERENCE

All means adjusted to single born, single raised, ram lambs, from 3 year old dams.

Table A.6 Least squares means (standard error) for scrotal circumference at 5, 10 and 16 months of age for each year of birth[A]

	Year	Model 1	Model 2	Model 3
SC5	1989	25.9 (0.52)^{a}	16.5 (0.30)^{a}	19.3 (0.41)^{a}
	1990	13.7 (0.34)^{b}	19.3 (0.26)^{b}	18.4 (0.27)^{b}
	1991	16.5 (0.36)^{c}	17.9 (0.26)^{c}	17.6 (0.26)^{c}
	1992	16.3 (0.34)^{c}	16.9 (0.24)^{a}	16.4 (0.24)^{d}
SC10	1989	30.1 (0.50)^{a}	26.3 (0.30)^{a}	27.1 (0.42)^{ac}
	1990	24.5 (0.34)^{b}	26.5 (0.37)^{a}	26.3 (0.28)^{b}
	1991	25.9 (0.34)^{c}	28.1 (0.28)^{b}	28.0 (0.28)^{a}
	1992	27.4 (0.33)^{d}	26.6 (0.26)^{a}	26.4 (0.27)^{bc}
SC16	1989	33.8 (0.44)^{a}	32.3 (0.28)	32.3 (0.38)
	1990	32.4 (0.29)^{b}	32.1 (0.16)	32.1 (0.25)
	1991	31.9 (0.30)^{b}	31.8 (0.17)	31.8 (0.26)
	1992	31.1 (0.29)^{c}	32.3 (0.15)	32.2 (0.25)

[A] Within a cell means with no superscript or with a common superscript do not differ significantly ($P > 0.05$) from each other within each model and age of scrotal circumference.

Table A.7 **Least squares means (standard error) for scrotal circumference at 5, 10 and 16 months of age for each flock**[A]

	Flock	Model 1	Model 2	Model 3
SC5	1	18.4 (0.35)	18.0 (0.26)^a	18.2 (0.25)^a
	2	18.5 (0.35)	17.1 (0.26)^b	17.5 (0.26)^b
	3	17.8 (0.37)	17.4 (0.27)^b	17.7 (0.26)^b
	4	17.8 (0.35)	18.2 (0.26)^a	18.2 (0.25)^a
SC10	1	27.6 (0.34)^{ac}	27.1 (0.27)^a	27.2 (0.27)^a
	2	27.8 (0.34)^a	27.2 (0.27)^a	27.3 (0.27)^a
	3	25.3 (0.35)^b	25.9 (0.28)^b	26.0 (0.29)^b
	4	27.2 (0.33)^c	27.1 (0.27)^a	27.2 (0.27)^a
SC16	1	32.4 (0.29)^a	32.2 (0.25)^a	32.2 (0.25)^a
	2	33.0 (0.30)^b	32.5 (0.25)^a	32.5 (0.26)^a
	3	31.2 (0.31)^c	31.5 (0.26)^b	31.5 (0.27)^b
	4	32.6 (0.29)^{ab}	32.2 (0.25)^a	32.2 (0.25)^a

[A] Within a cell means with no superscript or with a common superscript do not differ significantly ($P > 0.05$) from each other within each model and age of scrotal circumference.

Table A.8 **Least squares means (standard error) for scrotal circumference at 5, 10 and 16 months of age for rams born and reared as singles (11), twins raised as singles (21) , or twins raised as twins (22)**[A]

	Tobr	Model 1	Model 2	Model 3
SC5	11	19.2 (0.14)^a	17.2 (0.10)^a	17.7 (0.10)^a
	21	18.2 (0.28)^b	17.6 (0.21)^b	17.9 (0.21)^{ab}
	22	16.8 (0.18)^c	17.9 (0.13)^b	18.0 (0.13)^b
SC10	11	26.7 (0.13)^a	26.1 (0.10)^a	26.2 (0.11)^a
	21	27.0 (0.28)^a	26.8 (0.22)^b	26.9 (0.23)^b
	22	26.2 (0.17)^b	26.7 (0.14)^b	26.8 (0.14)^b
SC16	11	32.0 (0.11)^a	31.7 (0.09)^a	31.7 (0.10)^a
	21	32.4 (0.25)^b	32.2 (0.20)^b	32.2 (0.21)^b
	22	31.8 (0.15)^a	32.0 (0.13)^{ab}	32.0 (0.13)^{ab}

[A] Within a cell means with no superscript or with a common superscript do not differ significantly ($P > 0.05$) from each other within each model and age of scrotal circumference.

A.4 GENETIC CORRELATIONS BETWEEN FEMALE AND MALE REPRODUCTION TRAITS AT ALL AGES OF MEASUREMENT

Table A.9 Genetic correlations (standard error) between scrotal circumference and number of lambs weaned at different ages

	Model	SC5	SC10	SC16
NLW28	1	-0.02 (0.178)	0.34 (0.191)	0.34 (0.192)
	2	-0.19 (0.179)	0.14 (0.197)	0.12 (0.194)
	3	-0.16 (0.181)	0.16 (0.194)	0.14 (0.193)
NLW40	1	1.01 (0.756)	0.92 (0.723)	1.35 (0.989)
	2	0.75 (0.825)	0.44 (0.615)	0.88 (0.937)
	3	0.81 (0.833)	0.45 (0.597)	0.92 (0.925)
NLW52	1	0.19 (0.234)	0.56 (0.284)	0.55 (0.289)
	2	0.29 (0.253)	0.45 (0.286)	0.44 (0.286)
	3	0.24 (0.250)	0.43 (0.282)	0.47 (0.286)
NLW64	1	0.50 (0.208)	0.69 (0.239)	0.86 (0.251)
	2	0.12 (0.206)	0.26 (0.231)	0.45 (0.233)
	3	0.20 (0.208)	0.29 (0.228)	0.47 (0.231)

Table A.10 Genetic correlations (standard error) between scrotal circumference and fertility at different ages

	Model	SC5	SC10	SC16
Fert28	1	0.11 (0.180)	0.39 (0.193)	0.45 (0.192)
	2	-0.18 (0.189)	0.06 (0.206)	0.11 (0.203)
	3	-0.14 (0.189)	0.09 (0.203)	0.14 (0.201)
Fert40	1	0.41 (0.280)	0.35 (0.306)	0.27 (0.309)
	2	0.47 (0.294)	0.28 (0.296)	0.04 (0.289)
	3	0.47 (0.297)	0.28 (0.296)	0.07 (0.290)
Fert52	1	-0.04 (0.273)	0.57 (0.360)	0.04 (0.314)
	2	0.18 (0.285)	0.59 (0.362)	0.07 (0.306)
	3	0.20 (0.278)	0.60 (0.344)	0.09 (0.296)
Fert64	1	0.28 (0.184)	0.45 (0.209)	0.39 (0.210)
	2	0.20 (0.185)	0.16 (0.205)	0.13 (0.204)
	3	0.24 (0.188)	0.17 (0.205)	0.12 (0.205)

Table A.11 Genetic correlations (standard error) between scrotal circumference and litter size at different ages

	Model	SC5	SC10	SC16
LS28	1	0.10 (0.208)	0.11 (0.238)	-0.22 (0.232)
	2	0.23 (0.206)	0.10 (0.237)	-0.37 (0.230)
	3	0.23 (0.211)	0.10 (0.233)	-0.35 (0.226)
LS40	1	0.22 (0.200)	0.29 (0.239)	0.26 (0.244)
	2	0.08 (0.201)	0.12 (0.228)	0.08 (0.223)
	3	0.04 (0.203)	0.09 (0.228)	0.09 (0.225)
LS52	1	0.08 (0.200)	0.30 (0.245)	0.75 (0.285)
	2	0.06 (0.204)	0.12 (0.234)	0.53 (0.250)
	3	0.03 (0.208)	0.11 (0.234)	0.54 (0.253)
LS64	1	0.22 (0.159)	0.33 (0.192)	0.46 (0.202)
	2	0.08 (0.166)	0.47 (0.202)	0.38 (0.190)
	3	0.08 (0.168)	0.33 (0.191)	0.41 (0.190)

Table A.12 Genetic correlations (standard error) between scrotal circumference and rearing ability at different ages

	Model	SC5	SC10	SC16
RA28	1	0.26 (0.170)	0.49 (0.181)	0.53 (0.180)
	2	-0.04 (0.185)	0.15 (0.202)	0.19 (0.198)
	3	0.01 (0.184)	0.18 (0.198)	0.21 (0.195)
RA40	1	0.88 (0.308)	0.87 (0.328)	0.96 (0.346)
	2	0.75 (0.328)	0.64 (0.325)	0.69 (0.332)
	3	0.79 (0.331)	0.64 (0.320)	0.73 (0.332)
RA52	1	0.19 (0.162)	0.28 (0.182)	0.37 (0.183)
	2	0.15 (0.169)	0.08 (0.186)	0.26 (0.184)
	3	0.16 (0.171)	0.08 (0.185)	0.28 (0.184)
RA64	1	0.28 (0.134)	0.39 (0.151)	0.48 (0.152)
	2	0.20 (0.138)	0.22 (0.153)	0.31 (0.151)
	3	0.20 (0.140)	0.21 (0.152)	0.31 (0.151)

A.5 CALCULATION OF CORRELATED RESPONSE FOR NUMBER OF LAMBS WEANED

Response to selection for a single trait is (Falconer and Mackay 1960):

$$\mathrm{R}_1 = h_1^2 i \sigma_{P_1} \qquad \text{(Equation 3.1)}$$

where R_1 is the response to selection, h_1^2 is the heritability, i is the selection intensity and σ_{P_1} is the standard deviation.

For number of lambs weaned using a selection intensity of 1, heritability of 0.16 (Table 3.6) and standard deviation of √0.178 (Table 3.4), the response to selection for number of lambs weaned is

$\mathrm{R}_1 = 0.16 * 1 * 0.422 = 0.068$ lambs per ewe per generation.

The correlated response in trait 2 when selecting for Trait 1 is (Falconer and Mackay 1960):

$$\mathrm{CR}_{2.1} = r_{A_1 A_2} \sqrt{h_1^2 h_2^2}\, i_p \sigma_{P_2} \qquad \text{(Equation 3.2)}$$

where $\mathrm{CR}_{2.1}$ is the correlated response, $r_{A_1 A}$ is the correlation between trait 1 and 2, h_1^2 is the heritability of trait 1, h_2^2 is the heritability of trait 2, i_p is the selection intensity and σ_{P_2} is the standard deviation of trait 2.

Correlated response in number of lambs weaned when selecting for litter size at 28 months.

$\mathrm{CR}_{2.1} = 0.78\sqrt{0.16 * 0.16} * 1 * \sqrt{0.178}$

$\mathrm{CR}_{2.1} = 0.052$ lambs per ewe per generation

Correlated response in number of lambs weaned when selecting for scrotal circumference at 10 months.

$\mathrm{CR}_{2.1} = 0.29\sqrt{0.40 * 0.16} * 1 * \sqrt{0.178}$

$\mathrm{CR}_{2.1} = 0.031$ lambs per ewe per generation

Appendix B

B.1 COMPARISON OF CORRELATIONS BETWEEN FLEECE AND REPRODUCTION TRAITS, WITH AND WITHOUT ADJUSTMENT FOR LAMBING STATUS

Table B.1 Genetic and phenotypic variances, and heritabilities of fleece traits with (Model 2) and without (Model 1) adjustment for lambing status[a]

		Age of measurement							
		28		40		52		64	
		Model 1	Model 2	Model 1	Model 2	Model 1	Model 2	Model 1	Model 2
CFW	V_g	0.248	0.237	0.235	0.241	0.286	0.281	0.338	0.315
	V_p	0.531	0.502	0.591	0.573	0.594	0.573	0.646	0.583
	h^2	0.47	0.47	0.40	0.42	0.48	0.49	0.52	0.54
FD	V_g	2.009	2.025	2.025	2.041	2.282	2.300	2.868	2.819
	V_p	2.906	2.864	3.402	3.379	3.655	3.563	4.091	3.951
	h^2	0.69	0.71	0.60	0.60	0.62	0.65	0.70	0.71
SL	V_g	44.50	45.96	61.72	46.48	61.51	61.17	61.85	63.16
	V_p	87.36	86.96	102.2	96.96	93.81	93.03	101.6	99.56
	h^2	0.51	0.53	0.60	0.48	0.66	0.66	0.61	0.63
SS	V_g	36.44	36.26	36.77	37.73	27.88	30.12	50.31	39.91
	V_p	96.06	94.53	121.0	115.2	131.5	126.6	144.2	128.2
	h^2	0.38	0.38	0.30	0.33	0.21	0.24	0.35	0.31

[a] Model 1: base model, Model 2: base model + number of lambs weaned. V_g = genetic variance, V_p = phenotypic variance, h^2 = heritability

B.2 LEAST SQUARES MEANS FOR FLEECE TRAITS – TURRETFIELD RESOURCE FLOCKS

All means adjusted to single born, single raised lambs, from 3 year old dams.

