

Chapter 1

General Introduction

Selection is a process of differential reproduction whereby certain individuals are permitted to contribute more offspring to the next generation than others. It is the primary technology available to the breeder to increase the frequency of desired genes within a livestock population for some intended purpose.

Selection experiments have been used widely in sheep populations to quantify direct and correlated responses to selection and weaning and yearling weight are the two most commonly utilised measures of growth and are included in most selection programs. In particular, selection for weaning weight has been an integral part of most performance recording schemes aimed at improving meat production in sheep. It is of significance because it is a measure of both growth and a dam's ability to raise heavier lambs.

The most consistent consequences of selection for weaning weight are increased food intake and growth rate, resulting in an increase in gross efficiency, and correlated responses in weights at all other ages. Selection for high and low weaning weight in sheep resulted in an increase and decrease in body weights respectively in subsequent generations (Pattie 1965b and Davis 1987) and at other ages including maturity (Pattie, 1965b, Thompson, Parks and Perry 1985 and Davis 1987). Numerous studies have also been conducted to examine the effect of selection on weaning weight for reproduction (Davis 1987, Herd *et al.* 1993), wool production (Pattie 1965b and Bradford *et al.* 1986), and body composition (Thompson and Butterfield 1985).

Knowledge of phenotypic and genetic parameters, and of the nature of selection responses in most important traits, is essential for any successful attempt to improve sheep

production by genetic means. This knowledge is needed because the potential for genetic improvement of a trait is largely dependent upon its heritability and its genetic correlations with other traits. Heritability estimates are used to predict the amount of genetic gain in future generations due to selection. Heritability of a trait is the proportion of superiority of selected parents above their contemporaries, which on average is passed on to their offspring. Phenotypic correlations between traits are gross correlations that include both the environmental and the genetic portions of the covariances. They are important because they directly affect the size of the selection differentials when several factors are used in a selection index. Genetic correlations exist when genes affecting one trait also affect another. Such correlations can influence the rate of progress when selection is for two or more traits.

Growth in live weight and wool reflects the genes an animal has inherited from its parents and a mix of seasonal and husbandry factors. In young animals, the milk supply of their dam and the maternal care she provides also contributes to their growth. For this reason, selection programs aimed at improving growth rate need to include both direct and maternal effects in order to achieve optimum genetic progress. Falconer (1989) enumerated the three causes of maternal effects. These are the maternal additive effect, which are due to the dam's own genotype for milking and mothering ability; the permanent environmental effects are those effects that are consistent between each lambing of a dam but not genetic in origin; and, those specific to one litter of a dam or the temporary environmental effect. If females have several litters at which they bear more than one young, variation due to each of those effects may be separated.

Studies have shown of significant maternal effects are of importance for growth traits in sheep with influence both before and after weaning. The influence is strongest with birth and decreases with age (Nasholm and Dannel 1994, Tosh and Kemp 1994, Mortimer and Atkins 1995). On the other hand, some reports for the maternal heritability estimates for fleece are found to be low and are not carried over as the animal aged (Hickson *et al.* 1995, Swan and Hickson 1994).

Animals have been raised in a wide variety of environments to which they have been well adapted through selection, both natural and artificial. In addition, there is much variability at both phenotypic and genetic levels between and within population and sub-populations. Woolaston (1985) suggested that different environments require different components of fitness, and desirable attributes in one environment are not necessarily an advantage in other environments. On the other hand, a genotype that is better adapted to a particular environment will have more genes to enable it to withstand the stresses imposed by that environment and the same genes may be of little use in another environment in which different stresses are imposed and will be of no value in a benign environment where stresses are minimal. A genotype x environment interaction is defined as a change in the relative performance of a character of two or more genotypes measured in two or more environments. Interactions can involve changes in rank order for genotypes between environments as well as changes in the absolute and relative magnitude of genetic and environmental sources of variations between environments. When there is greater diversity between genotypes, and between environments, genotype x environment interaction is more likely to exist. On the other hand, genotypes with narrow ranges of adaptive genes will be more sensitive to environmental variation. Wilson (1974) concluded that while there is clear evidence of genotype x environment interactions where environments differ greatly, the bulk of experimentation shows little evidence of serious interactions when the range of genotypes and environments is modest.

This thesis uses data from long-term weight Merino selection flocks to examine the impact of genotype by environment interactions and also to examine changes in direct and correlated responses as a result of suspension of selection in the same flocks. Chapter 2 provides a detailed description of the selection and random bred lines as well as the environmental conditions while chapter 3 examines line and environmental effects on lamb and hogget parameters and presents genetic and phenotypic estimates for these parameters.

Chapter 4 looks in detail at the genotype by environmental interactions resulting from evaluation of weight selected lines in two NSW environments. Finally chapter 5 examines the changes in direct and correlated responses in the weight-selected lines as a result of suspension of selection.

Chapter 2

Description of the Trangie Weight Selection Experiment

2.1 Sources of data

The data used in the studies reported in this thesis were recorded on animals at NSW Agriculture's Agricultural Research Centre at Trangie and the University of New England's (UNE) Kirby Research Station located on the Central Western Plains and the Northern Tablelands, respectively, New South Wales, Australia. The studies used animals from the Trangie Weight Selection Experiment maintained by the NSW Agriculture between 1951 and 1994.

2.2 The Trangie Weight Selection Lines

2.2.1 The Trangie flocks

Sheep in the Trangie Weight Selection lines were derived from Registered Flock No. 78, a stud founded at Yanco in 1912 and transferred to Trangie in 1915. The stud was established from medium-Peppin Merino ewes and rams, purchased from 'Cobran Estate,' 'Bundemar,' and 'Weemabung' studs. Additional ewes were obtained from the same studs until 1920. Between 1920 and 1943, thirteen more 'Bundemar' stud rams were purchased.

The Trangie stud, established to breed a Merino suited to the Western Plains and provide sheep of good quality for sale at a reasonable price (Dun and Eastoe, 1970), was managed as a commercial stud. Selection was based on improving fleece weights while maintaining wool quality. Culling was based on visual appraisal of animals and animals with obvious physical faults or black wool were culled. Fleece weight was visually assessed with the general opinion being that ‘the ideal sheep was robust with traditional heavy neck folds, but plain over the body and breech.’ A heavy, but attractive fleece cover was stressed, with plenty of classer’s density to repel dust and burr. Wool below the eye was not desired, but this had to be combined with a woolled poll, belly and legs. The sheep’s frame was required to be big-boned, with wide hocks and robust, wide horns – all signs of ‘constitution’ (Dun and Eastoe 1970). However, the visual appraisal of characters was found to be generally inaccurate resulting in minimal amount of selection over the period between 1920 and 1943 (Morley 1951). The management of the stud was based on a nucleus where the best ram was mated to the best ewes and a base of second stud ewes of lower quality which were mated to nucleus rams to produce flock rams for sale.

2.2.2 Selection lines

In 1951, four pairs of single-trait selection lines were established on the basis of high expression (plus) or low expression (minus) of the following traits – clean fleece weight, crimp frequency, skin fold score and live weight at weaning. For live weight at weaning, eighty ewes from the base flock of second stud ewes were selected on the basis of either their hogget or weaning weights to establish each of the plus and minus selection lines. The ewes ranged in age from 18 months to 8 years of age. Ewes of the selection lines were mated to five 18-month old rams selected on the basis of their weaning weights. The flocks were increased to 100 ewes per line in the following year and thereafter the flocks were closed.

The selection of ewe and ram replacements within each line was on the basis of the appropriate selection criterion: high weaning weight (Weight Plus) or low weaning weight (Weight Minus) . This policy was maintained from 1951 to 1983, with few exceptions. Due to drought, no matings were done in 1952. In the years 1966 and 1967, the selection lines were joined to Border Leicester rams and to Fertility flock rams in 1970.

Between 1983 and 1994, selection was suspended, with replacement rams and ewes chosen at random within each line. The selection lines were dispersed in 1995.

2.2.3 Random line

The Random line had a number of design changes during the experiment, resulting in a complex structure. Two separate sub-lines were split from the same base flock as the selection lines in 1951; one was mated in Autumn (denoted MR) and the other in Spring (denoted AR). Both random sub-lines were increased to a flock size of 100 ewes in the following year and were subsequently closed. Ewes of each of the sub-lines were mated to ten 18-year old rams per year which were randomly selected from within each sub-line.

From 1959 to 1961, there was a reciprocal exchange of rams between the sub-lines in order to reduce genetic drift between the lines and inbreeding within the lines. From 1962 to 1972, the sub-lines were again closed. However, the Spring-mated sub-line was mated in April (AR) and the Autumn-mated sub-line's mating was advanced to March (MR).

In 1973, the sub-lines were re-opened by mating MR line rams to AR line ewes and from 1974 to 1994 the two sub-lines were combined to form the composite Random line with no attempt to distinguish between sub-lines.

2.2.4 The Armidale flock

The Armidale flock was established in the latter part of 1982, with the transfer from Trangie of half of the breeding ewes from each of the selection lines and 100 Random ewes to the University of New England's Kirby Research Station. In the group were 166 ewes from the Weight Plus line and 109 ewes from the Weight Minus line. An additional group of 18-month old ewes were transported to Armidale in October 1983. Additional Random line ewes were also made available with the transfer of 120 ewes to Armidale in October 1983.

2.2.5 Selection procedure

The Trangie Weight Selection Experiment involved two lines of medium-Peppin Merinos for high live weight at weaning (Weight Plus) and low live weight at weaning (Weight Minus) and a randomly selected control line (Random). For the selection lines, the selection criterion used between 1951 and 1983 was weaning weight.

The adjustments for some fixed effects were altered over this period. From 1951 to 1957, selection was based on actual “over the scales” weaning weight, without any correction. From 1958 to 1961, all weights were corrected for age and birth type by using additive correction factors calculated from previous data. The adjustment factor of 0.113 kg per day was added (or subtracted) for all ewes for each day in age below (or above) the average age of the cohort. The corresponding adjustment factor for rams was 0.136 kg per day. For twin-born ewes, 2.3 kg was added and 3.2 kg for twin-born rams.

From 1962 to 1983, all weaning weights were adjusted for age by applying the following procedure:

$$WWC_i = \frac{(WW_i - BW_i)}{AAW_i} \times AAW + BW_i$$

where

WWC_i = corrected weaning weight for individual i ;

WW_i = observed weaning weight for individual i ;

BW_i = observed birth weight for individual i ;

AAW_i = age at weaning of individual i ;

AAW = age at weaning of cohort.

The weaning weights of twin-born rams and ewes were corrected using the difference between twin-and single-born lambs. Lambs with black wool or physical faults were culled at weaning in all lines throughout the experiment.

2.2.6 Suspension of selection

Between 1983 and 1994, selection was suspended in the selection lines. Replacement rams and ewes were chosen at random within each flock. The selection lines were dispersed in 1995.

2.3 Environments

2.3.1 Locations

The Trangie Agricultural Research Centre (A.R.C.), located outside the town of Trangie, is situated in the lower Macquarie Valley of the Central Western Plains of New South Wales. The research centre occupies approximately 4500 hectares of very flat flood plain. It has an elevation of 219 metres above sea level and is located at latitude 31°59'S. The UNE Kirby Research Station is located approximately 7 kilometres from the city of Armidale in the New England Region of New South Wales. The station comprises 746 hectares with an elevation of 1090 metres and is located at latitude 30°26'S.

2.3.2 The Trangie environment

2.3.2.1 Rainfall

The average annual rainfall based on meteorological data from 1987 to 1992 is approximately 484 mm. From 1983 to 1992, the average annual rainfall was 454 mm. For this ten-year period, the annual distribution of rainfall was variable with April registering the highest mean rainfall (88 mm) and September registering the lowest mean rainfall (24 mm) as shown in Figure 2.1. On a seasonal basis, the highest and lowest rainfall amounts were recorded during autumn and spring, respectively.

Evaporation levels were highest in late spring and summer indicating that autumn and winter rainfall is most effective. Biddiscombe *et al.* (1954) reported that the botanical composition and quantity of spring pastures were largely determined by the amount of rainfall in the months of March and April.

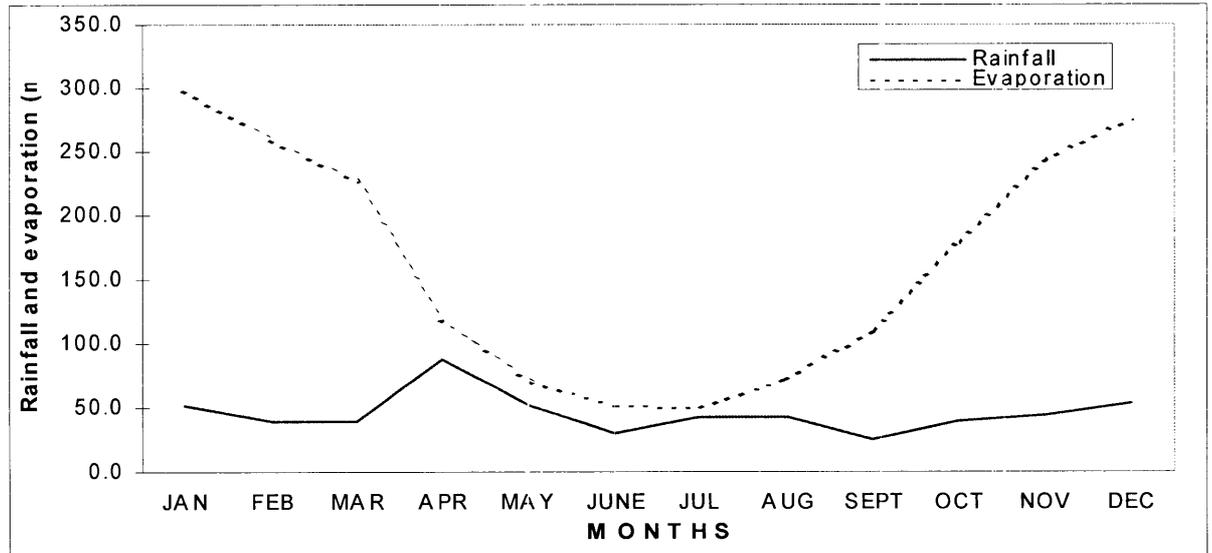


Figure 2.1 Monthly rainfall and pan evaporation at Trangie A.R.C, (1983-1992)

2.3.2.2 Temperature

Figure 2.2 shows the pattern of maximum and minimum screen monthly temperatures. For the ten year period, the highest maximum temperature was 32.8 °C in February and lowest was 15.0 °C in July. The highest average monthly minimum temperatures was 18.4 °C in February and lowest was 3.8 °C in July, respectively.

Frosts occurred from April to December with August as the peak month with 9.8 average frost days (Figure 2.3). There were on average 36 frost days annually within the ten-year period.

2.3.2.2 Soil

Approximately 75% of the Trangie district is composed of light textured soils (Biddiscombe 1953). This group includes greyish-brown sands, sandy loams and loams overlaying light clay. The remaining 25% of the soils are black earths and grey, brown and red clays. In general, these soils are extremely fertile and grass growth is rapid when rain falls.