Table B.2 Least squares means (standard error) of clean fleece weight (kg) for each year of birth, flock of origin and type of birth and rearing (Tobr)[A]

		Ram		Ewe				
		10	16	16	28	40	52	64
Year	**1989**	1.8^{a} (0.03)	2.3^{a} (0.04)	3.5^{a} (0.07)	4.2^{a} (0.08)	5.3^{a} (0.08)	5.0^{a} (0.09)	4.8^{a} (0.09)
	1990	2.2^{b} (0.02)	3.4^{b} (0.03)	4.4^{b} (0.04)	5.2^{b} (0.05)	4.8^{b} (0.05)	5.0^{a} (0.05)	5.3^{b} (0.06)
	1991	2.1^{b} (0.03)	3.3^{b} (0.03)	4.4^{b} (0.04)	5.2^{b} (0.05)	5.2^{a} (0.05)	5.5^{b} (0.05)	5.1^{c} (0.06)
	1992	2.8^{c} (0.02)	2.7^{c} (0.03)	4.9^{c} (0.04)	4.9^{c} (0.05)	5.5^{c} (0.05)	5.2^{c} (0.05)	ne
Flock	**1**	2.2^{a} (0.03)	2.9^{a} (0.03)	4.1^{a} (0.05)	4.5^{a} (0.05)	4.8^{a} (0.06)	4.7^{a} (0.06)	4.7^{a} (0.07)
	2	2.3^{b} (0.03)	3.1^{b} (0.03)	4.6^{b} (0.05)	5.2^{b} (0.05)	5.6^{b} (0.06)	5.4^{b} (0.06)	5.4^{b} (0.07)
	3	2.3^{ab} (0.03)	2.9^{a} (0.03)	4.5^{b} (0.05)	5.0^{b} (0.06)	5.4^{b} (0.07)	5.4^{b} (0.07)	5.4^{b} (0.10)
	4	2.2^{a} (0.03)	2.9^{a} (0.03)	4.2^{a} (0.04)	4.7^{a} (0.05)	5.1^{c} (0.06)	5.1^{c} (0.06)	4.9^{a} (0.07)
Tobr	**11**	2.2^{a} (0.01)	2.9^{a} (0.02)	4.4^{a} (0.02)	4.8^{a} (0.03)	5.2^{a} (0.03)	5.1^{a} (0.03)	5.1 (0.04)
	21	2.0^{b} (0.03)	2.8^{b} (0.04)	4.1^{b} (0.06)	4.6^{b} (0.07)	4.9^{b} (0.07)	4.8^{b} (0.08)	5.0 (0.09)
	22	2.0^{b} (0.02)	2.8^{b} (0.02)	4.1^{b} (0.03)	4.6^{b} (0.04)	4.9^{b} (0.04)	4.9^{b} (0.05)	4.9 (0.06)

[A] Within a cell means with no superscript or with a common superscript do not differ significantly ($P > 0.05$) from each other. ne = not estimable

Table B.3 Least squares means (standard error) of clean fleece weight (kg) for year of birth by flock of origin interaction[A]

		Ram		Ewe				
Year	**Flock**	**10**	**16**	**16**	**28**	**40**	**52**	**64**
1989	1	1.7^{a} (0.07)	2.3 (0.05)	3.3^{a} (0.13)	3.9 (0.09)	4.8^{ab} (0.16)	4.5 (0.10)	4.5 (0.11)
	2	1.8^{b} (0.06)	2.5 (0.05)	3.9^{b} (0.11)	4.5 (0.08)	6.0^{c} (0.13)	5.3 (0.10)	5.2 (0.10)
	3	1.8^{ab} (0.07)	2.3 (0.05)	ne	ne	ne	ne	ne
	4	1.8^{ab} (0.07)	2.3 (0.05)	3.3^{a} (0.11)	4.0 (0.09)	5.0^{ade} (0.13)	4.9 (0.10)	4.7 (0.10)
1990	1	2.3^{c} (0.05)	3.3 (0.04)	4.3^{cd} (0.07)	4.9 (0.06)	4.5^{b} (0.09)	4.5 (0.07)	4.9 (0.08)
	2	2.2^{cd} (0.05)	3.5 (0.04)	4.8^{ef} (0.08)	5.5 (0.06)	5.3^{de} (0.10)	5.2 (0.07)	5.6 (0.08)
	3	2.2^{cd} (0.05)	3.3 (0.04)	4.2^{d} (0.09)	5.3 (0.07)	4.8^{ab} (0.11)	5.2 (0.08)	5.5 (0.10)
	4	2.2^{cd} (0.05)	3.3 (0.04)	4.3^{cd} (0.08)	5.0 (0.06)	4.7^{ab} (0.10)	4.9 (0.07)	5.1 (0.08)
1991	1	2.1^{d} (0.05)	3.3 (0.04)	4.2^{d} (0.07)	4.9 (0.06)	4.7^{ab} (0.09)	5.0 (0.07)	4.7 (0.08)
	2	2.1^{cd} (0.05)	3.5 (0.04)	4.5^{cgh} (0.08)	5.5 (0.07)	5.2^{de} (0.10)	5.7 (0.08)	5.4 (0.09)
	3	2.1^{d} (0.07)	3.3 (0.04)	4.4^{cd} (0.11)	5.3 (0.08)	5.6^{f} (0.13)	5.8 (0.09)	5.3 (0.11)
	4	2.2^{cd} (0.05)	3.3 (0.04)	4.4^{cdh} (0.08)	5.0 (0.06)	5.2^{de} (0.10)	5.4 (0.07)	4.9 (0.08)
1992	1	2.8^{e} (0.04)	2.7 (0.04)	4.7^{fgh} (0.08)	4.5 (0.06)	5.0^{ade} (0.09)	4.7 (0.07)	ne
	2	3.0^{f} (0.05)	2.9 (0.04)	5.1^{i} (0.08)	5.2 (0.06)	5.8^{cf} (0.10)	5.4 (0.07)	ne
	3	3.0^{f} (0.05)	2.7 (0.04)	5.0^{ei} (0.08)	5.0 (0.07)	5.9^{cf} (0.10)	5.5 (0.08)	ne
	4	2.5^{g} (0.05)	2.7 (0.04)	4.7^{fg} (0.08)	4.7 (0.06)	5.3^{e} (0.10)	5.1 (0.07)	ne

[A] Within a column means with no superscript or with a common superscript do not differ significantly ($P > 0.05$) from each other. ne = not estimable

Table B.4 Least squares means (standard error) of fibre diameter (μm) for each year of birth, flock of origin and type of birth and rearing (Tobr)[A]

		Ram		Ewe				
		10	16	16	28	40	52	64
Year	1989	20.1^{a} (0.14)	21.6^{a} (0.17)	20.9^{a} (0.19)	23.3^{ab} (0.21)	25.0^{a} (0.21)	24.1^{a} (0.24)	24.7^{a} (0.25)
	1990	21.1^{b} (0.10)	23.2^{b} (0.12)	22.7^{b} (0.11)	24.5^{c} (0.12)	24.3^{b} (0.13)	24.9^{b} (0.14)	26.1^{b} (0.15)
	1991	21.0^{b} (0.11)	23.3^{b} (0.13)	21.6^{c} (0.12)	23.7^{a} (0.13)	24.0^{b} (0.14)	25.5^{c} (0.15)	24.5^{a} (0.16)
	1992	21.7^{c} (0.10)	21.6^{a} (0.12)	21.9^{c} (0.11)	23.2^{b} (0.12)	25.1^{a} (0.13)	24.8^{b} (0.14)	ne
Flock	1	21.7^{a} (0.11)	23.2^{a} (0.13)	22.4^{a} (0.12)	24.3^{a} (0.14)	25.2^{a} (0.14)	25.3^{a} (0.15)	25.4^{a} (0.20)
	2	22.0^{b} (0.11)	23.7^{b} (0.13)	23.0^{b} (0.12)	24.9^{b} (0.14)	26.0^{b} (0.14)	26.3^{b} (0.15)	26.5^{b} (0.20)
	3	19.7^{c} (0.12)	21.0^{c} (0.15)	20.4^{c} (0.15)	22.7^{c} (0.17)	23.5^{c} (0.18)	23.7^{c} (0.19)	24.1^{c} (0.27)
	4	20.4^{d} (0.11)	21.8^{d} (0.13)	21.3^{d} (0.12)	22.9^{c} (0.14)	23.7^{c} (0.14)	24.0^{c} (0.15)	24.2^{c} (0.20)
Tobr	11	21.0^{a} (0.06)	22.4 (0.07)	21.8^{a} (0.07)	23.7^{a} (0.08)	24.6 (0.09)	24.8^{a} (0.09)	25.2 (0.11)
	21	21.0^{a} (0.13)	22.5 (0.15)	22.0^{ab} (0.15)	23.8^{ab} (0.16)	24.8 (0.18)	25.1^{ab} (0.19)	25.6 (0.24)
	22	21.3^{b} (0.08)	22.6 (0.10)	22.2^{b} (0.09)	24.0^{b} (0.10)	24.9 (0.11)	25.2^{b} (0.12)	25.5 (0.16)

[A] Within a cell means with no superscript or with a common superscript do not differ significantly ($P > 0.05$) from each other. ne = not estimable

Table B.5 Least squares means (standard error) of staple length (mm) for each year of birth, flock of origin and type of birth and rearing (Tobr)[A]

		Ram		Ewe				
		10	16	16	28	40	52	64
Year	**1989**	55.0^{a} (0.45)	51.5^{a} (0.58)	103.7^{a} (1.10)	105.6^{a} (1.06)	110.9^{a} (1.08)	105.1^{a} (1.18)	108.0^{a} (1.21)
	1990	58.0^{b} (0.33)	69.7^{b} (0.43)	120.9^{b} (0.67)	110.9^{b} (0.64)	107.5^{b} (0.67)	109.5^{b} (0.71)	107.9^{a} (0.75)
	1991	55.9^{a} (0.35)	71.0^{c} (0.44)	115.6^{c} (0.74)	110.6^{b} (0.70)	111.0^{a} (0.70)	109.7^{b} (0.75)	101.4^{b} (0.79)
	1992	58.9^{b} (0.32)	62.5^{d} (0.40)	113.1^{d} (0.67)	109.5^{b} (0.63)	105.4^{b} (0.66)	101.5^{c} (0.71)	ne
Flock	**1**	58.2^{a} (0.40)	64.6^{a} (0.43)	114.7^{a} (0.79)	110.2^{a} (0.75)	110.4^{a} (0.72)	107.1^{a} (0.78)	105.6^{a} (0.96)
	2	59.8^{b} (0.38)	67.0^{b} (0.46)	118.7^{b} (0.75)	114.5^{b} (0.71)	113.9^{b} (0.72)	111.7^{b} (0.77)	111.8^{b} (0.98)
	3	53.6^{c} (0.41)	60.1^{c} (0.50)	110.0^{c} (0.91)	105.3^{c} (0.86)	104.3^{c} (0.90)	103.3^{c} (0.97)	101.0^{c} (1.30)
	4	56.2^{d} (0.36)	63.1^{d} (0.45)	111.5^{c} (0.75)	106.5^{c} (0.71)	106.3^{c} (0.72)	103.7^{c} (0.78)	102.4^{c} (0.97)
Tobr	**11**	57.0 (0.20)	63.7^{a} (0.25)	114.0 (0.42)	109.4 (0.40)	108.7 (0.43)	106.4 (0.46)	105.6^{a} (0.54)
	21	57.3 (0.48)	64.9^{b} (0.56)	113.8 (0.93)	110.4 (0.88)	109.7 (0.96)	107.4 (0.95)	109.2^{b} (1.24)
	22	57.1 (0.29)	64.2^{ab} (0.35)	113.8 (0.55)	109.2 (0.52)	108.5 (0.56)	106.8 (0.58)	106.4^{a} (0.77)

[A] Within a cell means with no superscript or with a common superscript do not differ significantly ($P > 0.05$) from each other. ne = not estimable

Table B.6 Least squares means (standard error) of staple length (mm) for year of birth by flock of origin interaction[A]

		Ram		Ewe				
Year	**Flock**	**10**	**16**	**16**	**28**	**40**	**52**	**64**
1989	1	57.0^{ab} (1.18)	52.4 (0.70)	103.0^{a} (2.21)	104.6^{ab} (2.09)	112.6 (1.23)	105.7 (1.35)	107.0 (1.48)
	2	58.2^{ae} (0.93)	54.8 (0.70)	110.6^{bcd} (1.69)	113.0^{cd} (1.63)	116.1 (1.16)	110.3 (1.26)	113.2 (1.40)
	3	51.6^{c} (0.95)	47.9 (0.70)	ne	ne	ne	ne	ne
	4	53.2^{c} (0.87)	50.9 (0.69)	97.6^{e} (1.81)	99.2^{e} (1.72)	108.5 (1.19)	102.4 (1.30)	103.8 (1.42)
1990	1	59.7^{de} (0.59)	70.6 (0.54)	123.2^{f} (1.24)	112.2^{cd} (1.18)	109.2 (0.88)	110.2 (0.94)	108.2 (1.07)
	2	61.6^{df} (0.70)	73.0 (0.58)	127.9^{g} (1.30)	116.4^{df} (1.24)	112.6 (0.91)	114.7 (0.96)	114.3 (1.13)
	3	52.9^{c} (0.77)	66.1 (0.61)	112.7^{bch} (1.47)	107.3^{agh} (1.41)	103.0 (1.01)	106.3 (1.07)	104.2 (1.37)
	4	58.0^{ae} (0.67)	69.1 (0.56)	119.7^{fi} (1.31)	107.6^{aghi} (1.24)	105.1 (0.90)	106.8 (0.96)	105.0 (1.12)
1991	1	57.6^{abe} (0.62)	71.9 (0.55)	118.1^{ij} (1.26)	112.2^{cd} (1.19)	112.7 (0.88)	110.4 (0.95)	101.7 (1.07)
	2	57.7^{abe} (0.67)	74.3 (0.58)	121.1^{fi} (1.38)	117.3^{f} (1.31)	116.2 (0.92)	114.9 (1.00)	107.8 (1.16)
	3	52.7^{c} (0.87)	67.4 (0.64)	108.1^{d} (1.82)	102.8^{be} (1.73)	106.6 (1.06)	106.5 (1.14)	97.7 (1.44)
	4	55.6^{b} (0.64)	70.4 (0.57)	115.1^{hj} (1.36)	110.1^{cgi} (1.27)	108.6 (0.91)	107.0 (0.99)	98.5 (1.13)
1992	1	58.7^{ae} (0.60)	63.4 (0.54)	114.6^{bhj} (1.27)	111.7^{cd} (1.20)	107.1 (0.89)	102.1 (0.95)	ne
	2	61.9^{f} (0.61)	65.8 (0.55)	115.1^{hj} (1.30)	111.4^{ci} (1.23)	110.6 (0.91)	106.7 (0.98)	ne
	3	57.0^{ab} (0.64)	58.9 (0.58)	109.0^{cd} (1.27)	105.9^{abh} (1.22)	101.0 (0.96)	98.3 (1.04)	ne
	4	58.0^{ae} (0.61)	61.9 (0.56)	113.7^{bh} (1.32)	109.1^{cghi} (1.25)	103.0 (0.91)	98.8 (0.98)	ne

[A] Within a column means with no superscript or with a common superscript do not differ significantly ($P > 0.05$) from each other. ne = not estimable

Table B.7 **Least squares means (standard error) of staple strength (N/ktex) for each year of birth, flock of origin and type of birth and rearing (Tobr)**[A]

		Ram		Ewe				
		10	16	16	28	40	52	64
Year	1989	35.7^{a} (0.81)	39.5^{a} (0.92)	19.8^{a} (0.88)	26.7^{a} (1.02)	30.7^{a} (1.06)	36.4^{a} (1.17)	30.0^{a} (1.16)
	1990	51.3^{b} (0.61)	41.2^{a} (0.66)	27.8^{b} (0.54)	32.1^{b} (0.61)	36.9^{b} (0.67)	31.4^{b} (0.66)	29.6^{a} (0.72)
	1991	41.2^{c} (0.60)	44.9^{b} (0.71)	20.3^{a} (0.57)	28.4^{a} (0.65)	27.1^{c} (0.69)	26.0^{c} (0.69)	26.5^{b} (0.76)
	1992	38.5^{d} (0.54)	52.2^{c} (0.64)	25.9^{c} (0.53)	24.7^{c} (0.61)	28.6^{ac} (0.66)	29.2^{b} (0.66)	ne
Flock	1	41.7 (0.62)	44.5^{a} (0.81)	24.6^{a} (0.58)	28.3 (0.66)	31.2 (0.70)	31.1 (0.70)	29.9 (0.90)
	2	41.8 (0.67)	44.4^{a} (0.76)	23.1^{a} (0.59)	28.0 (0.67)	31.4 (0.72)	31.1 (0.73)	28.8 (0.95)
	3	42.1 (0.70)	42.2^{b} (0.84)	21.3^{b} (0.74)	27.2 (0.85)	29.6 (0.90)	29.7 (0.91)	27.5 (1.28)
	4	41.2 (0.62)	46.7^{c} (0.73)	24.8^{a} (0.59)	28.4 (0.67)	31.2 (0.72)	31.1 (0.73)	27.7 (0.93)
Tobr	11	41.7 (0.35)	44.4 (0.40)	23.4^{a} (0.35)	28.0 (0.40)	30.8^{a} (0.43)	30.7 (0.45)	28.5 (0.53)
	21	41.2 (0.92)	44.5 (0.92)	25.2^{b} (0.82)	28.2 (0.93)	28.8^{b} (1.04)	29.0 (1.12)	28.0 (1.47)
	22	41.4 (0.53)	43.8 (0.57)	23.5^{a} (0.49)	27.5 (0.54)	29.7^{ab} (0.59)	29.6 (0.62)	28.0 (0.88)

[A] Within a cell means with no superscript or with a common superscript do not differ significantly ($P > 0.05$) from each other. ne = not estimable

Table B.8 Least squares means (standard error) of staple strength (N/ktex) for year of birth by flock of origin interaction[A]

		Ram	
Year	**Flock**	**10**	**16**
1989	1	34.8^{a} (1.76)	40.0^{ab} (2.38)
	2	36.0^{abc} (1.48)	38.6^{bc} (1.89)
	3	35.6^{ac} (1.64)	34.7^{c} (1.96)
	4	36.2^{abc} (1.48)	44.5^{de} (1.81)
1990	1	52.5^{d} (0.97)	39.0^{b} (1.20)
	2	52.0^{d} (1.22)	42.6^{abd} (1.38)
	3	53.9^{d} (1.45)	39.1^{b} (1.50)
	4	46.9^{e} (1.16)	44.1^{ade} (1.33)
1991	1	42.2^{f} (1.02)	46.9^{ef} (1.25)
	2	40.3^{fg} (1.13)	43.7^{ade} (1.35)
	3	40.2^{fg} (1.48)	44.6^{de} (1.77)
	4	42.2^{f} (1.08)	44.4^{de} (1.31)
1992	1	37.2^{abcg} (0.99)	52.1^{g} (1.19)
	2	38.8^{bcfg} (1.02)	52.7^{g} (1.22)
	3	38.6^{bcg} (1.08)	50.4^{fg} (1.28)
	4	39.4^{bfg} (1.01)	53.7^{g} (1.24)

[A] Within a column means with no superscript or with a common superscript do not differ significantly ($P > 0.05$) from each other.

Appendix C

C.1 LEAST SQUARES MEANS FOR WEIGHTS AND ADJUSTED FAT AND EYE MUSCLE DEPTH

All means adjusted to single born, single raised, ram lambs, from 3 year old dams.

Table C.1 Least squares means (standard error) for live weight (kg) at all ages for years and flocks[A]

	Year		Flock				
	2000	2001	Control	MPR	PCA	EWF	FM+
Birth	5.7 (0.06)	5.6 (0.05)	5.5^a (0.07)	5.7^{ab} (0.09)	5.7^b (0.09)	5.6^{ab} (0.08)	5.8^b (0.09)
Weaning	31.5^a (0.25)	28.7^b (0.23)	27.3^a (0.27)	31.3^b (0.33)	28.0^{ac} (0.33)	28.3^{cd} (0.32)	29.1^d (0.34)
4 months	33.5 (0.25)	33.1 (0.24)	30.7^a (0.28)	33.5^b (0.33)	31.2^{ac} (0.33)	31.8^{cd} (0.32)	32.1^d (0.34)
5 months	34.3^a (0.31)	36.1^b (0.29)	33.0^a (0.34)	34.3^{bc} (0.42)	32.7^a (0.42)	33.4^{ac} (0.40)	34.7^b (0.42)
7 months	36.1^a (0.29)	31.3^b (0.28)	31.0^a (0.34)	31.7^a (0.41)	30.8^a (0.40)	31.0^a (0.39)	34.3^b (0.41)
8 months	40.3^a (0.34)	38.5^b (0.32)	36.4^a (0.40)	37.2^a (0.50)	36.7^a (0.50)	36.7^a (0.47)	39.9^b (0.50)
10 months	47.1^a (0.36)	45.6^b (0.35)	44.5^a (0.39)	45.1^a (0.48)	44.6^a (0.48)	44.3^a (0.46)	47.6^b (0.48)
13 months	56.6^a (0.36)	52.9^b (0.35)	52.5^a (0.42)	53.1^a (0.51)	53.0^a (0.51)	52.5^a (0.49)	56.0^b (0.52)
16 months	67.8^a (0.42)	62.3^b (0.40)	62.8^a (0.48)	63.8^a (0.58)	63.7^a (0.58)	63.4^a (0.56)	66.8^b (0.59)

[A] Within a cell means with no superscript or with a common superscript do not differ significantly ($P > 0.05$) from each other. Control = Control flock, MPR = Measured performance records flock, PCA = Professional classer assessment flock, EWF = Elite wool flock, FM+ = Fibre meat plus flock

Table C.2 **Least squares means (standard error) for live weight (kg) at all ages for sex and type of birth and rearing**[A]

	Sex		Type of birth and rearing		
	Female	Male	11	21	22
Birth	5.3^{a} (0.04)	5.7^{b} (0.04)	5.7^{a} (0.04)	4.7^{b} (0.07)	4.8^{b} (0.05)
Weaning	26.3^{a} (0.19)	28.8^{b} (0.18)	28.8^{a} (0.18)	27.0^{b} (0.31)	24.9^{c} (0.19)
4 months	28.8^{a} (0.20)	31.9^{b} (0.19)	31.9^{a} (0.19)	30.2^{b} (0.33)	28.3^{c} (0.20)
5 months	29.9^{a} (0.24)	33.6^{b} (0.23)	33.6^{a} (0.23)	32.2^{b} (0.38)	30.8^{c} (0.24)
7 months	30.2^{a} (0.24)	31.8^{b} (0.23)	31.8^{a} (0.23)	30.5^{b} (0.39)	29.5^{c} (0.24)
8 months	32.6^{a} (0.29)	37.4^{b} (0.28)	37.4^{a} (0.28)	35.8^{b} (0.45)	35.0^{c} (0.29)
10 months	38.3^{a} (0.27)	45.2^{b} (0.27)	45.2^{a} (0.27)	43.6^{b} (0.46)	43.2^{b} (0.28)
13 months	41.7^{a} (0.30)	53.4^{b} (0.29)	53.4^{a} (0.29)	52.3^{b} (0.48)	51.6^{b} (0.30)
16 months	53.7^{a} (0.33)	64.1^{b} (0.33)	64.1^{a} (0.33)	63.3^{ab} (0.56)	62.3^{b} (0.35)

[A] Within a cell means with no superscript or with a common superscript do not differ significantly ($P > 0.05$) from each other.

Table C.3 Least squares means (standard error) of live weight (kg) for significant interactions^{A}

Year	Flock	BW	WW	WT4	WT5	WT7	WT8	WT10	WT13	WT16
2000	Control	5.5^{ab} (0.09)	31.0^{a} (0.36)	33.6^{abc} (0.38)	34.9^{abc} (0.45)	36.5^{a} (0.44)	40.4^{ab} (0.51)	47.8^{a} (0.53)	57.1^{a} (0.55)	67.9^{a} (0.64)
	MPR	5.7^{ab} (0.11)	32.5^{b} (0.45)	33.8^{ab} (0.44)	34.2^{bcd} (0.57)	35.7^{ab} (0.54)	40.0^{abc} (0.67)	46.9^{ab} (0.66)	56.5^{a} (0.68)	67.8^{ab} (0.78)
	PCA	5.7^{a} (0.10)	30.7^{a} (0.41)	32.7^{bc} (0.41)	33.1^{d} (0.52)	34.6^{bc} (0.49)	39.1^{bcd} (0.60)	46.0^{bc} (0.60)	55.8^{ab} (0.62)	67.1^{abc} (0.72)
	EWF	5.6^{ab} (0.11)	30.8^{a} (0.44)	33.5^{abc} (0.44)	33.8^{cd} (0.55)	34.6^{bc} (0.53)	39.0^{bcd} (0.63)	45.2^{c} (0.63)	54.8^{b} (0.66)	66.0^{bc} (0.76)
	FM+	6.1^{c} (0.11)	32.6^{b} (0.44)	34.0^{a} (0.45)	35.6^{abe} (0.55)	39.1^{d} (0.53)	42.9^{e} (0.64)	49.5^{d} (0.64)	59.0^{c} (0.66)	70.1^{d} (0.77)
2001	Control	5.5^{b} (0.08)	26.2^{c} (0.34)	30.7^{d} (0.35)	34.2^{bcd} (0.42)	29.4^{e} (0.41)	36.5^{f} (0.48)	43.4^{e} (0.49)	50.7^{d} (0.51)	59.6^{e} (0.60)
	MPR	5.6^{ab} (0.11)	32.6^{b} (0.45)	36.2^{e} (0.44)	37.6^{f} (0.57)	31.6^{f} (0.54)	38.4^{cd} (0.67)	45.6^{bc} (0.65)	52.5^{e} (0.68)	61.7^{f} (0.78)
	PCA	5.7^{ab} (0.10)	27.8^{d} (0.41)	32.5^{c} (0.41)	35.5^{ab} (0.51)	30.8^{f} (0.49)	38.4^{d} (0.59)	45.4^{bc} (0.59)	52.8^{e} (0.61)	62.2^{f} (0.71)
	EWF	5.7^{ab} (0.11)	28.4^{d} (0.42)	33.0^{abc} (0.42)	36.0^{ae} (0.53)	31.3^{f} (0.51)	38.4^{d} (0.62)	45.7^{bc} (0.61)	52.9^{e} (0.63)	62.7^{f} (0.73)
	FM+	5.6^{ab} (0.11)	28.2^{d} (0.44)	33.1^{abc} (0.45)	37.0^{ef} (0.56)	33.3^{c} (0.53)	40.8^{a} (0.64)	48.0^{ad} (0.64)	55.8^{ab} (0.67)	65.3^{c} (0.77)
	Tobr									
2000	11	5.7^{a} (0.06)	31.5^{a} (0.25)	33.5^{a} (0.25)	34.3^{a} (0.31)			47.1^{a} (0.36)		
	21	4.8^{bc} (0.09)	30.4^{b} (0.43)	32.4^{b} (0.46)	33.9^{a} (0.54)			46.0^{ab} (0.65)		
	22	4.9^{b} (0.06)	27.7^{c} (0.26)	30.2^{c} (0.27)	31.9^{b} (0.32)			45.2^{b} (0.38)		
2001	11	5.6^{a} (0.05)	28.7^{d} (0.23)	33.1^{ab} (0.24)	36.1^{c} (0.29)			45.6^{b} (0.35)		
	21	4.7^{c} (0.09)	26.3^{e} (0.41)	31.0^{c} (0.44)	33.9^{a} (0.51)			43.7^{c} (0.62)		
	22	4.7^{c} (0.06)	24.2^{f} (0.26)	28.9^{d} (0.27)	32.5^{b} (0.32)			43.1^{c} (0.37)		
	Sex									
2000	Male			33.5^{a} (0.25)	34.3^{a} (0.31)		40.3^{a} (0.34)		56.6^{a} (0.36)	
	Female			31.3^{b} (0.26)	30.7^{b} (0.32)		34.8^{b} (0.35)		45.0^{b} (0.37)	
2001	Male			33.1^{a} (0.24)	36.1^{c} (0.29)		38.5^{c} (0.32)		52.9^{c} (0.35)	
	Female			28.7^{c} (0.24)	31.8^{d} (0.29)		33.6^{d} (0.32)		40.6^{d} (0.34)	

[A] Within a cell means with no superscript or with a common superscript do not differ significantly ($P > 0.05$) from each other, Tobr = type of birth and rearing: 11 = single raised as single, 21 = multiple raised as single, 22 = multiple raised as multiple.