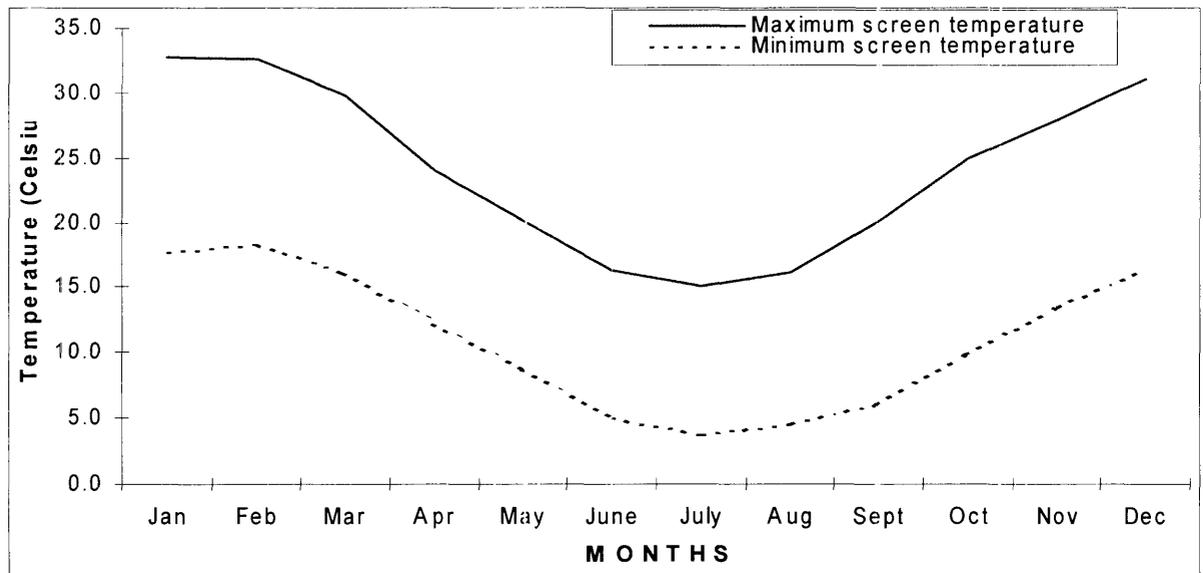


Figure 2.2 Average maximum and minimum screen temperature at Trangie A.R.C. (1983-1992)

2.3.2.3 Pasture species and grazing

Sheep involved in the experiment grazed natural pastures most of the year. Perennial grasses dominated these pastures, but under grazing pressure, increasingly higher proportions of annuals began to dominate. Perennial grasses, which dominated in spring and summer, included spear grass (*Stipa* spp), wallaby grass (*Danthonia semiannularis*), *Eragrostis*, *Digitaria* and *Enneapogon* species (Robards and Milchalk 1978). The annuals, which provided the bulk of feed during autumn and winter, included barley grass (*Hordeum leporinum*), crowfoot (*Erolium* spp) and medics (*Medicago* spp) (Biddiscombe *et al.* 1954). During periods of low pasture availability, the sheep were given free access to dry-land lucerne and in times of drought were supplemented with oaten grain.

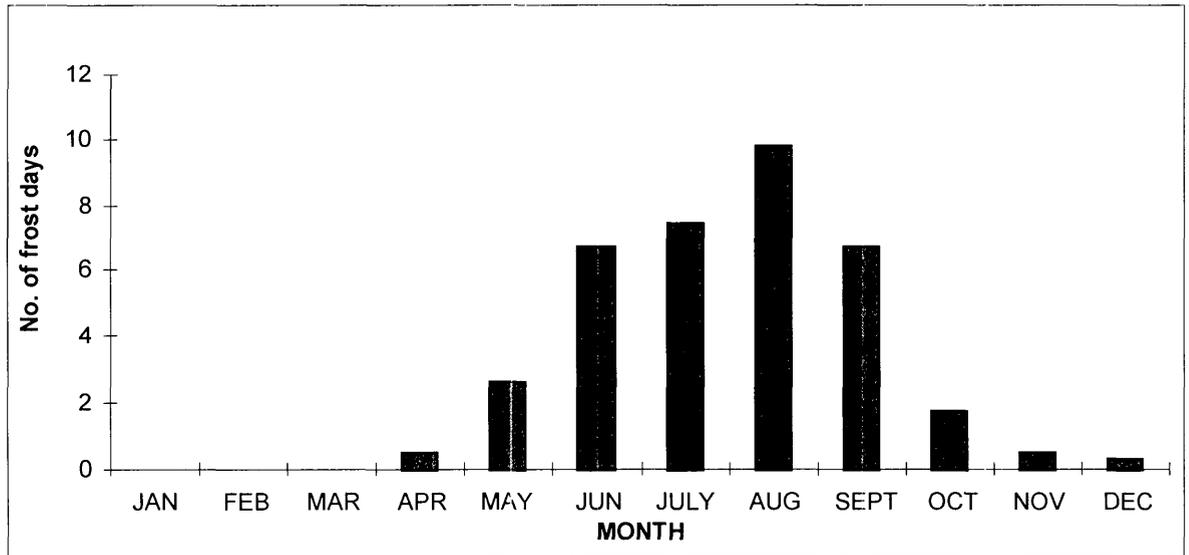


Figure 2.3 Monthly number of frost days at Trangie A.R.C. (1983-1992)

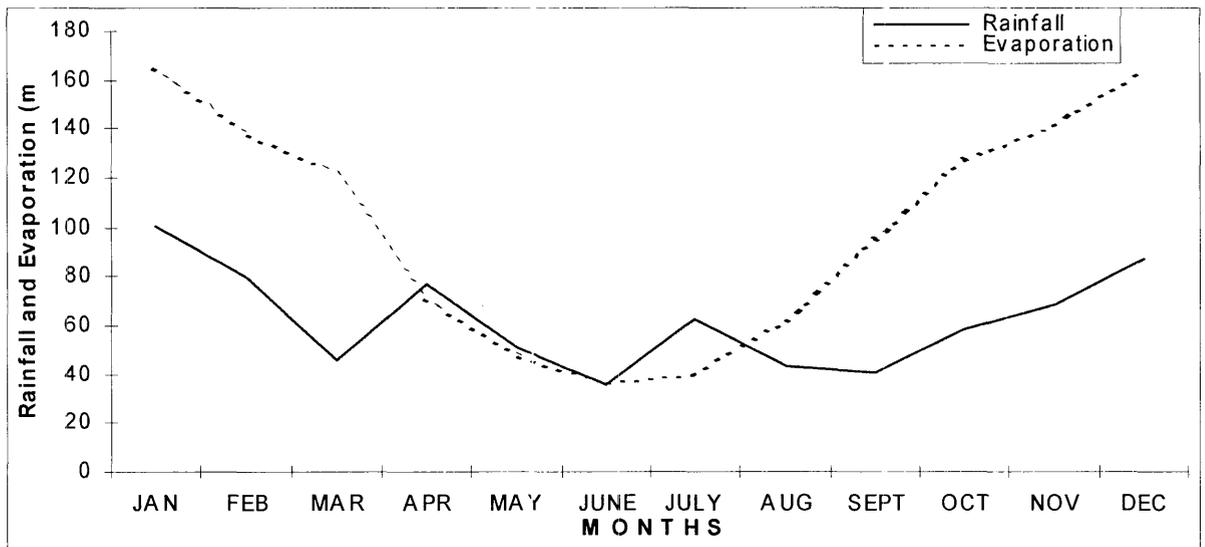


Figure 2.4 Monthly rainfall and evaporation at Armidale, NSW (1983- 1992)

2.3.3 The Armidale environment

2.3.3.1 Rainfall

The average annual rainfall of Armidale from 1983 to 1992 was 624.17 mm. Rainfall was highest during summer and lowest during the winter season. January was the wettest month (100.34 mm) and June the driest month (35.14 mm) (Figure 2.4). However, since evaporation is highest during summer and lowest during winter, rain is found to be most effective during the autumn and winter season (Davis 1987).

2.3.3.2 Temperature

For the ten-year period, the average monthly maximum temperature was observed to be highest in January at 25.9 °C and lowest in July at 11.6°C (Figure 2.5). Records showed that the average monthly temperature never exceeded 30°C between 1983 and 1992. July registered the lowest average monthly minimum temperature (0.2°C) and the highest was recorded in February (12.3°C). During the winter season, minimum monthly temperatures would sometimes be below freezing.

Frosts were observed on average for 90.6 days per year between 1983 and 1992. Frosts occurred from the month of March to December, with August as the peak month (18.1 days, see Figure 2.6.)

2.3.3.3 Grazing areas

The sheep normally grazed on a phalaris (*Phalaris tuberosa*) and white clover (*Trifolium repens*) pasture. Other grasses found in the pasture included perennial *Danthonia* species and the annuals *Poa* and *Festuca* species. During poor pasture conditions, the animals were supplemented with lucerne hay (*Medicago sativa*) and sorghum grain.

2.3.3.4 Soil

The part of Kirby Research Station on which the sheep grazed was a self-mulching soil of basalt origins. The soil is naturally fertile but additional phosphate fertilisers were added annually.

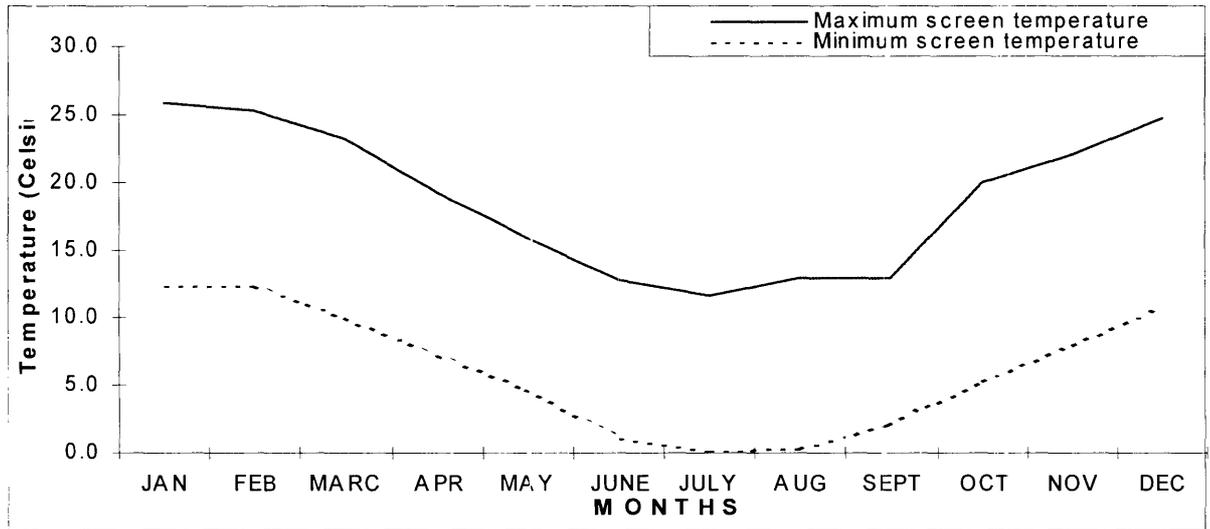


Figure 2.5. Average monthly maximum and minimum screen temperature at Armidale, NSW (1983-1992)

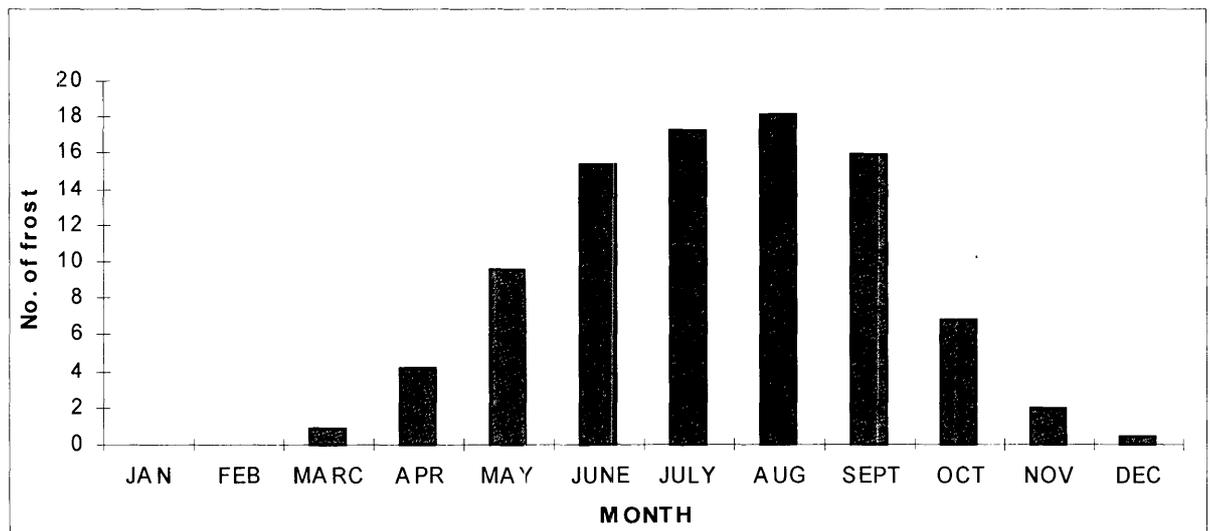


Figure 2.6 Monthly number of frosts at Armidale, NSW (1983-1992)

2.4 Management and observations

2.4.1 Mating routine at Trangie

Two or three weeks prior to the commencement of mating, all selected rams, including reserves, were electro-ejaculated to test for semen quality. Those failing to produce semen of good motility were rejected in favour of the reserves.

In the selection lines, artificial insemination (A.I.) was used in the period 1951-1961 (Marrant and Dun 1960). High dose rates of sperm were used and poor collection specimens were rejected. A.I. was carried out for three weeks and was followed by three weeks of natural mating using one ram to 40-50 ewes. For the Random line, 8 out of 10 selected sires were used for A.I. while the remaining two were used for single sire matings to 40-50 ewes each.

From 1962 to 1982, there was single-sire natural mating in the selection lines for five weeks, with one ram per twenty ewes. Rams were selected based on the selection procedures described in section 2.2.4. Rams were replaced if return to service rates were high as detected by sire-sire harnesses. From 1983 to 1992, single-sire natural mating was still being used but sires were selected at random in each line.

Ewe numbers for the selection lines were influenced by the following studies: a genotype x environment interaction experiment (1983 - 1987) reported here and a cross-over experiment designed to separate direct (or individual) and maternal components of selection response and evaluate effects of inbreeding (1989 - 1992).

From 1973 onwards, matings in the Random line were single-sire joinings using 25 rams to 200 ewes or one ram per eight ewes. Each joining lasted for 5 - 6 weeks and ewes were regularly inspected for return to service marks. In all years and in all lines, no artificial methods of synchronising ewes were used.

As in the selection lines, the ewe numbers were influenced by the same studies mentioned earlier, plus behavioural studies and other comparative studies of wool attributes.

2.4.2 Lambing routine at Trangie

From 1951 to 1961, ewes from the selection and Random lines were lambed together along with the ewes from the Folds Plus and Minus flocks described by Dun (1964), forming an initial lambing mob of 400-500 ewes. Lambs were identified with their mothers by a technique known as ‘mothering’ whereby ewes and their new-born lambs were mustered into a small portable yard every 2 to 3 days. This technique enabled lambs to be identified with their dams and subsequently ear-tagged and recorded. Ewes that did not possess a lamb were examined and were classed on their udder condition as ‘dry’ or having ‘lambled and lost’ the lamb or lambs.

McGuirk (1973) reported that this technique prevented recording of lambs that died shortly after birth, thus increasing the proportion of ewes classed as lambled and lost. In addition, the early death of one or more individuals from a litter may have resulted in the underestimation of litter size.

Lambs identified by the mothering technique were ear-tagged. All male lambs remained entire except for lambs born in 1951 and 1952. Lambs were tail-docked from 1 to 4 weeks of age and ‘mulesed’ against blowfly strike at weaning.

Between 1962 to 1992, ‘drift lambing’ was used as the lambing routine technique with the selection lines being lambed together in the same group. Drift lambing involved moving the lambing group so that ewes with lambs were left behind and dry ewes that had not lambed were moved to an adjacent paddock. This was a daily routine and thus newborn lambs were easily identified with their mothers and difficult births could be assisted. All lambs were ear-tagged and weighed, including those that died shortly after birth. Lambs were tail-docked and ‘mulesed’ at 4-7 weeks of age. Two days later, the lambs and their dams were removed from the drift paddocks.

The average age of lambs weaned from 1983 to 1992 ranged from 50 to 156 days, with earlier years generally having higher average weaning ages. All lambs were weighed and scored for degree of skin wrinkle (fold score) at weaning. All rams not selected were then disposed of and rams and ewes were managed separately.

2.4.3 Mating and lambing routines at Armidale

In 1983, selection for weaning weight was suspended. All joinings between 1983 and 1987 were conducted using rams selected randomly within each line from Trangie-bred rams. Five to ten rams per line were used each year. These rams were used at Trangie for joining in February - March and then transported to Armidale for an April joining. The first joining in Armidale occurred in April 1983.

All ewes were weighed prior to mating, then allocated to sire groups for single-sire joinings. The joinings lasted for five weeks and, a month later, ewes were joined with harnessed teaser rams to identify those ewes that had failed to conceive during the mating period.

Lambing was carried out using a drift system similar to that used for the Trangie flocks with lambs and ewes identified as they were removed from lambing paddocks 4 to 10 days post-partum. Lambs were marked, "mulesed" and vaccinated at 3-4 weeks. The average weaning age of lambs from 1983 to 1992 ranged from 60 to 160 days. All lambs were weighed and scored for degree of skin wrinkle (fold score) at weaning.

Table 2.1 Lamb and hogget production traits analysed in this study with their units and abbreviations.