Table C.4 Least squares means (standard error) for adjusted fat depth (mm) at all ages for years and flocks[A]

	Year		Flock				
	2000	2001	Control	MPR	PCA	EWF	FM+
4 months	1.9^{a} (0.03)	1.5^{b} (0.03)	1.8 (0.04)	1.6 (0.05)	1.7 (0.05)	1.7 (0.05)	1.7 (0.05)
5 months	1.3^{a} (0.03)	1.2^{b} (0.03)	1.3^{a} (0.04)	1.1^{b} (0.04)	1.1^{b} (0.04)	1.2^{a} (0.04)	1.1^{b} (0.04)
7 months	1.1 (0.03)	1.0 (0.03)	1.2^{a} (0.03)	1.0^{b} (0.04)	1.1^{b} (0.04)	1.1^{b} (0.04)	1.1^{b} (0.04)
8 months	1.1^{a} (0.03)	1.6^{b} (0.03)	1.5^{a} (0.03)	1.3^{b} (0.04)	1.4^{bc} (0.04)	1.4^{ac} (0.04)	1.4^{abc} (0.04)
10 months	1.9^{a} (0.04)	2.1^{b} (0.03)	2.2^{a} (0.04)	1.9^{b} (0.05)	2.0^{b} (0.05)	2.0^{b} (0.05)	2.0^{b} (0.05)
13 months	1.7^{a} (0.04)	2.8^{b} (0.03)	2.4^{a} (0.04)	2.2^{b} (0.05)	2.2^{b} (0.05)	2.2^{b} (0.05)	2.2^{b} (0.05)
16 months	2.0^{a} (0.04)	3.3^{b} (0.04)	2.7^{a} (0.04)	2.6^{b} (0.06)	2.5^{b} (0.06)	2.6^{b} (0.05)	2.6^{b} (0.06)

[A] Within a cell means with no superscript or with a common superscript do not differ significantly ($P > 0.05$) from each other. Control = Control flock, MPR = Measured performance records flock, PCA = Professional classer assessment flock, EWF = Elite wool flock, FM+ = Fibre meat plus flock

Table C.5 Least squares means (standard error) for adjusted fat depth (mm) at all ages for sex and type of birth and rearing[A]

	Sex		Type of birth and rearing		
	Female	Male	11	21	22
4 months	2.1^{a} (0.03)	1.7^{b} (0.02)	1.7 (0.02)	1.6 (0.04)	1.6 (0.03)
5 months	1.5^{a} (0.03)	1.2^{b} (0.03)	1.2 (0.03)	1.2 (0.04)	1.2 (0.03)
7 months	1.2^{a} (0.02)	1.1^{b} (0.02)	1.1 (0.02)	1.1 (0.04)	1.1 (0.02)
8 months	1.6^{a} (0.03)	1.4^{b} (0.02)	1.4^{a} (0.02)	1.5^{b} (0.04)	1.5^{b} (0.03)
10 months	2.4^{a} (0.03)	2.0^{b} (0.03)	2.0^{a} (0.03)	2.1^{a} (0.04)	2.2^{b} (0.03)
13 months	2.9^{a} (0.03)	2.2^{b} (0.03)	2.2 (0.03)	2.3 (0.04)	2.3 (0.03)
16 months	3.5^{a} (0.03)	2.6^{b} (0.03)	2.6^{a} (0.03)	2.7^{ab} (0.04)	2.7^{b} (0.03)

[A] Within a cell means with no superscript or with a common superscript do not differ significantly ($P > 0.05$) from each other.

Table C.6 Least squares means (standard error) of adjusted fat depth (mm) for significant interactions[A]

Year	Flock	FAT4	FAT5	FAT7	FAT8	FAT10	FAT13	FAT16
2000	Control				1.2^{a} (0.05)	2.1^{ab} (0.05)	1.8^{a} (0.05)	2.2^{a} (0.06)
	MPR				1.0^{b} (0.06)	1.8^{c} (0.07)	1.6^{b} (0.07)	1.9^{b} (0.08)
	PCA				1.1^{ac} (0.05)	1.9^{bd} (0.06)	1.7^{b} (0.06)	1.9^{b} (0.07)
	EWF				1.1^{ac} (0.06)	1.8^{cd} (0.06)	1.7^{ab} (0.07)	1.9^{b} (0.07)
	FM+				1.0^{bc} (0.06)	1.8^{cd} (0.06)	1.5^{b} (0.07)	1.8^{b} (0.07)
2001	Control				1.6^{d} (0.04)	2.2^{a} (0.05)	2.9^{c} (0.05)	3.3^{c} (0.05)
	MPR				1.5^{e} (0.06)	2.1^{ab} (0.07)	2.7^{de} (0.07)	3.2^{c} (0.08)
	PCA				1.5^{e} (0.05)	2.0^{b} (0.06)	2.7^{e} (0.06)	3.2^{c} (0.07)
	EWF				1.6^{de} (0.05)	2.1^{ab} (0.06)	2.8^{cde} (0.06)	3.3^{c} (0.07)
	FM+				1.7^{d} (0.06)	2.2^{a} (0.06)	2.9^{cd} (0.07)	3.3^{c} (0.07)
	Tobr							
2000	11	1.9^{a} (0.03)	1.3^{ab} (0.03)				1.7^{a} (0.04)	
	21	1.8^{b} (0.05)	1.3^{a} (0.05)				1.6^{a} (0.06)	
	22	1.7^{b} (0.03)	1.2^{b} (0.03)				1.8^{b} (0.04)	
2001	11	1.5^{c} (0.03)	1.2^{b} (0.03)				2.8^{c} (0.03)	
	21	1.5^{c} (0.05)	1.2^{ab} (0.04)				2.9^{c} (0.06)	
	22	1.6^{c} (0.03)	1.2^{ab} (0.03)				2.9^{c} (0.04)	
	Sex							
2000	Male		1.3^{a} (0.03)		1.1^{a} (0.03)	1.9^{a} (0.04)		2.0^{a} (0.04)
	Female		1.6^{b} (0.03)		1.4^{b} (0.03)	2.2^{b} (0.04)		2.8^{b} (0.04)
2001	Male		1.2^{c} (0.03)		1.6^{c} (0.03)	2.1^{c} (0.03)		3.3^{c} (0.04)
	Female		1.7^{d} (0.03)		1.8^{d} (0.03)	2.6^{d} (0.03)		4.3^{d} (0.04)

[A] Within a cell means with no superscript or with a common superscript do not differ significantly ($P > 0.05$) from each other, Tobr = type of birth and rearing: 11 = single raised as single, 21 = multiple raised as single, 22 = multiple raised as multiple.

Table C.7 Least squares means (standard error) for adjusted eye muscle depth (mm) at all ages for years and flocks[A]

	Year		Flock				
	2000	2001	Control	MPR	PCA	EWF	FM+
4 months	20.8^{a}	18.3^{b}	20.0^{a}	19.5^{b}	19.1^{c}	19.4^{bc}	19.5^{bc}
	(0.11)	(0.11)	(0.12)	(0.17)	(0.17)	(0.15)	(0.16)
5 months	18.6^{a}	18.4^{b}	18.9^{a}	18.1^{b}	18.0^{b}	18.2^{b}	18.4^{c}
	(0.11)	(0.11)	(0.15)	(0.17)	(0.17)	(0.17)	(0.17)
7 months	15.9^{a}	17.1^{b}	17.1^{a}	16.1^{b}	16.3^{b}	16.2^{b}	16.5^{b}
	(0.15)	(0.14)	(0.16)	(0.23)	(0.22)	(0.21)	(0.21)
8 months	19.9^{a}	20.2^{b}	20.6^{a}	19.6^{b}	19.9^{bc}	19.9^{bc}	20.2^{ac}
	(0.13)	(0.12)	(0.15)	(0.20)	(0.20)	(0.19)	(0.20)
10 months	22.9^{a}	22.4^{b}	23.2^{a}	22.5^{b}	22.5^{b}	22.4^{b}	22.8^{ab}
	(0.13)	(0.12)	(0.14)	(0.20)	(0.20)	(0.18)	(0.19)
13 months	23.7^{a}	23.3^{b}	24.1^{a}	23.3^{b}	23.4^{b}	23.2^{b}	23.4^{b}
	(0.14)	(0.12)	(0.14)	(0.19)	(0.19)	(0.18)	(0.19)
16 months	25.7^{a}	25.3^{b}	26.0^{a}	25.4^{b}	25.3^{b}	25.2^{b}	25.6^{b}
	(0.14)	(0.12)	(0.15)	(0.20)	(0.20)	(0.18)	(0.19)

[A] Within a cell means with no superscript or with a common superscript do not differ significantly ($P > 0.05$) from each other. Control = Control flock, MPR = Measured performance records flock, PCA = Professional classer assessment flock, EWF = Elite wool flock, FM+ = Fibre meat plus flock

Table C.8 Least squares means (standard error) for adjusted eye muscle depth (mm) at all ages for sex and type of birth and rearing[A]

	Sex		Type of birth and rearing		
	Female	Male	11	21	22
4 months	19.6^{a}	20.1^{b}	19.5	19.6	19.4
	(0.09)	(0.09)	(0.09)	(0.13)	(0.09)
5 months	18.0^{a}	18.7^{b}	18.3	18.4	18.4
	(0.12)	(0.12)	(0.11)	(0.15)	(0.12)
7 months	16.8	16.7	16.4^{a}	16.8^{b}	16.9^{b}
	(0.12)	(0.12)	(0.12)	(0.17)	(0.12)
8 months	19.4^{a}	21.0^{b}	20.1^{a}	20.5^{b}	20.5^{b}
	(0.11)	(0.11)	(0.11)	(0.16)	(0.11)
10 months	22.4^{a}	23.6^{b}	22.7^{a}	23.3^{b}	23.1^{c}
	(0.10)	(0.10)	(0.10)	(0.15)	(0.10)
13 months	23.2^{a}	24.7^{b}	23.5^{a}	23.9^{b}	23.6^{ab}
	(0.10)	(0.10)	(0.11)	(0.15)	(0.11)
16 months	25.9^{a}	26.5^{b}	25.5^{a}	25.7^{ab}	25.8^{b}
	(0.10)	(0.10)	(0.11)	(0.16)	(0.11)

[A] Within a cell means with no superscript or with a common superscript do not differ significantly ($P > 0.05$) from each other.

Table C.9 Least squares means (standard error) of eye muscle depth (mm) for significant interactions[A]

Year	Flock	EMD4	EMD5	EMD7	EMD8	EMD10	EMD13	EMD16
2000	Control		19.0^{ab} (0.17)	16.5^{ab} (0.22)	20.5^{abc} (0.20)		24.6^{a} (0.20)	26.6^{a} (0.20)
	MPR		18.6^{abcd} (0.22)	15.9^{bcd} (0.31)	19.7^{de} (0.28)		23.7^{b} (0.26)	25.9^{b} (0.28)
	PCA		18.3^{cdef} (0.19)	15.8^{cd} (0.26)	19.7^{de} (0.23)		23.6^{b} (0.23)	25.5^{bcd} (0.24)
	EWF		18.5^{bcde} (0.21)	15.8^{bcd} (0.27)	19.9^{cde} (0.25)		23.3^{bc} (0.24)	25.2^{cd} (0.25)
	FM+		18.4^{cde} (0.20)	15.5^{d} (0.28)	19.6^{de} (0.25)		23.3^{bc} (0.24)	25.4^{bcd} (0.25)
2001	Control		19.0^{a} (0.15)	17.8^{e} (0.20)	20.7^{ab} (0.18)		23.7^{b} (0.17)	25.6^{bcd} (0.18)
	MPR		17.8^{f} (0.22)	16.4^{abc} (0.31)	19.4^{e} (0.27)		23.0^{c} (0.25)	25.0^{d} (0.27)
	PCA		18.0^{ef} (0.19)	17.0^{af} (0.26)	20.1^{bcd} (0.23)		23.2^{bc} (0.22)	25.1^{d} (0.23)
	EWF		18.2^{def} (0.20)	16.8^{a} (0.27)	19.9^{cde} (0.25)		23.1^{bc} (0.23)	25.3^{cd} (0.25)
	FM+		18.7^{abc} (0.20)	17.6^{ef} (0.27)	20.8^{a} (0.26)		23.6^{bc} (0.24)	25.8^{bc} (0.25)
	Tobr							
2000	11	20.8^{a} (0.11)						
	21	20.7^{a} (0.19)						
	22	20.5^{a} (0.11)						
2001	11	18.3^{b} (0.11)						
	21	18.7^{c} (0.18)						
	22	18.5^{bc} (0.11)						
	Sex							
2000	Male		18.9^{a} (0.11)			23.8^{a} (0.13)	25.0^{a} (0.12)	
	Female		18.7^{b} (0.11)			21.9^{b} (0.13)	23.7^{b} (0.13)	
2001	Male		18.8^{ab} (0.10)			23.3^{c} (0.12)	24.6^{c} (0.12)	
	Female		18.4^{c} (0.10)			22.9^{d} (0.12)	22.7^{d} (0.11)	

[A] Within a cell means with no superscript or with a common superscript do not differ significantly (P > 0.05) from each other, Tobr = type of birth and rearing: 11 = single raised as single, 21 = multiple raised as single, 22 = multiple raised as multiple.

C.2 PHENOTYPIC AND GENETIC CORRELATIONS FOR UNADJUSTED FAT AND EYE MUSCLE DEPTH (MODEL 1)

Table C.10 Phenotypic (above diagonal) and genetic (below diagonal) correlations (standard error) between unadjusted fat depth at different ages

	FAT4	FAT5	FAT7	FAT8	FAT10	FAT13	FAT16
FAT4		0.46 (0.021)	0.35 (0.023)	0.27 (0.025)	0.25 (0.025)	0.22 (0.026)	0.25 (0.026)
FAT5	0.91 (0.068)		0.35 (0.023)	0.33 (0.024)	0.29 (0.024)	0.33 (0.024)	0.29 (0.025)
FAT7	0.58 (0.113)	0.68 (0.127)		0.51 (0.019)	0.38 (0.022)	0.33 (0.024)	0.30 (0.021)
FAT8	0.64 (0.111)	0.87 (0.098)	0.89 (0.073)		0.45 (0.021)	0.42 (0.022)	0.35 (0.020)
FAT10	0.69 (0.095)	0.85 (0.096)	0.83 (0.092)	1.03 (0.045)		0.46 (0.021)	0.39 (0.022)
FAT13	0.41 (0.118)	0.73 (0.102)	0.77 (0.105)	0.97 (0.059)	0.98 (0.049)		0.47 (0.021)
FAT16	0.48 (0.113)	0.58 (0.128)	0.59 (0.000)	0.89 (0.000)	0.91 (0.074)	0.93 (0.059)	

Table C.11 Phenotypic (above diagonal) and genetic (below diagonal) correlations (standard error) between unadjusted eye muscle depth at different ages

	EMD4	EMD5	EMD7	EMD8	EMD10	EMD13	EMD16
EMD4		0.66 (0.015)	0.52 (0.020)	0.47 (0.021)	0.46 (0.022)	0.44 (0.022)	0.39 (0.023)
EMD5	0.92 (0.035)		0.61 (0.017)	0.55 (0.019)	0.52 (0.020)	0.37 (0.024)	0.45 (0.021)
EMD7	0.82 (0.061)	0.94 (0.039)		0.72 (0.013)	0.64 (0.016)	0.44 (0.022)	0.39 (0.023)
EMD8	0.78 (0.068)	0.88 (0.053)	0.94 (0.029)		0.70 (0.014)	0.62 (0.016)	0.55 (0.019)
EMD10	0.84 (0.061)	0.91 (0.049)	0.94 (0.037)	0.98 (0.024)		0.67 (0.014)	0.60 (0.017)
EMD13	0.78 (0.080)	0.57 (0.108)	0.78 (0.080)	0.93 (0.045)	0.96 (0.035)		0.66 (0.015)
EMD16	0.79 (0.086)	0.75 (0.087)	0.79 (0.086)	0.84 (0.072)	0.97 (0.043)	0.93 (0.043)	

C.3 PHENOTYPIC CORRELATIONS BETWEEN WEIGHT, ADJUSTED FAT AND EYE MUSCLE DEPTH (MODEL 2)

Table C.12 Phenotypic correlations (standard error) between live weight and adjusted fat depth

	BW	WW	WT4	WT5	WT7	WT8	WT10	WT13	WT16
FAT4	-0.19 (0.027)	0.10 (0.030)	0.35 (0.029)	0.24 (0.029)	-0.10 (0.029)	-0.10 (0.029)	-0.11 (0.028)	-0.12 (0.028)	-0.14 (0.027)
FAT5	-0.15 (0.026)	0.02 (0.030)	0.26 (0.029)	0.27 (0.032)	0.02 (0.030)	0.01 (0.030)	-0.05 (0.029)	-0.04 (0.029)	-0.08 (0.028)
FAT7	-0.23 (0.027)	-0.22 (0.029)	-0.24 (0.028)	-0.23 (0.029)	0.15 (0.034)	0.16 (0.032)	-0.13 (0.030)	-0.11 (0.029)	-0.11 (0.029)
FAT8	-0.28 (0.027)	-0.36 (0.026)	-0.36 (0.026)	-0.34 (0.026)	0.12 (0.032)	0.23 (0.033)	-0.15 (0.031)	-0.11 (0.031)	-0.13 (0.029)
FAT10	-0.30 (0.026)	-0.28 (0.027)	-0.32 (0.026)	-0.32 (0.026)	-0.28 (0.028)	-0.24 (0.030)	0.30 (0.032)	0.23 (0.030)	-0.18 (0.030)
FAT13	-0.25 (0.028)	-0.24 (0.028)	-0.22 (0.028)	-0.16 (0.029)	-0.11 (0.030)	-0.07 (0.031)	0.35 (0.028)	0.42 (0.028)	0.05 (0.033)
FAT16	-0.19 (0.028)	-0.12 (0.029)	-0.15 (0.029)	-0.14 (0.030)	-0.09 (0.030)	-0.08 (0.031)	-0.02 (0.032)	0.00 (0.033)	0.13 (0.035)

Table C.13 Phenotypic correlations (standard error) between live weight and adjusted eye muscle depth

	BW	WW	WT4	WT5	WT7	WT8	WT10	WT13	WT16
EMD4	-0.19 (0.026)	0.26 (0.029)	0.72 (0.015)	0.62 (0.017)	0.09 (0.030)	0.08 (0.029)	0.01 (0.029)	-0.01 (0.028)	-0.06 (0.028)
EMD5	-0.11 (0.028)	0.18 (0.030)	0.50 (0.023)	0.51 (0.024)	0.12 (0.030)	0.12 (0.030)	0.28 (0.030)	0.02 (0.030)	-0.02 (0.029)
EMD7	-0.24 (0.027)	-0.11 (0.030)	-0.06 (0.031)	-0.03 (0.031)	0.46 (0.026)	0.46 (0.025)	0.13 (0.030)	0.12 (0.030)	0.05 (0.030)
EMD8	-0.26 (0.026)	-0.20 (0.028)	-0.20 (0.028)	-0.17 (0.029)	0.08 (0.032)	0.12 (0.034)	0.10 (0.031)	0.10 (0.030)	0.04 (0.030)
EMD10	-0.20 (0.028)	-0.12 (0.029)	-0.09 (0.029)	-0.07 (0.030)	0.07 (0.031)	0.11 (0.032)	0.06 (0.035)	0.08 (0.033)	0.09 (0.031)
EMD13	-0.18 (0.027)	-0.04 (0.029)	-0.03 (0.029)	-0.02 (0.030)	0.08 (0.030)	0.09 (0.031)	0.31 (0.029)	0.32 (0.030)	0.79 (0.010)
EMD16	-0.21 (0.027)	-0.05 (0.029)	-0.06 (0.029)	-0.05 (0.030)	0.04 (0.030)	0.05 (0.030)	0.09 (0.031)	0.13 (0.031)	0.58 (0.022)

Table C.14 Phenotypic correlations (standard error) between adjusted fat depth and adjusted eye muscle depth

	EMD4	EMD5	EMD7	EMD8	EMD10	EMD13	EMD16
FAT4	0.40 (0.022)	0.25 (0.025)	0.25 (0.026)	0.20 (0.026)	0.23 (0.026)	0.17 (0.027)	0.21 (0.026)
FAT5	0.28 (0.025)	0.37 (0.022)	0.24 (0.025)	0.21 (0.026)	0.18 (0.026)	0.19 (0.026)	0.19 (0.026)
FAT7	0.21 (0.025)	0.21 (0.026)	0.40 (0.022)	0.30 (0.024)	0.25 (0.025)	0.19 (0.026)	0.24 (0.025)
FAT8	0.17 (0.026)	0.18 (0.026)	0.28 (0.025)	0.34 (0.023)	0.25 (0.025)	0.17 (0.026)	0.24 (0.025)
FAT10	0.21 (0.025)	0.21 (0.026)	0.27 (0.025)	0.27 (0.025)	0.37 (0.023)	0.26 (0.025)	0.25 (0.025)
FAT13	0.20 (0.026)	0.17 (0.027)	0.23 (0.026)	0.23 (0.026)	0.24 (0.026)	0.28 (0.025)	0.25 (0.026)
FAT16	0.17 (0.026)	0.14 (0.027)	0.22 (0.026)	0.18 (0.027)	0.19 (0.027)	0.24 (0.026)	0.33 (0.024)

Table C.15 Heritabilities (on diagonal), phenotypic correlations (above diagonal) and genetic correlations (below diagonal) (standard error) between live weight, unadjusted fat and eye muscle depth (Model 1)