Traits	Abbreviations	Units
<i>Lamb traits</i>		
Birth weight	BWT	kg
Birth-coat score	BCS	score
Weaning weight	WWT	kg
Growth rate	GR	grams/day
Nine-month weight	NMWT	kg
<i>Hogget production traits</i>		
Greasy fleece weight	GFW	kg
Skirted fleece weight	SFW	kg
Clean fleece weight	CFW	kg
Yield	YLD	percent (%)
Fibre diameter	FD	microns
Off-shear live weight	OBWT	kg
Live weight	LW	kg

2.4.4 Measurements

Measurements were taken on lambs and hoggets for the various traits throughout the experiment. Not all traits measured at Trangie were recorded at Armidale (e.g. fleece traits) and there were some data not recorded in some years. Abbreviations of the various traits are shown in Table 2.1 and these abbreviations will be used where possible throughout the thesis.

The description of the environments, flocks, selection policy and the traits recorded for the weaning weight selection flock provides the bases for the detailed examination of the data that follows. In the chapters that follow various aspects of the direct and correlated responses to selection for weaning weight, genotype by environment interactions and the impact of suspension of selection will all be examined.

Chapter 3

Line, environmental and direct and maternal effects for lamb and hogget traits

3.1 Introduction

Selection is a differential reproductive rate resulting from the deliberate choice of animals to be parents of the next generation. It is one of the primary forces by which breeders can improve the genetic composition of their herds. Selection for weaning weight is generally recommended as an integral part of most performance recording schemes aimed at improving meat production in sheep. It is a common practice to select on weaning weight because it is a measure of both growth and a dam's ability to raise heavier lambs.

Live weights, in particular birth and weaning weights, and wool traits are determined not only by its own genetic potential but also by maternal environment. In young animals, the milk supply of their dam, and her mothering ability contributes greatly to their growth. Effects of the uterine environment and extra-chromosomal inheritance may also have an effect (Meyer 1992a). Studies have clearly shown that the genotype of the dam clearly affects the phenotype of the young through a sample of her direct, additive genes for growth as well as through her genotype for maternal effect on growth. Hence, selection programmes aimed at improving growth need to account for both direct and

maternal effects in order to achieve optimum genetic progress. To achieve optimum progress in a selection programme, it is therefore important that both direct and maternal components should be taken into account.

Falconer (1989) enumerated the three causes of maternal effects. These are the maternal additive effect, which are due to the dam's own genotype for milking and mothering ability; the permanent environmental effects are those effects that are consistent between each lambing of a dam but not genetic in origin; and, those specific to one litter of a dam or the temporary environmental effect. If females have several litters at which they bear more than one young, variation due to each of those effects may be separated.

The Restricted Maximum Likelihood (REML) has become a popular tool in the estimation of (co)variance components and genetic parameters. Meyer (1994) reported that REML analyses allow direct and maternal effects and (co)variance components to be separated when fitting both dam's genetic and dam's permanent environmental effects. In univariate analyses of birth, weaning, yearling and final weights for three breeds of Australian beef cattle, Meyer (1992a) reported that direct heritability estimates were inflated substantially, in particular for growth till weaning, when maternal effects were ignored. Significant maternal effects were also found in all analyses except for final weight in Angus and there were marked differences between breeds in the relative magnitude of direct heritability and the maternal heritability, and the direct-maternal genetic correlation. In sheep production, recent analyses of data from random-bred populations of Merino sheep, fitting animal models and using REML procedures (Hickson *et al.* 1991, Mortimer and Atkins 1994, Swan and Hickson 1994 and Vaez Torshizi *et al.* 1995) have shown that maternal effects carry over to influence live weights recorded post-weaning in growing Merino sheep. Mortimer and Atkins (1996 – personal communication) also reported that allowing for significant maternal effects in models avoided over-estimation of genetic parameters, and in the improvement of Merino growth, ignoring maternal effects caused substantial errors in prediction of responses from direct and particularly indirect selection.

Year, season, sex, type of birth and rearing and age of dam exert important influences on sheep productivity. The superiority of some animals could be due to more favourable environmental conditions than any genetic advantage that they may have. Since selection for breeding rams and ewes involves comparison of animals under varying

environmental conditions, accuracy of selection could be enhanced if attention was given to accounting for environmental factors before any selection was carried out.

The main purpose of the present study was to estimate variance components and genetic parameters using an animal model fitting direct additive, maternal genetic and permanent maternal environmental effects for lamb and hogget production traits of Merino sheep selected for weaning after the suspension of selection. The effects of environmental line and environmental factors such as sex, year, birth and rearing types and age of dam are also presented.

3.2 Review of Literature

3.2.1 Environmental effects on production traits

Selection for breeding rams and ewes involves the comparison of individual records in a variety of environmental states. These conditions may include sex, type of birth and rearing, year of birth and age of dam. The superiority of selected animals may be due to more favourable environmental conditions rather than to any genetic advantage. Confusion of environmental advantage with genetic gain will reduce the effectiveness of selection to produce genetic improvement. Thus, accuracy of selection may be increased by adjusting for important environmental effects before selection is made.

3.2.1.1 Sex effects

3.2.1.1.1 Growth traits and lamb survival

Current selection practices in Australian Merinos are such that selection is carried out within each sex. Therefore, there is no need to adjust information in this respect or consider it in selection decisions except when using information from various relatives in selection decisions when relatives are of differing sexes. Results suggest that sex adjustment would be required for weaning weight, growth rate, clean fleece weight, fibre diameter, crimps and staple length but not for yield. Caution is required in the

interpretation of results related to sex effects since the separation of the sexes after weaning may contribute to the observed differences (Walkley *et al.* 1987; Davis 1987a).

Sex has been shown to be a significant source of variation for most growth traits with ram lambs heavier at birth and at weaning (Davis 1987, Sidwell and Miller 1971b, Hohenboken *et al.* 1976b). Male lambs expressed a weight advantage over female lambs at birth of 0.21 - 0.29 kg for Merinos, 0.30 - 0.54 kg for Corriedales and 0.73 kg for Polwarths in the study of Mullaney (1969). Similar differences were also reported by Hight and Jury (1970) and Lax and Turner (1965) for Merinos and by Gunn and Robinson (1963) for English breeds. Bichard and Cooper (1966) also reported that at birth, male lambs were 5% heavier than female lambs and the difference was maintained at 21 to 42 and 112 days old. Ercanback and Price (1972) reported a significant influence of sex on growth rate of both inbred and non-inbred lambs to weaning.

Female lambs normally have had higher survival rates than male lambs (Lax and Turner 1965, Mullaney 1969). Hight and Jury (1977) reported a difference of 4.6% which agrees with the 1 - 9% estimates reviewed by Gunn and Robinson (1963)., However, Atkins (1978) and Davis (1987) found no influence of sex on lamb survival. On the other hand, the death rate of males is generally higher than that of females at any time prior to weaning (Mullaney 1969).

3.2.1.1.2 Wool traits

Yearling rams outperformed yearling ewes in most fleece traits. Greasy fleece weights, clean fleece weights, staple length and face covering were greater for rams, with the greatest difference found in greasy fleece weight in the study of Terril *et al.* (1948b). Walkley *et al.* (1987) also found that ram lambs have finer wool with lower crimps. Jackson and Roberts (1970) reported significant differences between sexes for face cover, neck fold, body folds, yield, total folds, fibre diameter and fibre density. However, crimp frequency, character, handle and colour, were non-significantly different. Young *et al.* (1965), disagreed, reporting that sex differences were negligible for fleece weights.

3.2.1.2 Birth and birth-rearing types

3.2.1.2.1 Growth traits and lamb survival

The growth handicap of twins is the result of both pre-natal and post-natal influences. The pre-natal influence on growth handicap of twins is due to the competition between foetuses for a limited supply of nutrients (Dun and Grewal 1963). Single born lambs have been found to be generally heavier than twins or multiple-born lambs (Purser and Young 1964, Mullaney 1969, Carter *et al.* 1981b, Sidwell and Miller 1971b, Hohenboken *et al.* 1976b, Smith 1977, Hinch *et al.* 1977, Davis 1987). These differences are usually in the order of 15 to 25% (Bogart *et al.* 1957, Starke *et al.* 1958, Turner 1961; Purser and Young 1964, Atkins 1978). Atkins (1978) noted that type of birth was a greater source of variation in both birth weight and growth rate than sex or age of dam, a finding which confirmed the results of previous studies by Blackwell and Henderson (1955), Vesely and Peters (1964), Sidwell and Miller (1971b) and Hight and Jury (1977).

The post-natal handicap for twins has been linked to the mother's inability to feed and care for several lambs as adequately as she can care for one. Milk supply per lamb is reduced (Dun and Grewal 1963) and the association between milk supply and growth rate is most marked during the first few weeks of life when the lamb is entirely dependent on milk for nutrients (Guyer and Dyer 1954, Slen and Banky 1961). Birth and rearing type has an effect on weaning weight according to various reports (Hohenboken *et al.* 1976, Walkley *et al.* 1987). Reported differences range from 7.5% (Sidwell and Miller 1971b); 11% (Dun and Grewal 1963 and Young *et al.* 1965, to a high of 14% (Davis 1987). Walkley (1987) and Gregory and Ponzoni (1981b) reported an average difference between single and twin born lambs of 2.05 kg and 2.09 kg at weaning, respectively.

The effect of an animal born as multiple and raised as a single is intermediate between the effects of single-single and multiple-multiple birth-rearing types for weaning and mature live weights (Walkley *et al.* 1987, Mortimer and Atkins 1989). Differences between singles and twins have been found to be greater at weaning than at other ages, and with weight penalties still evident at 15-16 months of age (Lax and Brown 1967) and even up to 18 months when a 3% difference was reported by Lax and Turner (1967). Post-weaning average daily gain is also influenced by rearing type. Sidwell and Miller (1971b) reported a 9.29 % difference and Davis (1987) a 14% difference between single and twin

born lambs. Olson *et al.* (1976) and Carter *et al.* (1971b) reported similar findings. In contrast, Hohenboken (1977) found no significant influence of birth type on post-weaning average daily gain.

Higher survival rates are associated with single-born lambs across many genotypes (Sidwell *et al.* 1962, Mullaney 1969, Sidwell and Miller 1971b, Hight and Jury 1970; Smith 1977). Dalton *et al.* (1980) reported an overall mean survival rate of 83% for singles and 73% for multiples for a variety of breeds. However, the advantage of an extra lamb born was still apparent as the survival rate of the twin lambs to weaning was not less than half that of the single lambs (Mullaney 1969, Hight and Jury 1970, Lax and Turner 1965).

3.2.2.1.2 Wool traits

Mortimer and Atkins (1989 and 1993) reported that birth and rearing types had large effects on hogget fleece weights (clean fleece weight, greasy fleece weight and skirted fleece weight), wool quality (fibre diameter and staple length) and component traits of the hogget fleece (fold cover, leg cover, neck fold, body fold, suint, dust penetration, follicle density and follicle ratio). Birth and rearing types was a relatively large source of variation for greasy fleece weight, clean fleece weight and skirted fleece weight, accounting for 3 - 6% of the total within-flock variation. For fibre diameter and live weight, this effect accounted for only 1%. The effect of multiple birth type raised as a single on fleece weight is intermediate between the effects of single-single and multiple-multiple birth-rearing types, with the penalty in fleece weight suffered by multiple born and reared ewes being about 7% (Mortimer and Atkins 1993). Turner (1961) found 5.3% less clean wool for multiple born lambs compared to single born lamb.

Other published reports have shown that type of birth and rearing significantly influence greasy fleece weight and clean fleece weight but not yield, staple length and fibre diameter (Terril *et al.* 1948a and 1948b, Walkley *et al.* 1987, Sidwell *et al.* 1971). Differences for greasy fleece weight between singles and twin born and reared lambs ranged from a low of 0.18 - 0.23 kg to a high 0.37 - 0.47 kg. Between singles and twins reared as singles, differences ranged from 0.09 kg to 0.17 - 0.29 kg (Terril *et al.* 1948b, Turner 1961, Young *et al.* 1965). For clean fleece weight, Atkins (1978) reported that

animals born and reared as multiples produced 0.2 kg (0.44 lb) less clean wool, similar to the estimates of Turner (1961).

Lambs born as multiples suffered penalties that were still evident up to 18 to even 30 months of age (Mullaney and Brown 1967). Multiple born animals were handicapped for fleece weight at 18 months, with 32% and 26% less grease and clean wool weight than single born animals (Young *et al.* 1965). The reduction in clean wool production in twins is apparently entirely associated with a reduced number of secondary fibres per sheep, the effect of the twins' decreased surface area being balanced by a proportionate increase in the density of primary fibres (Dun and Grewal 1963). The maturation of secondary follicles is delayed due to the limited nutrient supply in the early post-natal period (Schinkel, 1953, 1955). Turner (1961) showed that a reduced secondary to primary follicle ratio was still apparent in 15 months old twins and accounted for the majority of their reduced clean wool production.

3.2.1.3 Year effects

3.2.1.3.1 Growth traits and lamb survival

Many published reports have concluded that year is a major factor influencing various measures of pre-weaning and post weaning growth traits, and that differences between years are often highly significant due to large variations in climatic conditions. Year has been shown to significantly affect birth weight (Atkins 1978, Carter *et al.* 1971b, Sidwell and Miller 1971b, Hight and Jury 1970, Smith 1977, Davis 1987, Hohenboken 1988), weaning weight (Carter *et al.* 1971a, Sidwell and Miller 1971, Hohenboken *et al.* 1976b and 1977, Smith 1977, Hight and Jury 1970, Atkins 1978, Walkley *et al.* 1987, Davis 1987), mature weight (Brash *et al.* 1997) and growth rate (Atkins 1978, Davis 1987). Demiroren *et al.* (1993) reported that although year effects were important for most traits, they appeared to be random and to follow no consistent trend. Hinch *et al.* (1985) suggested that there are environmental and /or management influences over and above nutritional differences associated with varying lamb birth weights.

Survival rate is also significantly influenced by year effects (Carter *et al.* 1971a, Hight and Jury 1977, Atkins 1978, Sidwell *et al.* 1971b). Year effects caused a range in

mean survival rate from 66 to 85% in the study of a variety of breeds by Dalton *et al.* (1980).

3.2.1.3.2 Wool traits

Differences between years was the most important effect upon yearling wool traits of Rambouillet, Columbia and Targhee rams in the studies of Terril *et al.* (1948a and b). Differences between years were significant for greasy fleece weight, clean fleece weight and neck folds and for staple length in the Rambouillet lambs. A similar significant effect of year has also been recorded for staple length, fibre diameter and coefficient for variability of fibre diameter (Sidwell *et al.* 1971, Atkins 1978, Walkley *et al.* 1987).

Mortimer and Atkins (1989,1993) reported that year was a significant source of variation in Merinos for various hogget fleece weights and wool quality traits. They found that the maximum differences between years over all flocks in average performance were 4.0 to 4.7 kg for greasy fleece weight, 19.5 to 21.9 mm for fibre diameter, 27.9 to 43.8 kg for live weight and 88.0 to 104 mm for staple length. Year also accounted for less than 10% of the total variance for component traits of hogget fleece except for follicle ratio (22.4%) and dust preparation (37.7%). The range between years in mean follicle ratio was 13.7 to 20.4 total follicles per primary follicle and dust penetration 35.3 to 61.2 mm. Brash *et al.* (1997) reported similar significant year effects for greasy and clean fleece weights, fibre diameter for 10-month old Merinos and greasy and clean fleece weights for 16-month old Merinos.

3.2.1.4 Age of Dam

3.2.1.4.1 Growth traits and lamb survival

Age of dam shows a characteristic curvilinear effect on the birth weight of lambs with maximum performance from progeny of intermediate age and lower performance from progeny of 2-year old and older ewes (Hohenboken *et al.* 1976). In the studies of Atkins (1978), Bichard and Cooper (1966) and Mullaney (1969), birth weight increased progressively with increasing dam age up to five years and to the third pregnancy for English hill flocks (Yalcin and Bichard 1964).

Weaning weight is also significantly influenced by age of dam (Sidwell and Miller 1971b, Hohenboken *et al.* 1976). Shelton and Campbell (1962) studied the influence of dam age on the weaning weight of Rambouillet lambs for ages 2 to 10 years and older. They found a steady rise in weaning weight to 5 years, followed by a steady decline thereafter. Using the progeny of 2-year old dams as a base, they estimated an increase of 9.2 % for the progeny of 5-year old ewes and a decrease of 5.5% for the progeny of ewes 10 years and older. Vesely *et al.* (1965, 1966) found a similar rise and fall in the weaning weight for Canadian breeds, but with smaller differences: progeny of 4-year old ewes were 5.2% above and those of 7-year old ewes less than 1% below those of 2 year-old ewes.