	Bw	Ww	Wt4	Wt5	Wt7	Wt8	Wt10	Wt13	Wt16	Fat4	Fat5	Fat7	Fat8	Fat10	Fat13	Fat16	Emd4	Emd5	Emd7	Emd8	Emd10	Emd13	Emd16
Bw	**0.34** **(0.088)**	0.37 (0.024)	0.36 (0.023)	0.30 (0.024)	0.27 (0.026)	0.24 (0.026)	0.27 (0.026)	0.25 (0.026)	0.26 (0.025)	-0.05 (0.027)	-0.02 (0.026)	-0.05 (0.027)	-0.08 (0.027)	-0.12 (0.027)	-0.11 (0.028)	-0.08 (0.028)	0.09 (0.028)	0.10 (0.029)	0.03 (0.029)	0.01 (0.029)	0.03 (0.029)	0.00 (0.028)	-0.01 (0.028)
Ww	0.24 (0.194)	**0.26** **(0.074)**	0.87 (0.006)	0.76 (0.011)	0.68 (0.015)	0.64 (0.016)	0.61 (0.017)	0.57 (0.018)	0.58 (0.172)	0.41 (0.022)	0.32 (0.024)	0.20 (0.025)	0.12 (0.026)	0.09 (0.026)	0.06 (0.027)	0.10 (0.028)	0.62 (0.017)	0.56 (0.019)	0.41 (0.023)	0.37 (0.024)	0.34 (0.024)	0.32 (0.024)	0.30 (0.024)
Wt4	0.26 (0.225)	0.83 (0.078)	**0.20** **(0.067)**	0.81 (0.009)	0.72 (0.013)	0.69 (0.014)	0.64 (0.015)	0.61 (0.016)	0.60 (0.017)	0.45 (0.021)	0.36 (0.023)	0.22 (0.025)	0.17 (0.025)	0.10 (0.026)	0.08 (0.026)	0.12 (0.027)	0.67 (0.015)	0.61 (0.017)	0.45 (0.022)	0.42 (0.022)	0.37 (0.023)	0.34 (0.023)	0.33 (0.024)
Wt5	0.33 (0.192)	0.71 (0.115)	0.86 (0.071)	**0.28** **(0.076)**	0.78 (0.010)	0.75 (0.012)	0.70 (0.013)	0.68 (0.014)	0.65 (0.015)	0.32 (0.024)	0.40 (0.022)	0.27 (0.024)	0.23 (0.025)	0.14 (0.026)	0.17 (0.026)	0.15 (0.027)	0.59 (0.018)	0.66 (0.015)	0.52 (0.020)	0.48 (0.021)	0.43 (0.022)	0.40 (0.023)	0.37 (0.023)
Wt7	0.11 (0.211)	0.41 (0.186)	0.62 (0.152)	0.82 (0.077)	**0.24** **(0.072)**	0.86 (0.007)	0.78 (0.010)	0.74 (0.012)	0.69 (0.014)	0.26 (0.025)	0.32 (0.024)	0.44 (0.021)	0.35 (0.023)	0.21 (0.025)	0.21 (0.025)	0.19 (0.027)	0.52 (0.020)	0.56 (0.019)	0.69 (0.014)	0.61 (0.017)	0.52 (0.020)	0.46 (0.021)	0.43 (0.022)
Wt8	0.14 (0.208)	0.48 (0.172)	0.69 (0.130)	0.86 (0.068)	1.00 (0.018)	**0.26** **(0.076)**	0.85 (0.007)	0.80 (0.009)	0.74 (0.012)	0.24 (0.025)	0.30 (0.024)	0.41 (0.022)	0.49 (0.020)	0.29 (0.024)	0.27 (0.024)	0.22 (0.026)	0.49 (0.021)	0.53 (0.020)	0.65 (0.016)	0.73 (0.013)	0.59 (0.018)	0.50 (0.020)	0.46 (0.021)
Wt10	0.08 (0.217)	0.51 (0.173)	0.63 (0.154)	0.77 (0.099)	0.92 (0.052)	0.92 (0.043)	**0.24** **(0.073)**	0.86 (0.007)	0.79 (0.010)	0.21 (0.026)	0.25 (0.025)	0.30 (0.024)	0.36 (0.023)	0.40 (0.022)	0.29 (0.024)	0.24 (0.026)	0.42 (0.023)	0.48 (0.021)	0.56 (0.019)	0.62 (0.017)	0.65 (0.016)	0.54 (0.019)	0.47 (0.021)
Wt13	0.00 (0.222)	0.50 (0.179)	0.56 (0.176)	0.76 (0.106)	0.93 (0.061)	0.91 (0.058)	0.95 (0.033)	**0.20** **(0.068)**	0.88 (0.006)	0.18 (0.026)	0.25 (0.025)	0.30 (0.024)	0.36 (0.023)	0.32 (0.023)	0.35 (0.023)	0.29 (0.025)	0.39 (0.023)	0.46 (0.022)	0.53 (0.020)	0.59 (0.018)	0.59 (0.018)	0.60 (0.017)	0.55 (0.019)
Wt16	0.29 (0.217)	0.58 (0.172)	0.67 (0.152)	0.80 (0.103)	0.78 (0.111)	0.82 (0.090)	0.83 (0.087)	0.82 (0.087)	**0.18** **(0.064)**	0.15 (0.026)	0.19 (0.026)	0.25 (0.025)	0.28 (0.024)	0.24 (0.025)	0.28 (0.024)	0.33 (0.024)	0.34 (0.024)	0.41 (0.023)	0.46 (0.022)	0.51 (0.020)	0.51 (0.020)	0.54 (0.019)	0.59 (0.018)
Fat4	-0.55 (0.141)	0.33 (0.135)	0.34 (0.149)	0.05 (0.159)	0.11 (0.167)	0.13 (0.159)	0.01 (0.169)	-0.03 (0.179)	-0.29 (0.216)	**0.43** **(0.068)**	0.46 (0.021)	0.35 (0.023)	0.27 (0.025)	0.25 (0.025)	0.22 (0.026)	0.25 (0.026)	0.57 (0.018)	0.39 (0.024)	0.32 (0.025)	0.27 (0.026)	0.27 (0.026)	0.23 (0.026)	0.24 (0.026)
Fat5	-0.30 (0.194)	0.37 (0.166)	0.41 (0.175)	0.34 (0.164)	0.40 (0.169)	0.43 (0.160)	0.28 (0.182)	0.33 (0.183)	0.05 (0.238)	0.91 (0.068)	**0.23** **(0.058)**	0.35 (0.023)	0.33 (0.024)	0.29 (0.024)	0.33 (0.024)	0.29 (0.025)	0.43 (0.022)	0.50 (0.020)	0.38 (0.023)	0.32 (0.024)	0.29 (0.025)	0.30 (0.025)	0.26 (0.025)
Fat7	-0.25 (0.165)	0.02 (0.189)	0.21 (0.201)	0.28 (0.166)	0.50 (0.144)	0.51 (0.142)	0.35 (0.164)	0.37 (0.170)	0.02 (0.212)	0.58 (0.113)	0.68 (0.127)	**0.28** **(0.057)**	0.51 (0.019)	0.38 (0.022)	0.33 (0.024)	0.30 (0.021)	0.30 (0.021)	0.33 (0.024)	0.57 (0.018)	0.46 (0.021)	0.37 (0.023)	0.32 (0.024)	0.32 (0.024)
Fat8	-0.50 (0.152)	0.12 (0.190)	0.28 (0.205)	0.38 (0.165)	0.39 (0.170)	0.51 (0.145)	0.33 (0.171)	0.35 (0.177)	0.25 (0.197)	0.64 (0.111)	0.87 (0.098)	0.89 (0.073)	**0.27** **(0.058)**	0.45 (0.021)	0.42 (0.022)	0.35 (0.020)	0.24 (0.022)	0.28 (0.025)	0.44 (0.022)	0.56 (0.018)	0.41 (0.022)	0.35 (0.023)	0.34 (0.023)
Fat10	-0.66 (0.116)	0.30 (0.171)	0.33 (0.195)	0.42 (0.161)	0.48 (0.181)	0.58 (0.161)	0.26 (0.180)	0.34 (0.185)	0.15 (0.206)	0.69 (0.095)	0.85 (0.096)	0.83 (0.092)	1.03 (0.045)	**0.29** **(0.061)**	0.46 (0.021)	0.39 (0.022)	0.21 (0.026)	0.23 (0.026)	0.34 (0.024)	0.39 (0.023)	0.51 (0.020)	0.40 (0.022)	0.33 (0.024)
Fat13	-0.53 (0.131)	-0.05 (0.180)	0.02 (0.199)	0.31 (0.161)	0.50 (0.178)	0.61 (0.160)	0.36 (0.168)	0.44 (0.168)	0.28 (0.188)	0.41 (0.118)	0.73 (0.102)	0.77 (0.105)	0.97 (0.059)	0.98 (0.049)	**0.37** **(0.069)**	0.47 (0.021)	0.17 (0.027)	0.23 (0.026)	0.31 (0.025)	0.35 (0.024)	0.37 (0.024)	0.43 (0.022)	0.36 (0.023)
Fat16	-0.42 (0.140)	-0.05 (0.143)	-0.10 (0.152)	-0.01 (0.142)	0.05 (0.152)	0.15 (0.150)	0.13 (0.157)	0.09 (0.164)	0.11 (0.179)	0.48 (0.113)	0.58 (0.128)	0.59 (0.000)	0.89 (0.000)	0.91 (0.074)	0.93 (0.059)	**0.40** **(0.068)**	0.18 (0.027)	0.20 (0.027)	0.28 (0.026)	0.26 (0.026)	0.29 (0.025)	0.37 (0.024)	0.45 (0.021)
Emd4	0.03 (0.155)	0.70 (0.074)	0.73 (0.072)	0.63 (0.085)	0.65 (0.092)	0.61 (0.101)	0.47 (0.129)	0.45 (0.137)	0.31 (0.167)	0.78 (0.066)	0.73 (0.101)	0.54 (0.000)	0.54 (0.000)	0.63 (0.118)	0.29 (0.138)	0.33 (0.121)	**0.42** **(0.070)**	0.66 (0.015)	0.52 (0.020)	0.47 (0.021)	0.46 (0.022)	0.44 (0.022)	0.39 (0.023)
Emd5	0.20 (0.144)	0.69 (0.079)	0.74 (0.084)	0.73 (0.078)	0.80 (0.071)	0.77 (0.082)	0.70 (0.094)	0.72 (0.092)	0.00 (0.134)	0.52 (0.101)	0.67 (0.100)	0.64 (0.112)	0.53 (0.129)	0.61 (0.120)	0.52 (0.122)	0.23 (0.133)	0.92 (0.035)	**0.42** **(0.074)**	0.61 (0.017)	0.55 (0.019)	0.52 (0.020)	0.37 (0.024)	0.45 (0.021)
Emd7	0.02 (0.143)	0.43 (0.116)	0.52 (0.122)	0.56 (0.106)	0.78 (0.069)	0.74 (0.078)	0.63 (0.098)	0.60 (0.106)	0.39 (0.145)	0.53 (0.098)	0.63 (0.106)	0.79 (0.071)	0.71 (0.093)	0.71 (0.097)	0.67 (0.100)	0.39 (0.120)	0.82 (0.061)	0.94 (0.039)	**0.47** **(0.075)**	0.72 (0.013)	0.64 (0.016)	0.44 (0.022)	0.39 (0.023)
Emd8	0.03 (0.149)	0.53 (0.117)	0.66 (0.107)	0.72 (0.086)	0.80 (0.071)	0.79 (0.064)	0.70 (0.087)	0.68 (0.097)	0.49 (0.141)	0.45 (0.108)	0.66 (0.103)	0.68 (0.095)	0.70 (0.090)	0.64 (0.104)	0.60 (0.111)	0.37 (0.124)	0.78 (0.068)	0.88 (0.053)	0.94 (0.029)	**0.46** **(0.076)**	0.70 (0.014)	0.62 (0.016)	0.55 (0.019)
Emd 10	0.04 (0.153)	0.49 (0.126)	0.60 (0.123)	0.62 (0.106)	0.73 (0.090)	0.72 (0.086)	0.62 (0.103)	0.58 (0.116)	0.41 (0.154)	0.47 (0.108)	0.61 (0.113)	0.73 (0.094)	0.70 (0.099)	0.55 (0.110)	0.55 (0.114)	0.48 (0.116)	0.84 (0.061)	0.91 (0.049)	0.94 (0.037)	0.98 (0.024)	**0.41** **(0.073)**	0.67 (0.014)	0.60 (0.017)
Emd 13	-0.16 (0.162)	0.41 (0.149)	0.45 (0.160)	0.59 (0.120)	0.71 (0.113)	0.70 (0.108)	0.60 (0.121)	0.58 (0.125)	0.36 (0.165)	0.38 (0.122)	0.56 (0.128)	0.60 (0.118)	0.71 (0.105)	0.68 (0.106)	0.73 (0.092)	0.57 (0.108)	0.78 (0.080)	0.57 (0.108)	0.78 (0.080)	0.93 (0.045)	0.96 (0.035)	**0.37** **(0.071)**	0.66 (0.015)
Emd 16	-0.10 (0.171)	0.48 (0.151)	0.59 (0.154)	0.63 (0.122)	0.66 (0.130)	0.69 (0.120)	0.59 (0.132)	0.57 (0.134)	0.48 (0.154)	0.49 (0.493)	0.49 (0.146)	0.67 (0.117)	0.75 (0.108)	0.73 (0.109)	0.70 (0.106)	0.75 (0.087)	0.79 (0.086)	0.75 (0.087)	0.79 (0.086)	0.84 (0.072)	0.97 (0.043)	0.93 (0.043)	**0.33** **(0.071)**

Table C.16 Heritabilities (on diagonal), phenotypic correlations (above diagonal) and genetic correlations (below diagonal) (standard error) between live weight, adjusted fat and eye muscle depth (Model 2)

	Bw	Ww	Wt4	Wt5	Wt7	Wt8	Wt10	Wt13	Wt16	Fat4	Fat5	Fat7	Fat8	Fat10	Fat13	Fat16	Emd4	Emd5	Emd7	Emd8	Emd10	Emd13	Emd16
Bw										-0.19 (0.027)	-0.15 (0.026)	-0.23 (0.027)	-0.28 (0.027)	-0.30 (0.026)	-0.25 (0.028)	-0.19 (0.028)	-0.19 (0.026)	-0.11 (0.028)	-0.24 (0.027)	-0.26 (0.026)	-0.20 (0.028)	-0.18 (0.027)	-0.21 (0.027)
Ww										0.10 (0.030)	0.02 (0.030)	-0.22 (0.029)	-0.36 (0.026)	-0.28 (0.027)	-0.24 (0.028)	-0.12 (0.029)	0.26 (0.029)	0.18 (0.030)	-0.11 (0.030)	-0.20 (0.028)	-0.12 (0.029)	-0.04 (0.029)	-0.05 (0.029)
Wt4										0.35 (0.029)	0.26 (0.029)	-0.24 (0.028)	-0.36 (0.026)	-0.32 (0.026)	-0.22 (0.028)	-0.15 (0.029)	0.72 (0.015)	0.50 (0.023)	-0.06 (0.031)	-0.20 (0.028)	-0.09 (0.029)	-0.03 (0.029)	-0.06 (0.029)
Wt5										0.24 (0.029)	0.27 (0.032)	-0.23 (0.029)	-0.34 (0.026)	-0.32 (0.026)	-0.16 (0.029)	-0.14 (0.030)	0.62 (0.017)	0.51 (0.024)	-0.03 (0.031)	-0.17 (0.029)	-0.07 (0.030)	-0.02 (0.030)	-0.05 (0.030)
Wt7					Table C.12					-0.10 (0.029)	0.02 (0.030)	0.15 (0.034)	0.12 (0.032)	-0.28 (0.028)	-0.11 (0.030)	-0.09 (0.030)	0.09 (0.030)	0.12 (0.030)	0.46 (0.026)	0.08 (0.032)	0.07 (0.031)	0.08 (0.030)	0.04 (0.030)
Wt8										-0.10 (0.029)	0.01 (0.030)	0.16 (0.032)	0.23 (0.033)	-0.24 (0.030)	-0.07 (0.031)	-0.08 (0.031)	0.08 (0.029)	0.12 (0.030)	0.46 (0.025)	0.12 (0.034)	0.11 (0.032)	0.09 (0.031)	0.05 (0.030)
Wt10										-0.11 (0.028)	-0.05 (0.029)	-0.13 (0.030)	-0.15 (0.031)	0.30 (0.032)	0.35 (0.028)	-0.02 (0.032)	0.01 (0.029)	0.28 (0.030)	0.13 (0.030)	0.10 (0.031)	0.06 (0.035)	0.31 (0.029)	0.09 (0.031)
Wt13										-0.12 (0.028)	-0.04 (0.029)	-0.11 (0.029)	-0.11 (0.031)	0.23 (0.030)	0.42 (0.028)	0.00 (0.033)	-0.01 (0.028)	0.02 (0.030)	0.12 (0.030)	0.10 (0.030)	0.08 (0.033)	0.32 (0.030)	0.13 (0.031)
Wt16										-0.14 (0.027)	-0.08 (0.028)	-0.11 (0.029)	-0.13 (0.029)	-0.18 (0.030)	0.05 (0.033)	0.13 (0.035)	-0.06 (0.028)	-0.02 (0.029)	0.05 (0.030)	0.04 (0.030)	0.09 (0.031)	0.79 (0.010)	0.58 (0.022)
Fat4	-0.74 (0.094)	-0.06 (0.158)	0.10 (0.184)	-0.19 (0.165)	-0.38 (0.164)	-0.35 (0.152)	-0.48 (0.158)	-0.50 (0.165)	-0.79 (0.170)	**0.49** **(0.068)**	0.38 (0.022)	0.36 (0.023)	0.30 (0.024)	0.31 (0.024)	0.27 (0.025)	0.28 (0.025)	0.40 (0.022)	0.25 (0.025)	0.25 (0.026)	0.20 (0.026)	0.23 (0.026)	0.17 (0.027)	0.21 (0.026)
Fat5	-0.57 (0.147)	-0.16 (0.191)	0.14 (0.224)	0.06 (0.196)	-0.21 (0.216)	-0.15 (0.202)	-0.38 (0.207)	-0.31 (0.218)	-0.59 (0.225)	0.99 (0.058)	**0.29** **(0.070)**	0.29 (0.024)	0.30 (0.024)	0.30 (0.024)	0.30 (0.024)	0.28 (0.025)	0.28 (0.025)	0.37 (0.022)	0.24 (0.025)	0.21 (0.026)	0.18 (0.026)	0.19 (0.026)	0.19 (0.026)
Fat7	-0.58 (0.112)	-0.55 (0.122)	-0.48 (0.148)	-0.43 (0.139)	0.15 (0.193)	0.18 (0.187)	-0.36 (0.175)	-0.33 (0.187)	-0.58 (0.182)	0.74 (0.089)	0.73 (0.117)	**0.31** **(0.065)**	0.44 (0.021)	0.37 (0.023)	0.29 (0.024)	0.29 (0.024)	0.21 (0.025)	0.21 (0.026)	0.40 (0.022)	0.30 (0.024)	0.25 (0.025)	0.19 (0.026)	0.24 (0.025)
Fat8	-0.81 (0.079)	-0.56 (0.115)	-0.55 (0.137)	-0.49 (0.134)	0.06 (0.210)	0.21 (0.197)	-0.48 (0.168)	-0.46 (0.183)	-0.44 (0.201)	0.82 (0.088)	0.92 (0.090)	0.93 (0.070)	**0.30** **(0.067)**	0.41 (0.022)	0.37 (0.023)	0.34 (0.023)	0.17 (0.026)	0.18 (0.026)	0.28 (0.025)	0.34 (0.023)	0.25 (0.025)	0.17 (0.026)	0.24 (0.025)
Fat10	-0.86 (0.060)	-0.37 (0.133)	-0.34 (0.170)	-0.27 (0.156)	-0.38 (0.160)	-0.28 (0.167)	0.17 (0.193)	0.24 (0.199)	-0.45 (0.172)	0.83 (0.072)	0.86 (0.089)	0.85 (0.084)	1.05 (0.039)	**0.31** **(0.068)**	0.41 (0.022)	0.37 (0.023)	0.21 (0.025)	0.21 (0.026)	0.27 (0.025)	0.27 (0.025)	0.37 (0.023)	0.26 (0.025)	0.25 (0.025)
Fat13	-0.74 (0.080)	-0.57 (0.115)	-0.47 (0.154)	-0.21 (0.159)	-0.12 (0.183)	-0.00 (0.185)	0.45 (0.159)	0.52 (0.155)	-0.06 (0.196)	0.57 (0.097)	0.74 (0.097)	0.76 (0.103)	0.96 (0.060)	0.97 (0.056)	**0.40** **(0.074)**	0.43 (0.022)	0.20 (0.026)	0.17 (0.027)	0.23 (0.026)	0.23 (0.026)	0.24 (0.026)	0.28 (0.025)	0.25 (0.026)
Fat16	-0.63 (0.106)	-0.29 (0.140)	-0.39 (0.126)	-0.34 (0.122)	-0.27 (0.160)	-0.16 (0.165)	-0.19 (0.175)	-0.24 (0.183)	-0.06 (0.203)	0.67 (0.089)	0.70 (0.107)	0.74 (0.103)	0.96 (0.067)	1.00 (0.058)	0.99 (0.043)	**0.45** **(0.075)**	0.17 (0.026)	0.14 (0.027)	0.22 (0.026)	0.18 (0.027)	0.19 (0.027)	0.24 (0.026)	0.33 (0.024)
Emd4	-0.66 (0.122)	0.36 (0.138)	0.72 (0.073)	0.61 (0.087)	0.18 (0.171)	0.07 (0.175)	-0.18 (0.188)	-0.19 (0.197)	-0.46 (0.195)	0.79 (0.076)	0.62 (0.129)	0.61 (0.124)	0.62 (0.130)	0.68 (0.121)	0.46 (0.131)	0.60 (0.112)	**0.38** **(0.069)**	0.42 (0.022)	0.36 (0.023)	0.34 (0.024)	0.37 (0.023)	0.35 (0.023)	0.33 (0.024)
Emd5	-0.41 (0.160)	0.29 (0.150)	0.58 (0.109)	0.57 (0.101)	0.30 (0.145)	0.25 (0.148)	0.13 (0.190)	0.19 (0.193)	-0.28 (0.213)	0.66 (0.096)	0.59 (0.118)	0.63 (0.120)	0.46 (0.140)	0.55 (0.124)	0.50 (0.125)	0.34 (0.130)	0.91 (0.060)	**0.32** **(0.069)**	0.44 (0.022)	0.39 (0.023)	0.40 (0.023)	0.38 (0.023)	0.37 (0.023)
Emd7	-0.55 (0.114)	0.01 (0.157)	0.02 (0.155)	0.03 (0.173)	0.31 (0.135)	0.26 (0.136)	0.16 (0.177)	0.14 (0.185)	-0.24 (0.203)	0.66 (0.087)	0.58 (0.116)	0.76 (0.084)	0.72 (0.095)	0.72 (0.094)	0.69 (0.095)	0.58 (0.105)	0.89 (0.069)	0.99 (0.041)	**0.48** **(0.078)**	0.53 (0.019)	0.49 (0.021)	0.44 (0.022)	0.41 (0.023)
Emd8	-0.57 (0.111)	-0.11 (0.171)	0.03 (0.198)	0.09 (0.165)	0.31 (0.187)	0.32 (0.166)	0.12 (0.173)	0.09 (0.184)	-0.20 (0.197)	0.49 (0.105)	0.52 (0.124)	0.56 (0.118)	0.56 (0.117)	0.56 (0.111)	0.53 (0.115)	0.49(0.1 19)	0.82 (0.079)	0.82 (0.076)	0.97 (0.037)	**0.39** **(0.072)**	0.53 (0.019)	0.46 (0.018)	0.41 (0.019)
Emd 10	-0.10 (0.126)	-0.08 (0.170)	0.05 (0.193)	0.07 (0.161)	0.25 (0.180)	0.26 (0.169)	-0.04 (0.177)	-0.08 (0.188)	-0.22 (0.199)	0.51 (0.100)	0.49 (0.125)	0.67 (0.105)	0.67 (0.107)	0.52 (0.110)	0.52 (0.112)	0.59 (0.107)	0.90 (0.062)	0.85 (0.069)	0.96 (0.045)	0.98 (0.033)	**0.47** **(0.077)**	0.50 (0.017)	0.48 (0.018)
Emd 13	-0.52 (0.122)	-0.11 (0.170)	-0.08 (0.199)	0.09 (0.163)	0.22 (0.190)	0.21 (0.181)	0.31 (0.170)	0.32 (0.176)	-0.11 (0.207)	0.43 (0.112)	0.38 (0.136)	0.51 (0.125)	0.63 (0.117)	0.60 (0.114)	0.66 (0.100)	0.65 (0.100)	0.94 (0.066)	0.77 (0.091)	0.88 (0.062)	0.92 (0.058)	0.92 (0.053)	**0.41** **(0.075)**	0.51 (0.019)
Emd 16	-0.57 (0.117)	-0.06 (0.172)	0.05 (0.195)	0.11 (0.166)	0.15 (0.196)	0.18 (0.186)	0.12 (0.188)	0.12 (0.199)	-0.27 (0.200)	0.54 (0.105)	0.37 (0.142)	0.73 (0.104)	0.69 (0.115)	0.72 (0.101)	0.66 (0.104)	0.78 (0.080)	0.95 (0.067)	0.80 (0.083)	0.95 (0.045)	0.85 (0.073)	0.99 (0.035)	0.95 (0.045)	**0.45** **(0.078)**

Table C.17 Genetic correlations (standard error) between growth rates using the standardised difference[A]

	FG	MG	FG adj	MG adj
WG	0.74 (0.153)	0.89 (0.133)	0.87 (0.138)	0.89 (0.131)
MG	0.85 (0.160)		0.48 (0.425)	

[A] Standardised difference = see equation 5.1, WG = weight gain, FG = fat depth gain, MG = eye muscle depth gain, FG adj = fat depth gain adjusted for weight gain, MG adj = eye muscle depth adjusted for weight gain

Appendix D

D.1 LEAST SQUARES MEANS FOR THE SELECTION DEMONSTRATION FLOCKS FLEECE TRAITS

Table D.1 **Least squares means (standard error) of fleece traits**[A]

		CFW (kg)	FD (µm)	SL (mm)	SS (N/ktex)
Year	**2000**	5.6^{a} (0.06)	20.5^{a} (0.12)	88.1 (0.73)	33.7 (0.72)
	2001	4.7^{b} (0.05)	19.1^{b} (0.12)	88.5 (0.69)	33.9 (0.70)
Flock	**Control**	4.9^{a} (0.07)	21.3^{a} (0.14)	88.4^{a} (0.83)	35.5^{a} (0.82)
	MPR	5.2^{b} (0.09)	19.1^{b} (0.20)	88.3^{a} (1.16)	30.9^{b} (1.00)
	PCA	4.9^{a} (0.09)	19.7^{c} (0.20)	85.4^{b} (1.16)	33.7^{a} (1.01)
	EWF	5.3^{b} (0.08)	19.5^{bc} (0.18)	88.7^{a} (1.05)	34.5^{a} (0.95)
	FM+	5.1^{ab} (0.10)	19.1^{b} (0.19)	87.8^{ab} (1.10)	34.3^{a} (1.03)
Sex	**Male**	5.1^{a} (0.04)	19.8 (0.10)	87.7 (0.57)	33.8 (0.57)
	Female	4.6^{b} (0.04)	19.7 (0.10)	88.5 (0.58)	32.8 (0.59)
Tobr	**11**	5.1^{a} (0.04)	19.8^{a} (0.10)	87.7 (0.57)	33.8 (0.57)
	21	4.9^{b} (0.06)	19.8^{a} (0.14)	88.8 (0.87)	33.7 (0.97)
	22	4.9^{b} (0.05)	20.1^{b} (0.10)	87.7 (0.61)	33.0 (0.61)

[A] Within a cell means with no superscript or with a common superscript do not differ significantly ($P > 0.05$) from each other. Control = Control flock, MPR = Measured performance records flock, PCA = Professional classer assessment flock, EWF = Elite wool flock, FM+ = Fibre meat plus flock

Table D.2 **Least squares means (standard error) of fleece traits for year by sex interaction**[A]

		CFW (kg)		FD (µm)		SL (mm)		SS (N/ktex)	
	Year	**2000**	**2001**	**2000**	**2001**	**2000**	**2001**	**2000**	**2001**
Sex	**Male**	5.6^{a} (0.06)	4.7^{c} (0.05)	20.5^{a} (0.12)	19.1^{c} (0.12)	88.2^{a} (0.72)	88.5^{a} (0.69)	33.5^{a} (0.72)	33.7^{a} (0.70)
	Female	4.8^{b} (0.06)	4.5^{d} (0.05)	20.1^{b} (0.12)	19.5^{d} (0.11)	90.4^{b} (0.74)	87.8^{a} (0.68)	29.5^{b} (0.75)	35.7^{c} (0.69)

[A] Within a cell means with no superscript or with a common superscript do not differ significantly ($P > 0.05$) from each other

Table D.3 Least squares means (standard error) of clean fleece weight (kg) for flock by sex interaction[A]

	Flock	Control	MPR	PCA	EWF	FM+
Sex	Male	4.9^{ab} (0.07)	5.2^{c} (0.09)	4.9^{ab} (0.09)	5.3^{c} (0.08)	5.1^{bc} (0.10)
	Female	4.3^{d} (0.07)	4.7^{a} (0.09)	4.7^{a} (0.09)	4.7^{a} (0.09)	4.4^{d} (0.10)

[A] Means with a common superscript do not differ significantly ($P > 0.05$) from each other. Control = Control flock, MPR = Measured performance records flock, PCA = Professional classer assessment flock, EWF = Elite wool flock, FM+ = Fibre meat plus flock

Table D.4 Least squares means (standard error) of clean fleece weight (kg) for year by flock by sex interaction[A]

		Flock				
Year	Sex	Control	MPR	PCA	EWF	FM+
2000	Male	5.6^{a} (0.09)	5.6^{ab} (0.13)	5.3^{b} (0.11)	5.8^{a} (0.11)	5.6^{ab} (0.12)
	Female	4.6^{defg} (0.09)	4.9^{cde} (0.13)	5.0^{c} (0.11)	5.0^{c} (0.12)	4.6^{fg} (0.12)
2001	Male	4.4^{gh} (0.09)	4.9^{cd} (0.13)	4.6^{defg} (0.11)	4.8^{cdef} (0.11)	4.6^{defg} (0.12)
	Female	4.3^{h} (0.09)	4.7^{cdef} (0.13)	4.6^{efg} (0.11)	4.6^{fg} (0.11)	4.4^{gh} (0.12)

[A] Means with a common superscript do not differ significantly ($P > 0.05$) from each other. Control = Control flock, MPR = Measured performance records flock, PCA = Professional classer assessment flock, EWF = Elite wool flock, FM+ = Fibre meat plus flock

D.2 PHENOTYPIC AND GENETIC CORRELATIONS BETWEEN FLEECE AND UNADJUSTED FAT AND EYE MUSCLE DEPTH (MODEL 1)

Table D.5 Phenotypic correlations (standard error) between fleece traits and unadjusted growth traits (Model 1)

Age (months)		4	5	7	8	10	13	16
FAT	CFW	0.01 (0.028)	0.02 (0.027)	0.07 (0.027)	0.14 (0.027)	0.03 (0.028)	0.05 (0.029)	0.06 (0.029)
	FD	0.05 (0.029)	0.10 (0.028)	0.20 (0.027)	0.25 (0.026)	0.20 (0.027)	0.20 (0.028)	0.20 (0.028)
	SL	0.04 (0.028)	0.10 (0.027)	0.16 (0.027)	0.18 (0.027)	0.13 (0.027)	0.12 (0.028)	0.11 (0.028)
	SS	0.04 (0.027)	0.03 (0.027)	0.12 (0.026)	0.18 (0.026)	0.15 (0.026)	0.14 (0.026)	0.10 (0.026)
EMD	CFW	0.12 (0.028)	0.16 (0.028)	0.17 (0.028)	0.23 (0.027)	0.21 (0.027)	0.24 (0.027)	0.23 (0.027)
	FD	0.06 (0.029)	0.12 (0.029)	0.24 (0.028)	0.24 (0.028)	0.22 (0.028)	0.24 (0.028)	0.24 (0.027)
	SL	0.11 (0.029)	0.13 (0.029)	0.23 (0.028)	0.26 (0.027)	0.21 (0.027)	0.22 (0.027)	0.21 (0.027)
	SS	0.01 (0.027)	0.05 (0.028)	0.11 (0.027)	0.20 (0.026)	0.19 (0.026)	0.15 (0.026)	0.10 (0.026)

Table D.6 Genetic correlations (standard error) between fleece traits and unadjusted growth traits (Model 1)