Olson *et al.* (1976) reported that lambs from 3 to 7 year-old ewes grew faster than lambs from younger and older ewes from 0 to 14 weeks. However, lambs from very young and very old ewes compensated their pre-weaning handicap by growing faster after 18 weeks. The curvilinear age of dam effect in growth rate is similar to the findings of Thrift and Whiteman (1969) and Dickerson *et al.* (1972). Bichard and Cooper (1966) reported that lambs from one-year old ewes were 25% lighter at birth than lambs from mature ewes and 10% lighter than those from 2-year old ewes. At 21 and 42 days, weights of lambs from mature ewes retain their advantage but by 112 days, age of dam became less important. Similarly, Demiroren (1995) reported that ewes lambing at 20 months produced significantly more total lamb weight than did 12-month old ewes by 48% at birth, 39% at 21 days and 35% at 91 days. The decline towards weaning is possibly due to the increasing independence of lambs from their mother's milk. Sidwell and Miller (1971b) reported variations in average daily gain although differences were less marked. However, the data reported by Davis (1987) for the weaning weight selection lines suggested that age of dam was not a significant source of variation for either weaning weight or growth rate to weaning although no reason was given.

Lamb survival has been shown to increase with ewe age until a peak is attained between four and seven years of age (Bowman 1966, Lax and Turner 1965, Turner and Dolling 1965, Vesely and Peters 1965, Sidwell and Miller 1971a). The lower survival rate of lambs from younger ewes suggests that 2-year old ewes require better management than the older group of ewes (Dalton *et al.* 1980). Lax and Turner (1965) reported that the age of ewe effect on lamb survival varies with environment. In a nutritionally poor environment, the relationship between survival and age of ewe was very marked, reaching

a peak at 5 years. Improving the pasture increased the survival rate and decreased the dependence on age of dam with a peak still at five years. In a nutritionally good environment, there was little relationship between survival rate and age of dam. They concluded that improved environment and proper management increases the survival rate of all lambs.

Hinch *et al.* (1985) and Dalton *et al.* (1980) stated that effects of ewe age were accounted for by differences in the birth weights of lambs from young and older ewes. They argued that ewe age is probably of minor importance to overall lamb survival in high fecundity flocks as the proportion of 2-year old ewes having large litters (>3) is lower than older ewes (Allison *et al.* 1982) and the proportion of 2-year old ewes in commercial flocks rarely exceeds 30%. They recommended preferential husbandry (feeding and management) of prolific young ewes which may advantage lamb survival.

3.2.1.4.2 Wool traits

Mortimer and Atkins (1989,1993) reported significant effects of age of dam on greasy fleece weight, clean fleece weight, skirted fleece weight, live weight and staple length but non-significant effect for fibre diameter, yield and for all component traits of the hogget fleece. However, variations due to age of dam were a negligible proportion of the within-flock variation for all traits. The progeny of 2-year old ewes were less productive as hoggets than progeny of adult ewes, although the effects were much smaller and were in broad agreement with the estimates reported by Young and Turner (1969). Terril *et al.* (1948a, b) found significant effects of dam age only for greasy fleece weight from Columbia sheep and for clean fleece weight from Rambouillet sheep. The advantage of mature dams over 2-year old dams was 0.41 kg for clean fleece weight for Columbia sheep and 0.14 kg for Rambouillet sheep.

Lax and Brown (1967) examined dams grouped into four-age-groups: 2, 3, 4-7, 8-10 years. They reported that greasy and clean wool weights and wrinkle score rose for offspring of both sexes to a peak for 4 - 7 year-old dams, followed by a slight decline. Fibre diameter and staple length reached a peak for 3 year-old dams for ewe progeny and for 4 - 7 year-old dams for ram progeny. They concluded that the small decline in older dam age-groups was not sufficient to invalidate the usual practice of adjusting only the progeny of 2-year old dams. Vesely *et al.* (1965) reported that in general, the progeny of

2-year old ewes have lower wool weights, wrinkle score and number of fibres per sq. mm. of skin. However, staple length and the effect for fibre diameter was variable and only available for one flock (Vesely *et al.* 1965).

Although no dam age effect was found to be significant for the traits studied, Walkley *et al.* (1987) observed the tendency for offspring of 2-year old dams to have lower greasy fleece weight, clean fleece weight and weaning weight. For clean fleece weight, lambs of 2-year old ewes were 0.06 kg lighter which is similar to the 0.08 kg reported by Gregory and Ponzoni (1984 and 1985) but less than the WOOLPLAN adjustment factor for 2-year old ewes of 0.2 kg. Sidwell *et al.* (1971) found no significant effects of dam age on wool traits studied.

3.2.2 Phenotypic and genetic parameters

Heritability, phenotypic and genetic correlations are the genetic and phenotypic parameters that are important in designing any selection program. This review presents recent estimates of genetic and phenotypic parameters for growth and wool production traits for Australian Merinos. Estimates for other breeds are also presented for the purpose of comparison.

3.2.2.1 Heritability

Heritability is arguably the most important single concept in the application of animal breeding (Hill 1994). Heritability refers to that portion of the total phenotypic variation controlled by genes. It is that part of the total variation that can be transmitted to the next generation by the gametes (Stufflebeam 1989). Heritability can be defined in two different ways:

Heritability in the narrow sense (h^2) is defined as the ratio of the additive variance to the phenotypic variance;

$$h^2 = \frac{V_A}{V_P}$$

where V_A is the additive genetic variance and V_P is the phenotypic variance.

Heritability in the narrow sense determines the degree of resemblance between relatives and is therefore of the greatest importance in breeding programs (Falconer, 1989). It is the proportion observed variance that can be passed on from generation to generation. Because the concept of heritability is most commonly used with animals in relation to selection programs, and since it is breeding values that are of prime importance in selection programs, the term *heritability* is normally used in this narrow sense.

Heritability in the broad sense (h^2_B) describes the relative contribution of genotypic variance to phenotypic variance:

$$h^2_B = \frac{V_G}{V_P}$$

where V_A is the total genetic variance and V_P is the phenotypic variance.

$$V_G = V_A + V_D + V_E$$

where V_D is dominance and V_E is epistasis.

In this case, it describes the proportion of the total variance that is due to the differences among the breeding values of the individuals in the population (Van Vleck *et al.* 1987). It is also called the *degree of genetic determination* and is of more theoretical interest than practical importance (Falconer 1989).

Turner and Young (1969) classified traits of economic importance in sheep based on arbitrary limits of heritability estimates as follows: values of 0.3 or more were regarded as high levels of heritability; values between 0.1 and 0.3 as intermediate or moderate; and those below 0.1 as low levels of heritability.

Many published estimates for heritability are calculated from the intra-class correlation of paternal half-sibs (PHS estimates). Estimates can be obtained from the regression of offspring on parent performance and when the parent is the dam this is referred to as dam-offspring regression (DOS) (Davis, 1987).

Robertson (1977) reported that using analysis of variance techniques to estimate within and between sire variance components results in a biased PHS estimates of heritability when sires are selected and the magnitude of this can be calculated. DOS estimates may be systematically different to PHS estimates when there are maternal

effects on the trait but it does not suffer from selection bias when calculated within sires. Differences between PHS and DOS estimates of h^2 in randomly mating populations have been used as evidence for possible maternal effects on a trait.

In any population with pedigree records it will often be possible to estimate the heritability from different sorts of relatives. It is obviously desirable to make use of all the data by combining the estimates from different relationships, suitably weighted. The preferred procedure for doing this is known as REML (Restricted Maximum Likelihood) which calculates the heritability that would give the greatest likelihood of fitting the observed phenotypic values of all the individuals in the data set (Falconer 1989).

Published heritability estimates by various workers for some traits relevant to this thesis are presented in Table 3.1 on Merinos and other breeds of sheep. Estimates calculated by various methods are also shown.

3.2.2.1.1 Growth traits

Heritability estimates for Merino birth weight have been found to vary from low (Thrift *et al.* 1973, Hancock *et al.* 1979, Davis and Kinghorn 1986, and Davis, 1987) to moderate (Hancock *et al.* 1969, Lewer *et al.* 1994) and to high (Tallis 1960, Lewer *et al.* 1994 and Vaez Torshizi *et al.* 1995). Lewer *et al.* (1994) found birth weight to be moderately heritable for male Merino hoggets and highly heritable among female hoggets, but reported that the difference was not significant. Davis (1987) reported a low heritability for birth weight estimated by Generalized Linear Model (GLM) procedure and moderate heritability estimated by REML.

Most estimates show weaning weight as a highly heritable trait for Merinos (Lewer *et al.* 1994, Lax and Jackson 1987, Davis 1987 and Davis and Kinghorn 1986). Young *et al.* (1965) and Pattie (1965a,b) reported high heritability levels for weaning weight calculated by dam-offspring correlation but only moderate levels when estimated by half-sib correlation. The dam-offspring estimates were greater due to maternal effects.

Growth rate to weaning was found to be moderately heritable by Davis (1987) and lowly heritable by Thrift *et al.* (1973). Post-weaning and mature live-weights are found to be moderately to highly heritable (Gregory 1982b, Skeritt *et al.* 1997, Purvis and Swan 1997, Brash *et al.* 1997).

3.2.2.1.2 Wool production traits

Birthcoat score is highly heritable in all published estimates both in the medium-Peppin (Morley 1955, Davis, 1987) and strong-wool Merino strains (Gregory 1982a). Except for the heritability estimate of 0.16 (Hancock *et al.* 1979) for index male progeny calculated by using half-sib analysis based on sire groups and the location-specific estimates of heritability by Lax and Jackson (1987), all other studies reviewed have shown moderate to high heritabilities for greasy fleece weight. The estimate suggests that heritability levels are similar for fine wool (Mullaley *et al.* 1970), medium fine wool (Young *et al.* 1960 and 1965, Davis, 1987, Mortimer and Atkins 1989) and strong wool types (Gregory 1962a). Mullaney (1970) also indicated a possible increase in heritability of greasy fleece weight from 0.30 to 0.51 with ages at 18 and 30 months, respectively. However, Brash *et al.* (1997) reported otherwise with 10 and 16 month-old Merinos registering heritabilities of 0.40 and 0.28, respectively.

Sex appears not to have an effect on heritability estimate (Lax and Jackson 1987, Young *et al.* 1965) but method of calculation used does (Gregory 1982, Young *et al.* 1965). The half-sib correlation method resulted in a lower heritability estimate than dam-offspring regression method in many reports *e.g.* Gregory 1982b, Hancock *et al.* 1979. The difference is possibly associated with the dam-offspring estimates being inflated by maternal effects (Young *et al.* 1965).

Clean fleece weight is also moderately to highly heritable in most studies with estimates ranging from 0.22 - 0.50 and similar to the values for greasy fleece weight (James *et al.* 1990, Gifford *et al.* 1994, Van Wyk *et al.* 1994). Skirted fleece weight is reported to be moderately heritable (Mortimer and Atkins, 1989), but within the range described for clean fleece weight.

Yield is a very highly heritable trait with most heritability estimates being above 0.35. Heritability estimates for fibre diameter are also high with the exception of the findings of Hancock *et al.* (1979) and Young *et al.* (1965) who used offspring - sire regression methodology. These observations were confusing as the expectation of bias in the regression estimates (*e.g.* maternal effects) predict an increase in the estimates of heritability. The authors attributed the low values of the offspring-sire regression estimates to be due in part to the fact that each ram was mated to several ewes.

3.2.2.1.3 Lamb survival

There are few published heritability estimates for lamb survival but those that have been published are of low level for Merinos (Davis 1987, Davis and Kinghorn 1986) and also for other breeds (Atkins, 1986).

3.2.2.2 Maternal heritability

The term maternal effect implies an influence of the mother on her offspring other than through the genes she transmits to it. The factors responsible for this maternal effect include the cytoplasm of the egg, the uterine environment and the post-natal environment. The post-natal environment includes both the dam's milk production and mothering ability. The dam, therefore, contributes in two ways to the phenotypic value of the offspring while a sire influence his offspring only through genes he transmits.

In a selection program for growth traits in farm animals, it is important that both direct and maternal components be taken into account. Meyer (1992) reported that maternal effects significantly influence traits of beef cattle measured up until weaning. Bradford (1972) suggested that maternal effects are more substantial in sheep than other livestock species because of greater relative variation in litter size in sheep and greater dependence of lambs on their mother milk supply until marketing period or until reaching market weight. Maria *et al.* (1993), Nasholm and Danell (1996), Lewis and Beatson (1996), Notter and Hough (1997) estimated maternal heritability in various lamb weights with the estimates indicating that maternal effects have a significant impact on lamb weights.

Maternal traits of economic importance in Australia have been examined. Analyses by Mortimer and Atkins (1994), Swan and Hickson (1994), Hickson *et al.* (1995) and Vaez Torshizi (1995) have shown that the maternal effects influence pre- and post-weaning weights of growing Merino sheep.

Published maternal heritability estimates by various workers for some traits relevant to this thesis are presented in Table 3.1.

3.2.2.2.1 Growth traits

Most estimates of the heritability of birth weight are moderate. Mortimer and Atkins (1996 – personal communication) reported a heritability estimate of 0.14 while Vaez Torshizi *et al.* (1995) reported a 0.29 estimate. However, Larsgard and Olese (1998) and Jara *et al.* (1998) estimates were in the high levels of heritability.

Most estimates for the maternal heritability of weaning weight are in the moderate level (Swan and Hickson 1994, Mortimer and Atkins 1996 – personal communication; Maria *et al.* 1994 and Vaez Torshizi *et al.* 1995). Jara *et al.* (1998) reported high estimates for weaning weight while Lewis and Beatson (1994b), and Notter (1998). Vaez Torshizi *et al.* (1995) and Lewis and Beatson (1999) reported a low maternal heritability estimate for mature live weight.

There is evidence of a possible decrease in maternal heritability with age as estimates for adult live weight are mostly in the low level, except for the estimates of Vaez Torshizi *et al.* (1994). Estimates for average daily gain were low (Nasholm and Dannel (1994b) to moderate Van Wyk *et al.* (1993).

3.2.2.2.2 Wool traits

Most maternal heritability estimates for the various wool traits were low (Mortimer and Atkins 1994, Swan and Hickson 1994, Olivier *et al.* 1994 and Lewis and Beatson 1999) except for the moderate and high estimates for greasy and clean fleece weights reported by Vaez Torshizi *et al.* (1995). The very low estimates for these traits may suggest that maternal effects need no immediate consideration in a breeding program (Swan and Hickson 1994). However, Hickson *et al.* (1994) reported that maternal genetic effects were important for clean and greasy fleece weights at both 10 and 16 months of age although they found no maternal effect on mean fibre diameter at 12 months.

Table 3.1 Summary of direct additive and maternal heritabilities, permanent environmental effects and direct additive correlations of various sheep breeds.

Trait	Breed	Parameters †				Reference
		h^2	m^2	c^2	r_{AM}	
BWT	Dorner	0.16 ± 0.03	0.43 ± 0.03			Van Wyk <i>et al</i> 1993
	Swedish	0.07	0.30			Nasholm and Dannel 1996
	Merino	0.23 ± 0.02	0.14 ± 0.02	0.12 ± 0.01	-0.40	Mortimer and Atkins 1995
	Romanov	0.04	0.22	0.10	-0.99	Maria <i>et al.</i> 1993
	Merino	0.38 ± 0.04	0.01 ± 0.03		0.57	Olivier <i>et al.</i> 1994
	Merino	0.30	0.29			Vaez Torshizi <i>et al.</i> 1995
	Merino	0.03 ± 0.02	0.13 ± 0.05		0.37	Pitono and James 1995
		0.22 ± 0.06	0.42 ± 0.01	0.04		
WWT	Dorner	0.13 ± 0.03	0.20 ± 0.03			Van Wyk <i>et al</i> 1993
	Merino	0.27 ± 0.03	0.11 ± 0.01	0.07 ± 0.01	-0.20	Mortimer and Atkins 1994
	Merino	0.01	0.1	0.09		Notter and Hough 1997
		0.10	0.05	0.08		
	Merino	0.27	0.42			Vaez Torshizi <i>et al.</i> 1995
	Romanov	0.34	0.25	0.00	-0.98	Maria <i>et al.</i> 1993
	Nor-Dala	0.12 ± 0.11	0.17 ± 0.05	0.10 ± 0.08	0.07	Larsgard and Olesen 1998
Merino	0.06 ± 0.03	0.09 ± 0.06	0.14 ± 0.03	0.201	Pitono and James 1995	
LW	Merino	0.26	0.05	0.05		Notter and Hough 1997
	Merino	0.33 (9mos)	0.08	0.00 ± 0.03	0.12	Mortimer and Atkins 1995
		0.39 (15 mos)	0.04	0.00 ± 0.03	0.42	
	Merino	0.33 ± 0.07	0.12 ± 0.03			Hickson <i>et al.</i> 1995
		0.35 ± 0.07	0.03 ± 0.05	0.13 ± 0.04		
	Merino	0.33 (16 mos)	0.07			Vaez Torshizi <i>et al.</i> 1995
		0.32 (22 mos)	0.08			
ADG	Dorner	0.13 ± 0.02	0.17 ± 0.03			Van Wyk <i>et al</i> 1993
	Romanov	0.26	0.17			Maria <i>et al.</i> 1993
	Merino	0.08	0.04			Pitono and James 1995
	Nor-Dala	0.09 ± 0.01	0.16 ± 0.08			Larsgard and Olesen 1998
GFW	Merino	0.32 ± 0.02 (10mos)	0.11		0.51	Hickson <i>et al.</i> 1995
		0.32 ± 0.04 (10mos)	0.02	0.00 ± 0.01	-0.35	
		0.51 ± 0.049 (12-16mos)	0.08 ± 0.03		-0.37	
		0.51 ± 0.04	0.08 ± 0.02	0.00 ± 0.02	-0.36	
	Merino	0.29 ± 0.04	0.06 ± 0.22			Mortimer & Atkins 1994
		0.33 ± 0.05	0.09		-0.23	
	Merino	0.21 ± 0.06	0.18 ± 0.03		-0.38	Swan & Hickson 1994
		0.29 ± 0.03 (weaner)	0.08 ± 0.03	0.04 ± 0.03		
		0.29 ± 0.04 (12mos)	0.05			

Table 3.1 continued

CFW	Merino	0.29 ± 0.02	0.03	0.00	-0.35	Olivier <i>et al.</i> 1994
		0.31 ± 0.04	0.05 ± 0.02			Olivier <i>et al.</i> 1994
		0.35 ± 0.05	0.09 ± 0.03		-0.31	
	Merino	0.55 ± 0.04	0.07 ± 0.02		-0.51	Hickson <i>et al.</i> 1995
		0.34 ± 0.04	0.13 ± 0.02			
		0.34	0.14		-0.49	
FD	Merino	0.44 ± 0.05		0.01 ± 0.03		Swan & Hickson 1994
		0.44 ± 0.05	0.01 ± 0.03			
	Merino	0.02	0.12		-0.27	Olivier <i>et al.</i> 1994
		0.54	0.17		-0.58	
	Merino	0.67				Mortimer & Atkins 1994
		0.61	0.004			
	Merino	0.62 ± 0.07	0.005 ± 0.03		-0.04	Swan & Hickson 1994
		0.44 ± 0.05		0.01 ± 0.03		
0.44 ± 0.05		0.01 ± 0.03				

† h^2 direct additive heritability; m^2 maternal heritability; c^2 permanent environmental effects; r_{AM} direct additive correlation

3.2.2.3 Permanent maternal environmental effects

Estimates for permanent environmental effects for live weights decrease with age. For birth weight, Mortimer and Atkins (1994) and Maria *et al.* (1994) both reported moderate permanent environmental effects while Tosh and Kemp (1994) reported high estimate of 0.37. Most estimates for weaning weight and mature weight were low (Maria *et al.* 1994, Notter and Hough 1997, Mortimer and Atkins 1994). Permanent maternal environmental effects have a very low influence on wool traits.

3.2.2.4 Phenotypic correlations

Phenotypic correlations between traits are gross correlations that include both the environmental and the genetic portions of the covariances. Phenotypic correlations for traits are important because they directly affect the size of the selection differentials when several factors are used in a selection index. This is especially true when the correlation is high, whether positive or negative (Lasley, 1972).

A correlation, whatever its nature, is the ratio of the covariance to the product of the two standard deviations. Thus, phenotypic correlation is;

$$r_p = \frac{Cov_{P_{XY}}}{\sigma_{P_X} \sigma_{P_Y}}$$

where r_p is the phenotypic correlation between the two traits X and Y, $Cov_{P_{XY}}$ is the phenotypic covariance of the two traits, σ_{P_X} is the phenotypic standard deviation for trait X and σ_{P_Y} is the phenotypic standard deviation for trait Y.

Table 3.2 presents a summary of published phenotypic correlations between traits within the categories of growth, lamb survival and wool production. Brown and Turner (1968) presented a classification to describe the magnitude of the correlation that is used here, as follows:

<u>Correlation</u>	<u>Classification</u>
< -0.60	high negative
-0.60 to -0.40	moderate negative
-0.40 to -0.20	low negative
-0.20 to +0.20	negligible or very low negative to very low positive
+0.20 to +0.40	low positive
+0.40 to +0.60	moderate positive
> 0.60	high positive.

This classification will be used in the following discussions.

3.2.2.4.1 Growth traits

Based on the published estimates of Davis (1987), Davis and Kinghorn (1986) and Lewer *et al.* (1994), birth weight and weaning weight have a low positive phenotypic correlation and the same is true between birth weight and post-weaning live-weights. Davis (1987) reported a very low but positive association between birth weight and

Table 3.2. A summary of published phenotypic (r_p) and genetic (r_g) correlations estimates for growth, lamb survival and wool production traits of Australian Merino and other breeds

Correlation		Reference	Correlation		Reference
Phenotypic	Genetic		Phenotypic	Genetic	
BWT 0.28±0.02 0.25±0.02	WWT 0.48±0.19 0.88±0.26	Davis and Kinghorn 1986 Davis 1987	0.20±0.02 0.38±0.02	0.07±0.19 0.26±0.02	Lewer <i>et al.</i> 1994
BWT 0.28±0.02 0.26±0.02	LWT 8 weeks 0.22±0.02 11 weeks 0.25±0.02	Lewer <i>et al.</i> 1994 Lewer <i>et al.</i> 1994	0.26±0.03 0.25±0.02	0.36±0.13 0.24±0.02	Davis and Kinghorn 1986 Lewer <i>et al.</i> 1994
WWT 0.84 0.57 0.65 0.63 0.49	LWT yearling 0.94±0.05 0.34±0.31 0.93 0.5 0.83 0.78	Van Wyk <i>et al.</i> 1985 Purvis <i>et al.</i> 1986 Pattie 1965 Gunawan <i>et al.</i> 1985	0.77 0.35	hogget 0.92±0.07 0.95	Van Wyk <i>et al.</i> 1985 Young <i>et al.</i> 1965
GFW 0.81 0.81 0.85±0.01 0.88±0.06 0.81±0.01 0.82 0.87±0.01 0.9	CFW 0.65 0.76 0.80±0.03 0.82±0.04 0.60±0.21 0.77±0.20 0.89±0.03 0.80±0.07	Morley 1955 Brown and Turner 1968 Mullaney <i>et al.</i> 1970 Hancock <i>et al.</i> 1979 Van Wyk <i>et al.</i> 1985 Davis 1987 Walkley <i>et al.</i> 1987	0.87±0.01 0.93 0.82±0.1 0.86±0.05 0.89±0.01 0.87±0.01 0.88±0.01 0.84±0.01	0.87±0.03 0.96±0.03 0.83±0.10 0.86±0.05 0.89±0.01 0.86±0.01 0.89±0.04 0.85±0.06	Mortimer and Atkins 1989 James <i>et al.</i> 1990 Lewer <i>et al.</i> 1994 Brash <i>et al.</i> 1997
GFW 0.04 -0.16±0.03 -0.06 0.02±0.04 -0.08 0.03±0.03 -0.14	YLD -0.18±0.12 -0.27 -0.39±0.10 -0.21 0.17±0.20 0.06 0.10±0.14 -0.11	Mullaney <i>et al.</i> 1970 Gregory 1982b Gunawan <i>et al.</i> 1985 Davis and Kinghorn 1986 James <i>et al.</i> 1987 Davis 1987 Walkley <i>et al.</i> 1987	-0.11±0.04 -0.29±0.16 -0.09±0.19 -0.11±0.02 -0.13±0.03 -0.06±0.03 -0.14±0.03	-0.09±0.13 -0.26±0.16 -0.12±0.18 -0.11±0.02 -0.13±0.03 0.17±0.20 -0.23±0.17	Mortimer and Atkins 1989 Lewer <i>et al.</i> 1994 Brash <i>et al.</i> 1997
GFW 0.06 0.13±0.02 0.36±0.03 0.31±0.04 0.45 0.28±0.03 0.21±0.04	FD 0.19±0.06 0.13±0.02 0.45±0.09 0.60±0.13 0.28±0.17 0.43±0.12 0.27±0.12	Beattie 1961,1962 Brown and Turner 1968 Mullaney <i>et al.</i> 1970 Davis and Kinghorn 1986 Walkley <i>et al.</i> 1987 Davis 1987 Mortimer and Atkins 1989	0.33 0.27±0.15 0.34±0.16 0.24±0.02 0.30±0.03 0.17±0.03 0.22±0.03	0.01±0.27 0.25±0.15 0.34±0.15 0.26±0.02 0.32±0.03 0.36±0.14 0.50±0.15	James <i>et al.</i> 1990 Lewer <i>et al.</i> 1994 Brash <i>et al.</i> 1997

Table 3.2 continued

CFW	YLD				
0.49	0.56	Mullaney <i>et al.</i> 1970	0.37±0.03	0.40±0.11	Mortimer and Atkins 1989
	0.50		0.32±0.03	0.22±0.16	Brash <i>et al.</i> 1994
0.56	0.64	Beattie 1961,1962	0.48±0.02	0.60±0.13	
0.54	0.52	Gunawan <i>et al.</i> 1985	0.03±0.16	0.32±0.01	Lewer <i>et al.</i> 1994
0.54	0.09	Gunawan and James 1986	0.43±0.05	0.40±0.15	
0.51±0.03	0.56±0.14	Davis and Kinghorn 1986	0.34±0.02	0.34±0.02	
0.50±0.02	0.56±0.10	Davis 1987	0.37±0.02	0.38±0.15	
0.27	0.48±0.11	Walkley <i>et al</i> 1987			
CFW	FD				
0.05	0.16±0.21	Beattie 1961, 1962	0.44	0.21±0.16	Walkley <i>et al.</i> 1987
0.85±0.01	0.80±0.03	Brown and Turner 1968	0.18±0.04	0.40±0.11	Mortimer and Atkins 1989
0.13±0.02	0.13±0.02		0.14±0.17	.014±0.16	Lewer <i>et al.</i> 1994
0.16±0.08	0.14±0.02		0.24±0.02	0.26±0.02	
0.88±0.06	0.82±0.04	Mullaney <i>et al.</i> 1970	0.28±0.16	0.29±0.16	
0.36±0.03	0.45±0.09		0.25±0.03	0.28±0.03	
0.31±0.03	0.35±0.10		0.15±0.03	0.38±0.14	Brash <i>et al</i> 1997
0.15±0.04	0.10±0.25	Hancock <i>et al.</i> 1979	0.22	0.14	Purvis and Swan 1997
0.24±0.03	0.33±0.13	Davis 1987	0.28	0.41±0.14	Skeritt <i>et al.</i> 1997
YLD	FD				
0.05	0.12	Brown and Turner 1968			
0.04	0.15	Gregory 1962	0.19±0.14	-0.18±0.14	Lewer <i>et al.</i> 1994
0.01	-0.03	Mullaney <i>et al.</i> 1970	0.02±0.03	0.02±0.03	
	-0.24		-0.08±0.17	-0.08±0.17	
-0.02±0.04	-0.12±0.20	Davis and Kinghorn 1986	-0.04±0.03	-0.05±0.03	
0.02	0.03	Beattie, 1961, 1962	-0.06	-0.41	James <i>et al.</i> 1987
0.00±0.03	-0.06±0.15	Davis 1987	-.03±0.03	0.11±0.16	Brash <i>et al</i> 1997
-0.02±0.04	0.34±0.11	Mortimer and Atkins 1989	-0.10±0.03	0.16±0.17	
0.02	-0.09	Walkley <i>et al.</i> 1987			

growth rate for Merinos while Vogt *et al.* (1967) found the correlation to be low and positive for Rambouillet x (Hampshire x Merino) crossbreds.

The correlation between weaning weight and live-weight at different ages have been found to be moderate to high (0.52 to 0.69). However, Young *et al* (1965), reported a low positive correlation estimated by using dam-offspring regression. Likewise, weaning weight is highly correlated to growth rate for Merinos (Davis, 987) and for other breeds (Ercanbrack and Price 1968). Growth rate and live weight correlation is low but positive for Merinos (Davis 1987) in contrast to the high correlation report of Price and Ercanbrack (1972) involving a crossbred and three other breeds.

3.2.2.4.2 Wool production traits

Greasy fleece weight is positively and highly correlated with clean fleece weight regardless of age, sex, breed and method of estimation, but correlation with yield is negligible and mostly negative. In most reports, greasy fleece weight has a low but positive correlation with fibre diameter (James *et al.* 1987, Mortimer and Atkins 1989, Lewer *et al.* 1994, Brash *et al.* 1997).

A low to moderate positive correlation exists between clean fleece weight and yield. Davis (1987) noted that these correlations contain a positive bias due to auto-correlation of measurement errors with clean fleece weight being directly calculated from greasy fleece weight and yield. Correlation estimates between clean fleece weight and fibre diameter generally are very low but positive.

Yield is negligibly correlated to fibre diameter both in Merinos and other sheep breeds. Correlations of birth-coat score with other wool traits are also negligible (Gregory 1982a, Morley 1955, Dolling 1970).

3.2.2.4.3 Growth traits and lamb survival

There are few published phenotypic correlation estimates between lamb survival and growth traits and those reports showed that lamb survival has a negligible phenotypic correlation with different growth traits: +0.06 correlation with birth weight; +0.08 correlation with weaning weight and +0.06 correlation with growth rate (Davis 1987, Davis and Kinghorn 1986). This is not surprising given that most lamb deaths occur within a few days of birth.

3.2.2.4.4 Growth and wool production traits

There is normally a very low to low positive correlation between birth weight and greasy fleece weight, birth weight and clean fleece weight and a negligible correlation between birth weight and yield and birth weight and fibre diameter (Hancock *et al.* 1979, Davis and Kinghorn 1986, Lewer *et al.* 1994).

The correlation between weaning weight and greasy fleece weight is generally low positive although Young *et al.* (1965) reported a high positive correlation estimate for rams

and a low positive correlation for ewes, and difference being associated with high sampling errors. Between weaning weight and clean fleece weight, the correlation is generally very low to low positive. Weaning weight, on the other hand, is negligibly correlated to yield and fibre diameter.

Post-weaning live-weight was positively correlated with greasy fleece weight and clean fleece weight in the studies of Merinos reported by Lewer *et al.* (1994), Brash *et al.* (1997), Skeritt *et al.* (1997) and Purvis and Swan (1997). Live-weight, on the other hand, has a negligible correlation with yield and a negligible to low and positive phenotypic correlation to fibre diameter.

3.2.2.5 Genetic correlations

Genetic correlations exist when genes affecting one trait also affect another. Such correlations can influence the rate of progress when selection is for two or more traits (Stufflebeam 1989). A positive correlation is apparent when selection in one trait results not only in a change in that trait, but also results in a change in a second trait. When two traits are negatively correlated, selection for progress in one will result in a loss of progress in the second. However, for many traits, no apparent genetic correlations exist.

Genetic correlation can be obtained by:

$$r_A = \frac{Cov_{XY}}{\sqrt{V_X V_Y}}$$

where r_A is additive genetic correlation between two traits X and Y, Cov_{XY} is the covariance of the two traits X and Y, V_x is the variance of trait X and V_y is the variance of trait Y.

A summary of genetic correlation estimates for various traits relevant to this thesis are shown in Table 3.2 for both Merino and other sheep breeds.

3.2.2.5.1 Growth traits

A moderate positive genetic correlation between birth weight and weaning weight was reported by Davis and Kinghorn (1987) for Merino sheep while Davis (1987) reported a very high positive correlation for an analysis of the same data. In contrast,

Lewer *et al* (1994) found the correlation between those traits to be negligible to low and positive and associated the low estimate with high standard errors. Genetic correlation between birth weight and growth rate was found to be high and positive by Davis (1987) while Vogt *et al.* (1987) found the correlation to be low and negative for Rambouillet x (Hampshire x Merino) crossbred when full-sib data was used. A correlation of unity was calculated when using estimates based on half-sib data. Sampling errors may account for some of the differences, but suggestions were made that there was more than sampling variations involved.