Age (months)		4	5	7	8	10	13	16
FAT	CFW	-0.25 (0.135)	-0.44 (0.167)	-0.48 (0.171)	-0.20 (0.173)	-0.12 (0.154)	-0.22 (0.146)	-0.18 (0.141)
	FD	0.00 (0.121)	-0.20 (0.155)	0.27 (0.143)	0.42 (0.130)	0.41 (0.127)	0.19 (0.131)	0.30 (0.128)
	SL	-0.02 (0.138)	-0.02 (0.174)	0.11 (0.154)	0.32 (0.142)	0.25 (0.145)	0.25 (0.138)	0.21 (0.141)
	SS	-0.07 (0.173)	0.01 (0.212)	0.31 (0.174)	0.34 (0.171)	0.26 (0.179)	0.09 (0.181)	0.11 (0.183)
EMD	CFW	-0.26 (0.143)	-0.15 (0.151)	-0.15 (0.144)	-0.11 (0.148)	-0.14 (0.150)	-0.18 (0.159)	-0.10 (0.162)
	FD	-0.15 (0.133)	-0.01 (0.135)	0.21 (0.120)	0.07 (0.130)	0.05 (0.134)	0.08 (0.136)	0.14 (0.140)
	SL	0.08 (0.146)	0.18 (0.142)	0.28 (0.127)	0.35 (0.124)	0.28 (0.132)	0.31 (0.140)	0.27 (0.149)
	SS	0.05 (0.188)	0.22 (0.173)	0.16 (0.166)	0.26 (0.163)	0.26 (0.166)	0.16 (0.181)	0.06 (0.196)

D.3 PHENOTYPIC CORRELATIONS BETWEEN FLEECE, WEIGHT AND ADJUSTED FAT AND EYE MUSCLE DEPTH (MODEL 2)

Table D.7 Phenotypic correlations (standard error) between fleece traits and adjusted growth traits (Model 2)

		Birth	Weaning	4	5	7	8	10	13	16
WT	**CFW**	0.27 (0.028)	0.30 (0.026)	0.30 (0.025)	0.27 (0.027)	0.29 (0.026)	0.36 (0.026)	0.37 (0.026)	0.40 (0.025)	0.43 (0.023)
	FD	-0.07 (0.030)	0.03 (0.029)	0.03 (0.028)	0.12 (0.028)	0.17 (0.027)	0.21 (0.027)	0.20 (0.027)	0.23 (0.027)	0.22 (0.028)
	SL	0.01 (0.029)	0.10 (0.028)	0.11 (0.027)	0.17 (0.027)	0.24 (0.026)	0.26 (0.026)	0.23 (0.026)	0.23 (0.026)	0.21 (0.026)
	SS	-0.02 (0.027)	-0.01 (0.027)	0.01 (0.026)	0.04 (0.027)	0.07 (0.026)	0.16 (0.026)	0.17 (0.026)	0.15 (0.026)	0.11 (0.026)
FAT	**CFW**			-0.11 (0.028)	-0.09 (0.028)	-0.07 (0.028)	-0.07 (0.028)	-0.15 (0.028)	-0.11 (0.029)	-0.11 (0.029)
	FD			0.05 (0.029)	0.06 (0.028)	0.14 (0.028)	0.17 (0.027)	0.12 (0.028)	0.13 (0.029)	0.13 (0.029)
	SL			-0.02 (0.029)	0.04 (0.028)	0.05 (0.028)	0.09 (0.028)	0.05 (0.028)	0.05 (0.028)	0.05 (0.029)
	SS			0.05 (0.027)	0.02 (0.027)	0.09 (0.026)	0.13 (0.026)	0.10 (0.026)	0.09 (0.027)	0.07 (0.027)
EMD	**CFW**			-0.06 (0.028)	-0.04 (0.028)	-0.03 (0.029)	-0.05 (0.029)	-0.06 (0.029)	-0.02 (0.029)	-0.06 (0.029)
	FD			0.05 (0.028)	0.06 (0.028)	0.18 (0.028)	0.13 (0.028)	0.11 (0.029)	0.12 (0.029)	0.12 (0.029)
	SL			0.05 (0.028)	0.03 (0.028)	0.12 (0.029)	0.13 (0.028)	0.10 (0.029)	0.10 (0.028)	0.11 (0.028)
	SS			0.01 (0.026)	0.03 (0.027)	0.09 (0.027)	0.12 (0.027)	0.11 (0.027)	0.08 (0.027)	0.04 (0.027)

Appendix E

Publications

Ingham, V.M. & Ponzoni, R.W. (2000). Genetic parameters for reproduction in South Australian merino sheep. *Asian-Australasian Journal of Animal Sciences, 13*(Supl.), 80-82.

NOTE:

This publication is included in the print copy
of the thesis held in the University of Adelaide Library.

Ingham, V. M. & Ponzoni, R. W. (2001). A progress report on the development of a meat Merino line in South Australia (the Fibre Meat Plus). In *Proceedings of the Association for the Advancement of Animal Breeding and Genetics*, *14*, 433-436.

GENETIC PARAMETERS FOR WEIGHT, FAT AND EYE MUSCLE DEPTH IN SOUTH AUSTRALIAN MERINO SHEEP

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SUMMARY

Data from the SARDI Selection Demonstration Flocks were used to estimate heritability of and genetic correlations between live weight, fat depth and eye muscle depth at five months of age under an animal model. Two models, with and without weight adjustment, were used for fat and eye muscle depth. Heritability estimates were 0.28 (0.08), 0.26 (0.06) and 0.35 (0.07) for weight, adjusted fat and adjusted eye muscle depth, respectively. Phenotypic correlations ranged from 0.27 to 0.66 and genetic correlations ranged from 0.16 to 0.73. The estimates reported here are similar to those previously reported for other sheep breeds. This suggests that sufficient genetic variation exists to enable selection to improve these traits for Merinos. Moderate heritabilities and correlations for weight adjusted traits suggest that there is potential for improvement in fat depth and eye muscle shape in Merinos. The similarity of these estimates to those reported for other sheep breeds indicates that selection used for meat breeds may be directly applicable to, or easily adapted for Merinos.

Keywords: Merino, sheep, selection, heritability, correlation

INTRODUCTION

Merinos have traditionally been selected for wool. Recent trends in wool and lamb prices, have increased the proportion of producer's income derived from lamb, and therefore a greater emphasis has been placed on growth and carcase attributes (Clarke *et al.* 2002; Davidson *et al.* 2002; Ingham and Ponzoni 2001; Safari *et al.* 2001). Parameter estimates are widely available for fleece traits and weight traits at birth, weaning and older ages (Ponzoni and Fenton 2000). However there are few genetic parameter estimates of weight traits between weaning and yearling ages, and fewer estimates of carcase traits at any age for Merinos. It is important for the further development and proper use of the Merino as a dual-purpose breed that the gaps in our knowledge of the interactions between weight and carcase traits be filled. An intensive schedule of weight and live carcase measurement has been carried out as part of the SARDI Selection Demonstration Flocks Project. This study presents genetic parameter estimates from the five month data obtained from these flocks.

MATERIALS AND METHODS

Animals. The 1761 lambs studied were from the 2000 and 2001 drops of SARDI Selection Demonstration Flocks (Ponzoni *et al.* 2000; Ingham and Ponzoni 2001). They were weaned at three months of age and measured at five months of age for body weight, ultrasonic fat and eye muscle depth (over the 12th rib, C site) by a Lambplan accredited scanner. There was no pedigree information available for the 86 sires and 1045 dams of the lambs. Table 1 shows the number of records available, the mean and the standard deviation for each of the traits.

Statistical analysis. Preliminary analyses to determine the fixed effects included in the model were carried out using univariate analysis with ASReml (Gilmour *et al.* 1999). Phenotypic and genetic correlations were estimated using multivariate analysis. Fat and eye muscle depth were analysed with and without adjustment for body weight. The base model included fixed effects for year of birth, flock, sex, age of dam (aod) and type of birth and rearing (tobr). Age fitted as day of birth (dob) was included as a linear covariate. Interactions fitted for all traits were; year x sex, year x flock, year x tobr, sex x dob and tobr x dob. The extended model used for fat and eye muscle depth included separate weight regressions for each sex. An animal term was fitted allowing optimal analysis of a finite, selected population. A dam term was included as a random effect for weight but was negligible and dropped from the final models for fat or eye muscle depth.

Table 1. Number of records available, simple means, standard deviations (s.d.) and range for weight (kg), fat and eye muscle depth (mm)

Trait	No. of records	Simple mean	s.d.	Range
Weight	1761	31.8	6.33	13 – 56
Fat depth	1657	1.4	0.59	0.5 – 3.5
Eye muscle depth	1657	18.9	3.08	10 – 28

RESULTS AND DISCUSSION

Fixed effects. *Weight.* There was a significant linear increase in weight associated with age of dam (Table 2a). Sex also had a major impact on weight with weight of males being greater than females. This difference was greater in 2001 drop lambs than in 2000 drop lambs (Table 2a). The regression on age was higher for males than females and higher for single born lambs than twins, and for single reared twins than twin reared twins (Table 2b).

Fat. Sex had a major impact on fatness interacting significantly with weight, tobr and year. Females were fatter than males and more so in the 2001 drop than the 2000 drop (Table 2a). The regression on weight was higher for females than for males. The regression on age was higher for females than for males and higher for twins than single born lambs, and for single reared twin lambs than for twin reared twin lambs (Table 2b)

Eye muscle depth. There was a significant linear decline in eye muscle depth associated with age of dam (Table 2a). Sex also had a major impact on eye muscle depth with muscle depth being less for females and the difference being greater in the 2001 drop lambs than the 2000 drop lambs (Table 2a). The regression on weight was lower for females than for males, however the pattern in age regressions for sex and tobr was similar to that for fat.

Heritability. The heritability estimates were 0.28 (0.08) for weight, 0.26 (0.07) for fat adjusted for weight and 0.35 (0.07) for eye muscle depth adjusted for weight (Table 3). There is a paucity of estimates for post weaning weight reported for Merinos. However the literature indicates that heritability of weight generally increases with age. Fogarty (1995) reports ranges in heritability of weaning weight for Merinos from 0.08 to 0.41 and post weaning weight in dual purpose breeds of 0.03 to 0.49. Our estimate is consistent with these values. The very small maternal genetic effect estimated for weight (0.04 SE 0.04) was not significant (P>0.05). There are also few estimates of carcase traits for Australian Merinos. Safari *et al.* (2001) reported heritabilities of 0.20 and 0.27 for weight adjusted fat depth (C site), and eye muscle depth respectively, measured in slaughtered 17 month old rams. Davidson *et al.* (2002) reported heritabilities of 0.28 (0.07) and 0.23 (0.07) for weight adjusted fat and eye muscle depth measured in the live animal at 16 months of age. Estimates from this study are in agreement with these for fat depth but are greater for eye muscle depth and are measured in much younger animals. Adjusting fat depth for weight had little effect on the heritability but reduced that of eye muscle depth by 0.06 due to a greater reduction in the genetic variance.

Table 2a. Predicted year x sex means, weight x sex regression coefficients and age of dam (aod) regression coefficients for weight, fat and eye muscle depth

			Weight	Fat depth	Eye muscle depth
aod			0.42	-	-0.07 (0.03)
weight		M		0.03 (0.002)	0.30 (0.01)
		F		0.04 (0.002)	0.28 (0.01)
year	2000	M	33.3 (0.31)	1.28 (0.03)	18.8 (0.11)
		F	29.8 (0.32)	1.43 (0.03)	18.7 (0.11)
	2001	M	34.5 (0.30)	1.29 (0.03)	19.1 (0.10)
		F	30.1 (0.30)	1.62 (0.02)	18.6 (0.10)

Table 2b. Regression coefficients of weight, fat and eye muscle depth on age (adjusted for weight), for sex, and type of birth and rearing (tobr) classes

	Weight			Fat depth			Eye muscle depth		
tobr	11	22	21	11	22	21	11	22	21
M	0.308 (0.010)	0.272 (0.010)	0.327 (0.010)	0.002 (0.001)	0.003 (0.001)	0.008 (0.001)	0.004 (0.005)	0.013 (0.005)	0.027 (0.005)
F	0.260 (0.010)	0.225 (0.010)	0.280 (0.010)	0.008 (0.001)	0.010 (0.001)	0.014 (0.003)	0.030 (0.005)	0.039 (0.005)	0.053 (0.005)

Correlations. Phenotypic correlations between weight and fat depth were moderate without weight adjustment but were lower with adjustment (Table 3). Genetic correlations were lower than phenotypic for both models. Correlations between weight and eye muscle depth were moderate to high but followed the same trend as weight and fat correlations when weight adjustment was included in the model. Correlations between fat and eye muscle depth were moderate to high. All estimates fit within reported ranges for other breeds (Fogarty 1995). These estimates suggest that selection for an increase in any of these traits, for example weight, will result in an increase in the other two component traits.

Table 3. Phenotypic variances, heritabilities (on diagonal), correlations (above the diagonal), and genetic correlations (below the diagonal) between body weight, fat depth and eye muscle depth at 5 months of age (± se in brackets)

Trait	Model	Phenotypic Variance	Weight	Fat depth	Eye muscle depth
Weight	1	17.9	0.28 (0.08)	0.40 (0.02)	0.66 (0.02)
	2			0.27 (0.03)	0.51 (0.02)
Fat depth	1	0.215	0.34 (0.16)	0.23 (0.06)	0.50 (0.03)
	2	0.140	0.16 (0.18)	0.26 (0.07)	0.36 (0.02)
Eye muscle depth	1	3.82	0.73 (0.08)	0.67 (0.10)	0.42 (0.07)
	2	2.93	0.57 (0.10)	0.60 (0.12)	0.35 (0.07)

CONCLUSIONS

This small group of 'new' parameters is encouraging for Merino breeders and producers as the moderate heritabilities and positive correlations between all traits suggests that enough genetic variation exists to enable selection to improve these traits. Moderate heritabilities and correlations for weight adjusted traits suggest that there is potential for improvement in fat depth and eye muscle depth in Merinos. The similarity of these estimates to those reported for other sheep breeds indicates that selection indicies used for meat breeds may be directly applicable to, or easily manipulated for Merinos. More work should be carried out to determine interactions between wool, growth and carcase traits for Merinos.

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