Weaning weight is highly associated with live-weight after weaning and growth rate and so is live-weight to growth rate (Davis and Kinghorn 1986, Davis 1987, Lewer *et al.* 1994). The high correlations suggest that the genetic control of weaning weight is largely determined by growth rate to weaning (Davis 1987).

3.2.2.5.2 Wool production traits

Most reports have found a high correlation between greasy fleece weight and clean fleece weight in various strains of Merino with the exception of the study of Hancock *et al.* (1979) for index-male progeny group calculated using half-sib analysis based on sire groups. Greasy fleece weight and yield correlation estimates range from high and negative to negligible. A large range of estimates (-0.36 to +0.73) have been reported between greasy fleece weight and fibre diameter but most are in the negligible to low positive levels (Jackson and James 1970, Hancock *et al.* 1979, Walkley *et al.* 1987, James *et al.* 1987). Davis and Kinghorn (1986) reported a high positive correlation estimated by REML procedures. The procedure used for estimation may impact on these findings.

The correlations between clean fleece weight and yield generally ranged from low to moderate and positive (Brown and Turner 1968, Mullaney *et al.* 1970, Gregory 1982b, Mortimer and Atkins 1989, Brash *et al.* 1997). In contrast, Beattie (1961) and Jackson and James (1970), reported a high and positive correlation estimate for the two traits which could have been inflated by sampling variations or unrecognised sources of bias. Clean fleece weight and fibre diameter correlation estimates are mostly in the low to moderate positive while the association between fibre diameter and yield is negligible.

Correlations between birth-coat score and other wool traits are generally negligible to low positive estimates (Morley 1955, Dolling 1970, Gregory 1982b). The low

estimates could be due to the fact that birth-coat score is recorded early in life relative to the other traits and thus less influenced by pre and post-natal effects (Davis 1987).

3.2.2.5.3 Growth and wool production traits

Birth weight has a negligible to moderate correlation to greasy fleece weight and clean fleece weight (Osman and Bradford 1965, Davis and Kinghorn 1987, Lewer *et al.* 1994). Hancock *et al.* (1979), on the other hand, reported some low negative and some high negative estimates for birth weight and clean fleece weight correlations. Associations between birth weight and yield are generally negative while the correlation between birth weight and fibre diameter ranges from highly negative to low and positive (Hancock *et al.* 1979, Davis and Kinghorn 1986, Lewer *et al.* 1994).

A low to moderate positive correlation appears to be common in reports of the relationship between weaning weight and greasy fleece weight (Walkley 1987, Pattie 1965) and between weaning weight and clean fleece weight (Walkley *et al.* 1987, Lewer *et al.* 1994). Pattie (1965) reported a negligible relationship when estimates were calculated by dam-offspring regression but estimates were moderate when estimates were by paternal half-sib methods. Weaning weight is negligibly correlated with yield in most reports except for the low positive estimate of Pattie (1965) when estimates were by paternal half-sib method of estimation. For weaning weight and fibre diameter, Davis and Kinghorn (1986) reported a moderate and positive estimate, while Walkley *et al.* (1987) and Lewer *et al.* (1994) reported correlation estimates which were low but also positive.

Turner (1958) suggested that live-weight was a component of wool production through its relationship with surface area. Genetic correlation estimates between live-weight and greasy fleece weight and between live-weight and clean fleece weight have been found to be low and positive. Low and negative associations, however, have been reported (Mortimer and Atkins 1989, Morley 1955). Young *et al.* (1965) reported a very high and negative correlation between live-weight and greasy fleece weight at weaning, a finding possibly biased upward by the inclusion of fleece weight in the live weight values used.

Most published genetic correlation estimates between live-weight and yield reports are negligible (Brown and Turner 1968, Dolling 1970, Gregory 1982b, Gunawan and

James 1986, Brash *et al.* 1997). James and Jackson (1970) found the correlations to be very high ($r_g = 0.80$).

Genetic correlation estimates of Lewer *et al.* (1994) between live-weight and fibre diameter were low and positive for males and negligible for females. Higher fibre diameter was associated with higher male live-weight, but had almost zero relationship with female live-weights and since none of the genetic correlations were different from zero, no firm conclusion were drawn from the data. Most other published estimates also showed correlation to be negligible except for the low, moderate and high positive estimates of Brash *et al.* (1997) and Purvis and Swan (1997), Skeritt *et al.* (1997) and Davis and Kinghorn (1986), respectively.

Birth-coat score and live-weight correlation is negligible (Morley, 1955, Dolling, 1970, Gregory 1982b) to low positive (Morley 1955).

3.2.2.5 Direct-maternal correlation

Direct-maternal correlation estimates are mostly negative for birth weight and with estimates increasing with age (Table 3.1). Nasholm and Danell (1996) reported an increase in correlation from 0.15 at birth to 0.635 at slaughter weight. The direct maternal correlation estimates for wool traits are negative and ranging from low to moderate for clean and greasy fleece weights and fibre diameter.

3.2.3 Conclusion

Environmental factors such as sex, birth and birth rearing types, year and age of dam, significantly influence most lamb and hogget traits and should therefore be given consideration when comparing individual records. The superiority of a selected animal may be due to more favourable environmental considerations rather than genetic advantage and this confounding may reduce the effectiveness of selection to produce genetic improvement. To increase the accuracy of selection, understanding and adjustment for environmental effects is a necessary part of any selection program.

Estimates of phenotypic and genetic parameters including heritability and phenotypic and genetic correlations are required for the prediction of genetic gains from selection and for planning selection procedures. Most parameter estimates presented for

the various traits showed a great variation in the ranges. Method of calculation used, lines within breeds and environmental differences are factors that caused the variations in the estimates. It must be noted, however, that advances in computing methodologies have improved the accuracy and precision of estimating genetic parameters.

Maternal effects have significant impact on lamb weights. While direct heritability increases with age, maternal heritability decreases with age. Greatest influence of maternal heritability is on birth weight, but is generally low in fleece traits suggesting that maternal effect need no immediate consideration in breeding programs. Although maternal genetic effects are important, but if not accounted for, then heritability estimates will be biased and will result in the reduction of selection efficiency. Permanent maternal environment effect estimates for live weights decrease with age and has a low influence on wool traits. Similarly, direct-maternal correlation increases with age and has also low influence on wool traits.

3.3 Materials and Methods

3.3.1 Source of data

The data used in this study come from the Trangie Weight Selection Experiment that was conducted by NSW Agriculture between 1951 and 1994. A description of the selection lines are presented in Chapter 2.

3.3.2 Experimental sheep and observations

The management, selection procedures and environment are described in Chapter 2. In this study, data on animals born at Trangie between 1983 and 1992 were used. Records were available from a total of 3082 sheep (Table 3.3): 837 in Weight Plus line (progeny of 49 sires), 426 in Weight Minus line (progeny of 52 sires) and 1819 in the Random line (progeny of 95 sires).

During the period of the study, the mating season was from February to March and animals were born during July and August and weaned in November. Animals, as hoggets (15 -16 months of age), were shorn around ten months after weaning.

3.3.2.1 Lamb traits

The traits observed on animals as lambs (lamb traits) included birth weight (BWT), weaning weight (WWT), growth rate to weaning (GR), lamb survival to weaning (LS), birth-coat score (BCS) and nine-month weight (NMWT). Growth rate was the average daily gain between birth and weaning. Lamb survival was determined as the ratio of lambs weaned to lambs born. Birth-coat score denoted the abundance of outer coat fibre (halo coat) upon the birth of the lamb where lambs were given a score varying from 0 for birth-coats with few or no projecting fibres to 7 where the whole birth-coat appeared hairy (Morley 1955).

Table 3.3. Number of lambs born, lambs weaned, total number of sires (N_s) and the average number of progeny per sire (K) for the ten-year period.

Year	All lambs				Lambs surviving to weaning			
	Random	Weight Plus	Weight Minus	Total	Random	Weight Plus	Weight Minus	Total
1983	123	46	26	195	94	35	19	148
1984	195	102	48	345	168	88	28	284
1985	157	81	27	265	135	73	23	231
1986	210	87	51	348	176	66	37	279
1987	179	128	56	363	147	105	38	290
1988	200	141	39	380	159	101	21	281
1989	207	48	38	293	156	39	26	271
1990	223	82	50	355	184	65	39	288
1991	216	51	41	308	177	38	28	243
1992	109	71	50	230	80	42	30	152
Total	1819	837	426	3082	1476	652	289	2417
N_s †	95	52	52	199	94	51	51	195
K †	19.1	16.1	8.2	14.4	15.7	12.8	5.8	11.4

† N_s total number of sires, k average number of progeny per sire

The number of records of lambs born and lambs surviving to weaning over the ten-year period (1983-1992) are given in Table 3.3 as well as the total number of sires (N_s) and the average number of progeny per sire (k) over this period.

3.3.2.2. Hogget production traits

Table 3.4 shows the number of records of hoggets of the selection lines and the control used in this study from 1983 to 1992.

The hogget production traits included greasy fleece weight (GFW), clean fleece weight (CFW), skirted fleece weight (SFW), yield (YLD), fibre diameter (FD) and off-shears live weight (OBWT) and were recorded on animals at 15-16 months of age. Greasy fleece weight was measured as the total weight of wool at its removal from the sheep while skirted fleece weight was greasy fleece after the removal of inferior wool at the edges of the fleece. Clean fleece weight was estimated as the product of greasy fleece weight and yield. Yield was the proportion of clean fleece wool obtained from greasy fleece wool after scouring method. Fibre diameter was measured as the fineness of wool in micrometer or microns by airflow method (Anderson 1956). Off-shear live weight was recorded as to the weight of the hogget after shearing at 15-16 months old.

Table 3.4. Number of hoggets by line for the ten-year period.

Year	L i n e s			
	Random	Weight Plus	Weight Min	Total
1983	86	31	18	135
1984	163	87	25	275
1985	132	73	19	224
1986	168	62	34	264
1987	143	101	33	277
1988	156	100	20	276
1989	151	39	23	213
1990	170	60	38	268
1991	173	36	29	238
1992	78	38	27	143
Total	1420	627	266	2313

3.3.3 Statistical Analysis

3.3.3.1 Line and environmental sources of variation

Least squares analyses of variance were used to estimate the effects of line and environmental sources of variation on the data for the lamb and hogget production traits. The general linear model procedure (GLM) of the Statistical Analysis System (SAS - 1990) program was used for all analyses.

The linear Model 3.1 was fitted to birth weight, birth-coat score and lamb survival:

$$\begin{aligned}
 y_{ijklmno} = & \mu + l_i + y_j + s_k(l,y_j) + m_l + t_m + d_n + b_1dob_{ijklmno} + \\
 & b_2dob^2_{ijklmno} + l_i y_j + l_i m_l + y_j m_l + y_i t_m + y_i d_n \\
 & + e_{ijklmno}
 \end{aligned} \tag{3.1}$$

where

- $y_{ijklmno}$ = individual observation,
- μ = overall mean,
- l_i = effect of the i th line ($i = 1, 2, 3$; 1 = Random, 2 = Weight Plus, 3 = Weight Minus),
- y_j = effect of the j th year of recording ($j = 1, 2, \dots, 10$; 1 = 1983, 2 = 1984, 3 = 1985, 4 = 1986, 5 = 1987, 6 = 1988, 7 = 1989, 8 = 1990, 9 = 1991, 10 = 1992),
- $s_k(l,y_j)$ = effect of the k th sire within i th line and j th year,
- m_l = effect of l th sex ($l = 1, 2$; 1 = male, 2 = female),
- t_m = effect of m th type of birth ($m = 1, 2$; 1 = single, 2 = multiple),
- d_n = effect of the n th age of dam ($n = 2, \dots, 7$: 2 = 2 years old, 3 = 3 years old, 4 = 4 years old, 5 = 5 years old, 6 = 6 years old, 7 = 7 years old and up),
- $b_1dob_{ijklmno}$ = linear regression effect due to the day of birth,
- $b_2dob^2_{ijklmno}$ = quadratic regression effect due to the day of birth

Line and environmental effects and genetic parameters

$$\begin{aligned}
 l_{ly_j} &= \text{interaction effect between line and year,} \\
 l_i m_l &= \text{interaction effect between line and sex,} \\
 y_j m_l &= \text{interaction effect between year and sex,} \\
 y_j t_m &= \text{interaction effect between year and birth type,} \\
 y_i d_n &= \text{interaction effect between year and age of dam,} \\
 e_{ijklmno} &= \text{random error effect assumed NID } \sim (0, s^2 e).
 \end{aligned}$$

Model 3.2 was fitted to weaning weight and growth rate traits:

$$\begin{aligned}
 y_{ijklmno} = & \mu + l_i + y_j + s_k(l_{ly_j}) + m_l + t_m + d_n + b_1 \text{wage}_{ijklmno} + \\
 & b_2 \text{wage}^2_{ijklmno} + l_{ly_j} + l_i m_l + y_j m_l + y_i t_m + y_i d_n + \\
 & e_{ijklmno}
 \end{aligned} \tag{3.2}$$

where

$$\begin{aligned}
 y_{ijklmno}, \mu, l_i, y_j, s_k(l_{ly_j}), m_l, d_n, l_{ly_j}, l_i m_l, y_j m_l, y_i t_m, \\
 y_i d_n \text{ and } e_{ijklmno} \text{ are as for Model 3.1 and} \\
 t_m &= \text{effect of the } m\text{th birth-rearing type } (m = 1, 2, 3; 1 = \\
 & \text{single born/single reared, 2 = multiple born / single} \\
 & \text{reared, 3 = multiple born / multiple reared),} \\
 b_1 \text{wage}_{ijklmno} &= \text{linear regression effect due to weaning age of lamb,} \\
 b_2 \text{wage}^2_{ijklmno} &= \text{quadratic regression effect due to weaning age of lamb.}
 \end{aligned}$$

For nine-month weight, Model 3.3 was fitted:

$$\begin{aligned}
 y_{ijklmno} = & \mu + l_i + y_j + s_k(l_{ly_j}) + m_l + t_m + d_n + b_1 \text{nage}_{ijklmno} + \\
 & b_2 \text{nage}^2_{ijklmno} + l_{ly_j} + l_i m_l + y_j m_l + y_i t_m + y_i d_n + \\
 & e_{ijklmno}
 \end{aligned} \tag{3.3}$$

where

$$\begin{aligned}
 y_{ijklmno}, \mu, l_i, y_j, s_k(l_{ly_j}), m_l, d_n, l_{ly_j}, l_i m_l, y_j m_l, \\
 y_i t_m, y_i d_n \text{ and } e_{ijklmno} \text{ are as for Model 3.1 and} \\
 b_1 \text{nage}_{ijklmno} &= \text{linear regression effect due to age at weighing of lamb,} \\
 b_2 \text{nage}^2_{ijklmno} &= \text{quadratic regression effect due to age at weighing of} \\
 & \text{lamb.}
 \end{aligned}$$

Model 3.4 was fitted to each of the hogget production traits:

Line and environmental effects and genetic parameters

$$\begin{aligned}
 y_{ijklmno} &= \mu + l_i + y_j + s_k(l_i y_j) + m_l + t_m + d_n + b_1 \text{sage}_{ijklmno} \\
 &+ b_2 \text{sage}^2_{ijklmno} + l_i y_j + l_i m_l + y_j m_l + y_i t_m + y_i d_n + e_{ijklmno}
 \end{aligned} \tag{3.4}$$

where

$$\begin{aligned}
 y_{ijklmno} &= \text{individual observation} \\
 \mu &= \text{overall mean} \\
 l_i &= \text{effect of the } i\text{th line } (i = 1, 2, 3; 1 = \text{Random}, \\
 &\quad 2 = \text{Weight Plus}, 3 = \text{Weight Minus}), \\
 y_j &= \text{effect of } j\text{th year of recording } (j = 1, 2, \dots, 10; \\
 &\quad 1 = 1983, 2 = 1984, 3 = 1985, 4 = 1986, 5 = 1987 \\
 &\quad 6 = 1988, 7 = 1989, 8 = 1990, 9 = 1991, 10 = 1992), \\
 s_k(l_i y_j) &= \text{effect of } k\text{th sire within } i\text{th line and } j\text{th year}, \\
 m_l &= \text{effect of the } l\text{th sex } (l = 1, 2; 1 = \text{male}, 2 = \text{female}), \\
 t_m &= \text{effect of the } m\text{th type of birth-rearing } (k = 1, 2, 3; 1 = \\
 &\quad \text{born single/reared single}, 2 = \text{multiple born /} \\
 &\quad \text{single reared}, 3 = \text{multiple born / multiple reared}), \\
 d_n &= \text{effect of the } n\text{th age of dam } (n = 2, \dots, 7; 2 = 2 \\
 &\quad \text{years old}, 3 = 3 \text{ years old}, 4 = 4 \text{ years old}, 5 = 5 \\
 &\quad \text{years old}, 6 = 6 \text{ years old}, 7 = 7 \text{ years old and up}), \\
 b_1 \text{sage}_{ijklmno} &= \text{linear regression effect due to the shearing age}, \\
 b_2 \text{sage}^2_{ijklmno} &= \text{quadratic regression effect due to the shearing age}, \\
 l_i t_m &= \text{interaction effect between line and birth type}, \\
 l_i y_j &= \text{interaction effect between line and year}, \\
 e_{ijklmno} &= \text{random error assumed NID } \sim (0, s^2 e)
 \end{aligned}$$

Model 3.5 was fitted to off-shear body weight as follows;

$$\begin{aligned}
 Y_{ijklmno} &= \mu + l_i + y_j + s_k(l_i y_j) + m_l + t_m + d_n + b_1 \text{nage}_{ijklmno} + \\
 &\quad b_2 \text{nage}^2_{ijklmno} + l_i y_j + l_i m_l + y_j m_l + y_i t_m + y_i d_n + e_{ijklmno}
 \end{aligned} \tag{3.5}$$

where

$$\begin{aligned}
 Y_{ijklmno}, \mu, l_i, y_j, s_k(l_i y_j), m_l, d_n, l_i y_j, l_i m_l, y_j m_l, y_i t_m, \\
 y_i d_n \text{ and } e_{ijklmno} &\text{ are as for Model 3.1 and} \\
 b_1 \text{nage}_{ijklmno} &= \text{linear regression effect due to age at weighing of hogget,}
 \end{aligned}$$

$b_2nage^2_{ijklmno}$ = quadratic regression effect due to age at weighing of hogget.

3.3.3.2 Estimation of variance components

Univariate analyses were used to estimate variance components and assess their significance. The basic linear model used in the study is as follows:

$$y = Xb + Z_a a + Z_m m + Z_c c + e \quad (3.6)$$

where

y is $n \times 1$ vector of the observations,

b is a vector of fixed effects in the model associated with matrix X ,

a is the vector of direct genetic effects with association matrix Z_a ,

m is the vector of maternal genetic effects with association matrix Z_m ,

c is the vector of permanent environmental effects with association matrix Z_c , and

e denotes the vector of residual effects.

Fixed effects included in the model were year (1983 – 1992), sex of lambs (male and female), age of dam (2 – 11) and birth and rearing type (single-born and-reared, multiple-born and single-reared and multiple-born and-reared). For birth weight, lamb survival and birth-coat score, birth-rearing type was replaced with birth type (single and multiple). Random effects included were direct additive genetic effects, maternal genetic effects and permanent maternal environmental effects. Covariates fitted included, day of birth for birth weight, lamb survival and birth-coat score, age at weaning for weaning weight and growth rate, age at weighing for nine-month weight, shearing age for greasy fleece weight, skirted fleece weight, clean fleece weight, fibre diameter and yield, and age at weighing for off-shear live weight.

The variance-covariance structure for the model was:

$$\mathbf{v} = \begin{bmatrix} \mathbf{a}_d \\ \mathbf{a}_m \\ \mathbf{c} \\ \mathbf{e} \end{bmatrix} \begin{bmatrix} \mathbf{A}\sigma_d^2 & \mathbf{A}\sigma_{am} & 0 & 0 \\ \mathbf{A}\sigma_{dm} & \mathbf{A}\sigma_m^2 & 0 & 0 \\ 0 & 0 & \mathbf{I}_c\sigma_c^2 & 0 \\ 0 & 0 & 0 & \mathbf{I}_n\sigma_e^2 \end{bmatrix}$$

where

\mathbf{A} is the numerator relationship matrix,

σ_a^2 is the additive direct variance,

σ_m^2 is the additive maternal variance,

\mathbf{I}_c is an identity matrix with order number of ewes, 0

σ_{pe}^2 is the permanent environmental variance,

\mathbf{I}_n is an identity matrix with order number of records, and

σ_e^2 is the residual variance,

Heritability for direct effect was calculated as:

$$h_d^2 = \sigma_a^2 / \sigma_p^2 \quad (3.7)$$

where

h_d^2 is the direct genetic heritability,

σ_a^2 is the additive genetic variance and

σ_p^2 is the phenotypic variance.

Phenotypic variance was estimated as;

$$\sigma_p^2 = \sigma_G^2 + \sigma_E^2$$

where

σ_G^2 = additive genetic variance

σ_E^2 = environmental variance

Heritability for additive maternal effects was estimated as:

$$h_m^2 = \sigma_m^2 / \sigma_p^2 \quad (3.8)$$

where

h_m^2 is the maternal genetic heritability,
 σ_a^2 is the additive maternal variance and
 σ_p^2 is the phenotypic variance.

The permanent maternal environmental effect was calculated as :

$$c^2 = \sigma_c^2 / \sigma_p^2 \quad (3.9)$$

where

c^2 is the permanent maternal environmental effect,
 σ_c^2 is the permanent maternal environmental variance and
 σ_p^2 is the phenotypic variance.

The genetic correlation between direct additive and maternal additive genetic effects was estimated as:

$$r_{am} = \sigma_{am} / (\sigma_a \sigma_m) \quad (3.10)$$

where

r_{am} is the direct-maternal genetic correlation,
 σ_{am} is the direct-maternal genetic covariance,
 σ_a is the direct additive variance and
 σ_m is the maternal genetic variance.

Bivariate analyses were performed for each pairing of the traits. Covariance components were estimated for direct additive genetic effects, maternal genetic effects, maternal environmental effects, direct-maternal genetic effects and temporary environmental effects where appropriate. From these covariance and variance components, direct genetic, maternal genetic, maternal environment, direct-maternal genetic and phenotypic correlations were estimated.

The variance- covariance components and other calculations were estimated by ASREML using the program of Gilmour (1999). ASREML is designed to fit the general linear model of the form:

$$Y = Xb + Zu + e$$

where

Y	=	vector of weaning weight
X	=	incidence matrix relating records to fixed effects
b	=	vector of fixed effects
Z	=	incidence of matrix relating to random effects
u	=	vector of random effects
e	=	vector of random residual errors

Table 3.5 Trait means, standard deviations and coefficient of variation and number of records, sires and dams for lamb and hogget production traits.

Traits	Mean	S.D	C.V.,%	No. of records	No. of sires	No. of dams
<i>Lamb traits</i>						
BWT (kg)	3.709	0.568	15.314	1811	85	426
BCS (score)	3.780	1.573	41.877	1820	85	426
LS (rate)	0.769	0.392	50.978	1818	92	373
GR (g/day)	144.619	32.544	22.503	1466	82	373
WWT (kg)	19.620	3.720	18.941	1469	82	374
NMWT (kg)	28.900	5.088	17.557	1341	80	347
<i>Hogget traits</i>						
GFW (kg)	3.945	0.609	15.416	1408	82	359
SFW (kg)	2.562	0.450	17.552	1237	77	325
CFW (kg)	2.642	0.462	17.427	1226	74	313
YLD (m)	65.100	5.358	8.105	1241	74	319
FD (microns)	21.180	1.446	6.917	1242	74	320
BOWT(kg)	40.080	4.738	11.825	1396	82	357

3.3.3.3 Data structure

The structure of the data used in the univariate analyses is presented in Table 3.5. The table shows the phenotypic mean, standard deviation, coefficient of variation and number of records, sire and dams for lamb and hogget production traits.

3.4 RESULTS

3.4.1 Line and environmental effects

3.4.1.1 Analyses of variance

The analyses of variance for lamb traits are summarised in Table 3.6. The model explained 57 %, 27 %, 21 %, 64 %, 72 % and 70 % of the variations in birth weight, weaning weight, growth rate, lamb survival, birth-coat score and nine-month weight, respectively. The analyses showed that line, year, sex, birth type or birth-rearing type and age of dam were significant.

Significant line x year interactions were observed for all traits ($P < 0.001$). Line x sex interactions for lamb survival and nine-month weight, year x sex interaction for nine-month weight, year x birth type interaction for birth weight and lamb survival, year x birth-rearing type interaction for growth rate and year x age of dam interactions for birth weight and lamb survival were also observed ($P < 0.05$). Day of birth covariates, fitted as a linear or quadratic regression, were significant for birth weight, birthcoat score and lamb survival. Weaning age, fitted as a linear or quadratic regression, showed no significant effect on weaning weight but significantly influenced growth rate. Age at weighing, also fitted as a linear or quadratic regression, had no significant effect on nine-month weight.

For hogget production traits, the models accounted 60 %, 57 %, 41 %, 54 %, 46 % and 78 % of the total variation in greasy, skirted, clean, yield, fibre diameter and off-shear live weight, respectively (Table 3.5). The main effects showed significant influence ($P < 0.001$) on most hogget production traits. However, birth-rearing type had no influence on yield or age of dam on fibre diameter. Significant line x year and year x sex interactions ($P < 0.05$) were observed for all traits and line x birth-rearing type for greasy fleeced weight, skirted fleece weight and off-shears live weight.

No significant effects of year x birth-rearing type or year x age of dam interaction were seen for any traits. Shearing age, fitted as linear and quadratic regressions, had no significant effects on hogget fleece traits nor age at weighing for off-shears live weight.

3.4.1.2 Line Effects

3.4.1.2.1 Lamb traits

Line effects were significant ($P < 0.001$) for birth weight, weaning weight and nine-month weight as shown in Figure 3.1. For birth weight, the Weight Plus lambs were superior to the Random and Weight Minus lambs by 12.0% and 22.6%, respectively. The Random lambs were heavier by 12% than the Weight Minus lambs at birth. The mean birth weight of Weight Plus lambs was 4.3 ± 0.02 , 3.7 ± 0.02 for the Random lambs and 3.3 ± 0.04 kg for the Weight Minus lambs. For weaning weight, Weight Plus lambs were 12.5% ($P > 0.0001$) heavier than the Random lambs, which in turn were heavier (22.2%) than the Weight Minus lambs. The difference in weaning weight between the two selection lines was 31.9%. The average weaning weight of the Weight Plus, Random and Weight minus lines were 22.4 ± 0.2 kg, 19.6 ± 0.13 kg and 15.2 ± 0.27 kg, respectively. At nine-months of age, the Weight Plus lambs were significantly ($P \leq 0.0001$) superior by 11.8% and 19.8% than the Random and Weight Minus lambs, respectively. The Random lambs were superior by 19.8% than the Weight Minus lambs. The Weight Plus lambs registered an average nine-month old weight of 33.1 ± 0.23 kg, 29.2 ± 0.16 kg for the Random line and 23.4 ± 0.34 for the Weight Minus line.

Line effects were significant ($P < 0.001$) for growth rate to weaning (Figure 3.2). The Weight Plus lambs grew faster by 11.1% than the Random lambs and 32.8% than the Weight Minus lambs. The Weight Plus line registered an average growth rate of 157.9 ± 1.56 g/day. On the other hand, the Random and Weight Minus lines had a growth rate to weaning of 140.3 ± 1.11 and 106.1 ± 2.30 g/day, respectively.

For lamb survival, line effects were significant ($P < 0.001$) as shown in Figure 3.3. Lamb survival for the Weight Plus and the Random lines were similar, but both were significantly superior than the Weight Minus lines by 13.3% and 15.6%, respectively. Lamb survival rates of the three lines were 0.75, 0.77 and 0.65, respectively.

Table 3.6. Analyses of variance for birth weight (BWT), birthcoat score (BCS), lamb survival at weaning (LS), weaning weight (WWT), and growth rate to weaning (GR).

Sources of Variation	d. f.	F - VALUES					
		BWT	BCS	LS	WWT	GR	NMWT
<i>Main Effect</i>							
Line	2	295.89***	51.04***	7.20***	306.35***	208.84***	359.19***
Year	9 / 8 ^a	48.18***	7.49***	4.03***	11.83***	13.37***	33.55***
Sex	1	58.64***	10.50***	8.12**	108.80***	87.74***	269.71***
Birth type	1	806.96***	9.76***	138.91***	-	-	-
Birth-rearing type	2	-	-	-	187.93***	136.13***	38.81***
Age of dam	5	21.35***	4.34***	3.52**	5.73***	4.24***	3.67**
Sire(line*year)	168/150 ^a /165 ^b	2.16***	2.86***	1.69***	3.90***	6.45***	2.32***
<i>Interactions</i>							
Line x year	18 / 16 ^a	4.89***	2.21***	2.28**	5.09***	8.73***	3.28***
Line x sex	2	0.56 ^{ns}	0.31 ^{ns}	3.44**	0.37 ^{ns}	0.36 ^{ns}	4.66**
Year x sex	9 / 8 ^a	1.19 ^{ns}	1.07 ^{ns}	0.44 ^{ns}	1.05 ^{ns}	1.25 ^{ns}	12.51***
Year x birth type	9	1.92*	1.83 ^{ns}	3.96***	-	-	-
Year x birth-rearing type	18 / 16 ^a	-	-	-	1.54 ^{ns}	2.03**	1.22 ^{ns}
Year x age of dam	45	2.02***	0.87 ^{ns}	1.74**	1.12 ^{ns}	1.03 ^{ns}	1.39 ^{ns}
<i>Regression</i>							
Day of birth (L)	1	6.42***	11.84***	4.52**	-	-	-
Day of birth (Q)	1	5.75***	12.37***	4.41*	-	-	-
Weaning age (L)	1	-	-	-	2.27 ^{ns}	8.93**	-
Weaning age (Q)	1	-	-	-	0.32 ^{ns}	9.52**	-
Nine-month age (L)	1	-	-	-	-	-	0.76 ^{ns}
Nine-month age (Q)	1	-	-	-	-	-	0.05 ^{ns}
Residual		0.30	1.74	0.14	10.11	750.41	13.96
Coefficient of determination		0.57	0.27	0.21	0.64	0.72	0.70

*** P<0.001, **P<0.01, *P<0.05 ^{ns} not significant a = for NMWT b = for WWT and GR

Table 3.7. Analyses of variance for greasy fleece weight (GFW), skirted fleece weight (SFW), yield (YLD), clean fleece weight (CFW), fibre diameter (FD) and off-shear-live weight (OBWT).

Sources of Variations	d. f.	F - V A L U E S					
		GFW	SFW	YLD	CFW	FD	OBWT
<i>Main effects</i>							
Line	2	82.11**	95.39***	5.95**	85.81***	101.89***	482.67***
Year	8 / 7 ^a /9 ^b	48.49***	33.92***	13.17***	25.68***	18.98***	43.85***
Sex	1	104.50***	41.66***	118.91***	30.03***	28.01***	1553.35***
Birth-rearing type	2	25.28***	26.23***	0.63 ^{ns}	22.03***	12.51***	20.77***
Age of dam	5	2.79*	2.78*	2.41*	3.38**	0.84 ^{ns}	2.39*
Sire (line *year)	146/131 ^a /164 ^b	1.91***	2.36***	3.29***	2.03***	3.23***	2.63***
<i>Interactions</i>							
Line x year	16/14 ^a /18 ^b	2.41***	2.26**	3.34***	2.09**	2.36**	4.52***
Line x birth-rearing type	2	5.78**	3.36*	0.76 ^{ns}	1.76 ^{ns}	2.42 ^{ns}	5.39***
Year x sex	8 / 7 ^a / 9 ^b	12.04***	13.10***	3.83***	12.35***	6.95***	16.74***
Year x birth-rearing type	16 / 14 ^a / 18 ^b	1.27 ^{ns}	1.55 ^{ns}	1.19 ^{ns}	0.92 ^{ns}	0.76 ^{ns}	1.26 ^{ns}
Year x age of dam	40/35 ^a / 45 ^b	1.10 ^{ns}	1.24 ^{ns}	1.20 ^{ns}	1.0 ^{ns}	1.33 ^{ns}	1.36 ^{ns}
<i>Regressions</i>							
Shearing age (L)	1	0.47 ^{ns}	0.96 ^{ns}	1.15 ^{ns}	0.85 ^{ns}	0.17 ^{ns}	-
Shearing age (Q)	1	0.16 ^{ns}	0.43 ^{ns}	1.10 ^{ns}	1.35 ^{ns}	0.21 ^{ns}	-
Age at weighing (L)	1	-	-	-	-	-	1.48 ^{ns}
Age at weighing (Q)	1	-	-	-	-	-	1.04 ^{ns}
Residual		0.30	0.16	22.20	0.15	1.61	19.71
Coefficient of correlation		0.60	0.57	0.41	0.54	0.46	0.78

*** P<0.001, **P<0.01, *P<0.05 ^{ns} not significant a = for SFW b = for GFW and OBWT

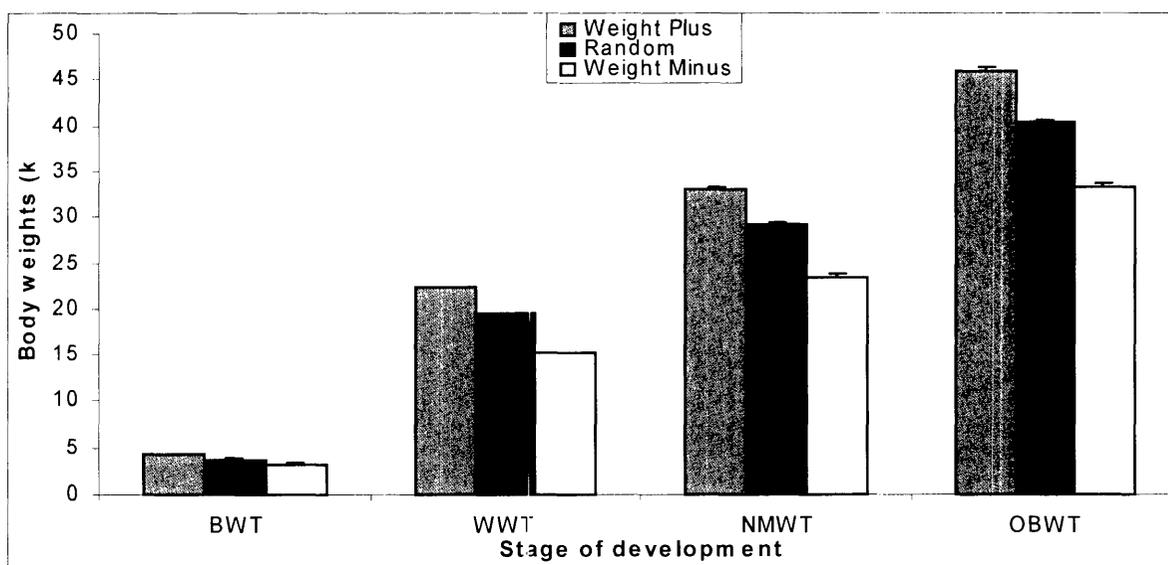


Figure 3.1 Least square means for birth weight, weaning weight, nine-month weight and off-shear weight of the Weight Plus, Random and Weight Minus lines

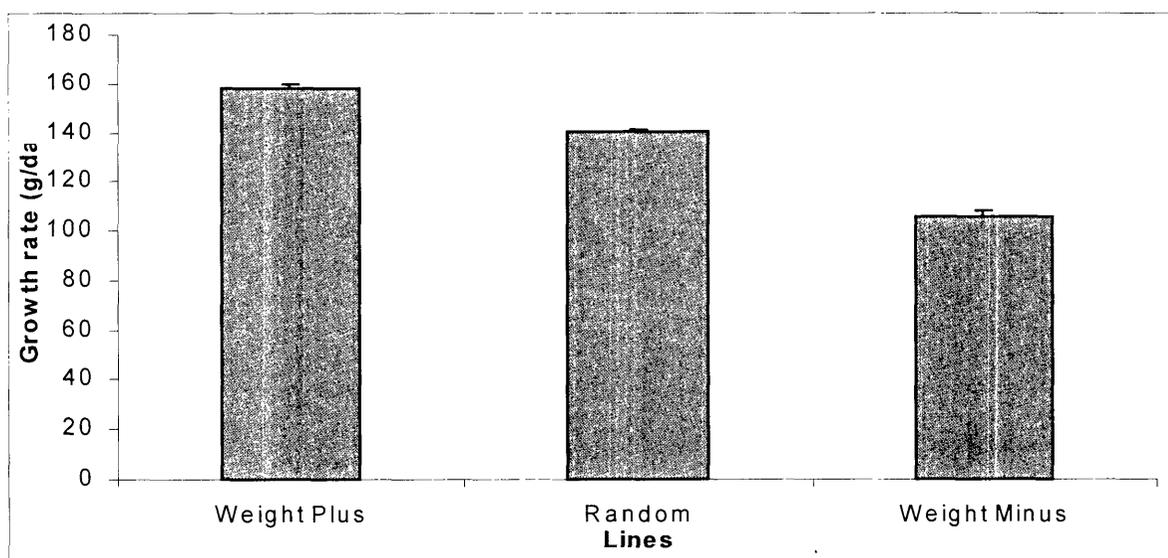


Figure 3.2 Least square means for growth rate to weaning (g/day) of the Weight Plus, Random and Weight Minus lines.

The line effects was significant ($P < 0.001$) for birth-coat score as shown in Figure 3.4. The Random line showed higher birth-coat score units than the Weight Plus line by 18.3% and 10.8% than the Weight Minus line. The Weight Minus line was superior to the Weight Plus line by 8.5%. The average birth-coat scores for the three lines were

3.81±0.04, 3.4±0.10 and 3.11±0.06 for the Random, Weight Minus and Weight Plus lines, respectively.

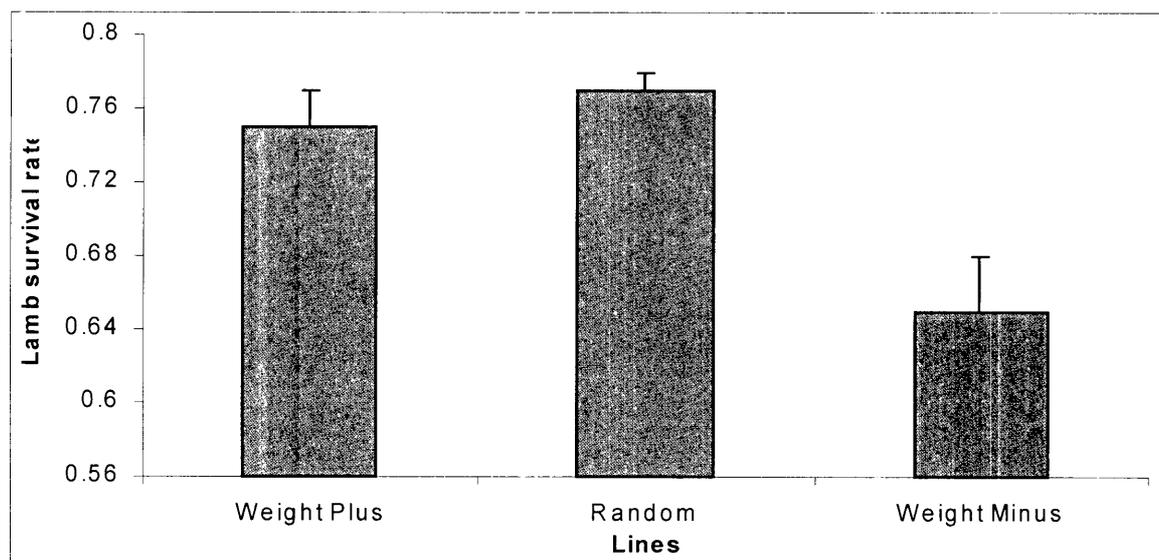


Figure 3.3 Least square means for lamb survival rates of the Weight Plus, Random and Weight Minus lines.

3.4.1.2.2 Hogget production traits

The least square means (Figure 3.5) show that hoggets of the Random line had significantly ($P < 0.0001$) higher greasy, skirted and clean fleece weights than the Weight Plus and Weight Minus hoggets. The Random line had greasy fleece weight that were 3.8% and 16% higher than the Weight Plus and Weight Minus groups, respectively. On the other hand, the Weight Plus lambs were 12.8% higher in greasy fleece weight than the Weight Minus lambs. The average greasy fleece weight of the three lines for the ten-year period were 4.0±0.02, 3.8±0.03 and 3.3±0.05 kg, respectively. For the skirted fleece weight, the same ranking of the lines was observed with the Random line significantly higher by 7.0% than the Weight Plus line and 27.2% than the Weight Minus hoggets. The Weight Plus line, on the other hand, was superior to the Weight Minus line by 15.5%. The average skirted fleece weights of the three lines were 2.6±0.02, 2.4±0.03 and 2.0±0.04 kg, respectively. For clean fleece weight, the Random line was also superior (3%) to the Weight Plus line and also to the Weight Minus line (18.7%). The difference in clean fleece weight between the two selection lines was 16.2%. Random line registered an average

clean fleece weight of 2.7 ± 0.02 , 2.6 ± 0.02 for the Weight Plus line and 2.2 ± 0.04 for the Weight Minus line.

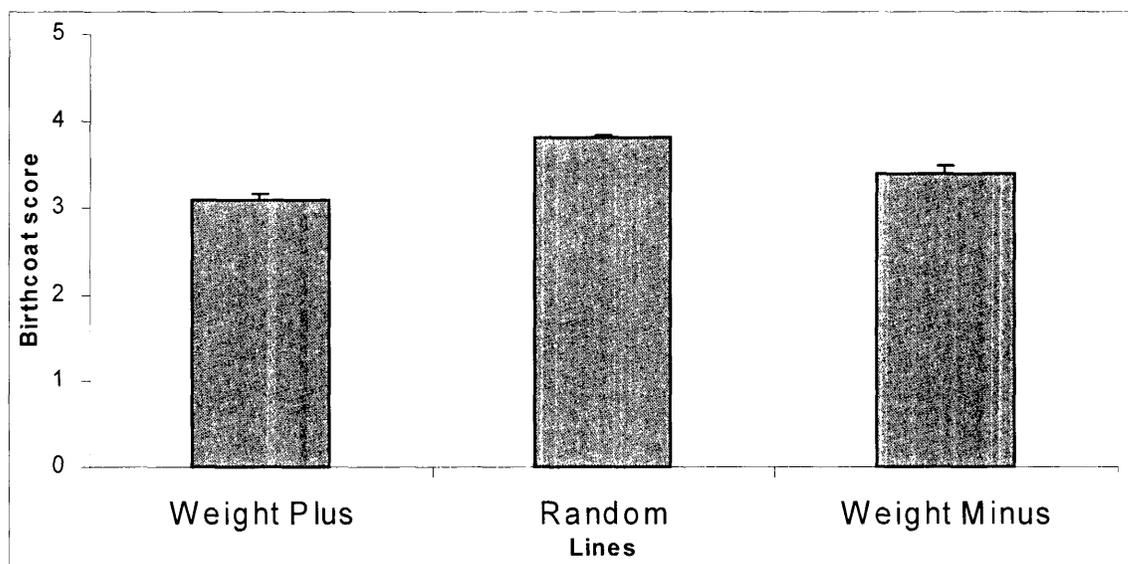


Figure 3.4 Least square means for birth-coat score of the Weight Plus, Random and Weight Minus lines.

Although, the Random hoggets had a higher yield than the Weight Plus hoggets the difference was not significant. However, the yields of both lines were significantly (2.4%, $P < 0.0001$) higher than the Weight Minus line (Figure 3.6). Average yield for the Random line was $65.8 \pm 0.22\%$, $65.8 \pm 0.30\%$ for Weight Plus line and $64.2 \pm 0.43\%$ for the Weight minus line. Fibre diameter of the Weight Plus lambs was significantly ($P < 0.0001$) finer than the Random and Weight Minus hoggets (Figure 3.7). The wool of the Weight Minus animals was finer (2.0%) than the Random line. On the average, the fleece diameter of the Weight Plus line was 19.7 ± 0.08 microns, 20.6 ± 0.12 microns for the Weight Minus line and 21.1 ± 0.06 microns for the Random line.

Significant line effects were observed for off-shear live weight as shown in Figure 3.1. The Weight Plus hoggets were significantly heavier than the Random hoggets by 12.2% and heavier by 27.8% than the Weight Minus hoggets. On the other hand, the Random hoggets were also significantly heavier 17.8% than the Weight Minus hoggets. On the average, the off-shear weight of the Weight Plus line was 46.01 ± 0.27 , 40.41 ± 0.19 for the Random line and 33.23 ± 0.38 for the Weight Minus line.

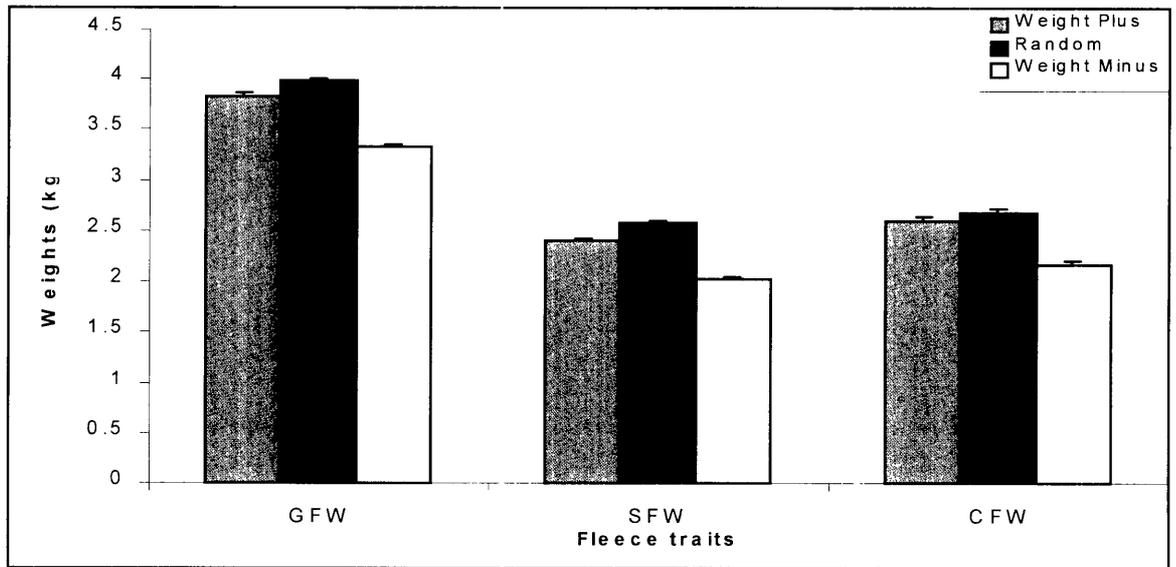


Figure 3.5 Least square means for greasy, skirted and clean fleeced weights (kg) of the Weight Plus, Random and Weight Minus lines.

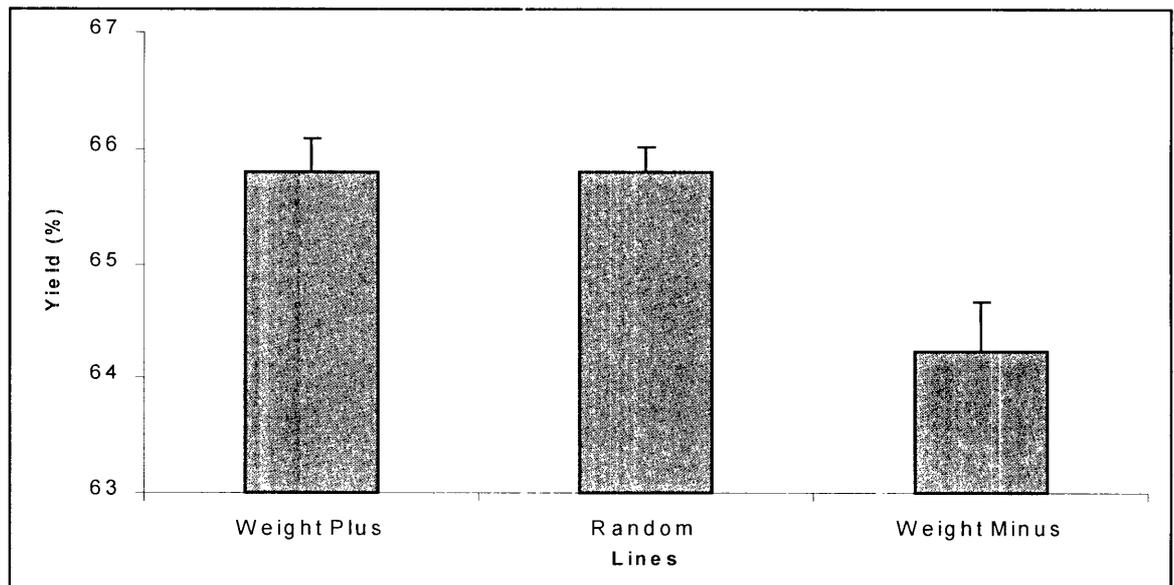


Figure 3.6 Least square means for yield (%) of the Weight Plus, Random and Weight Minus lines.

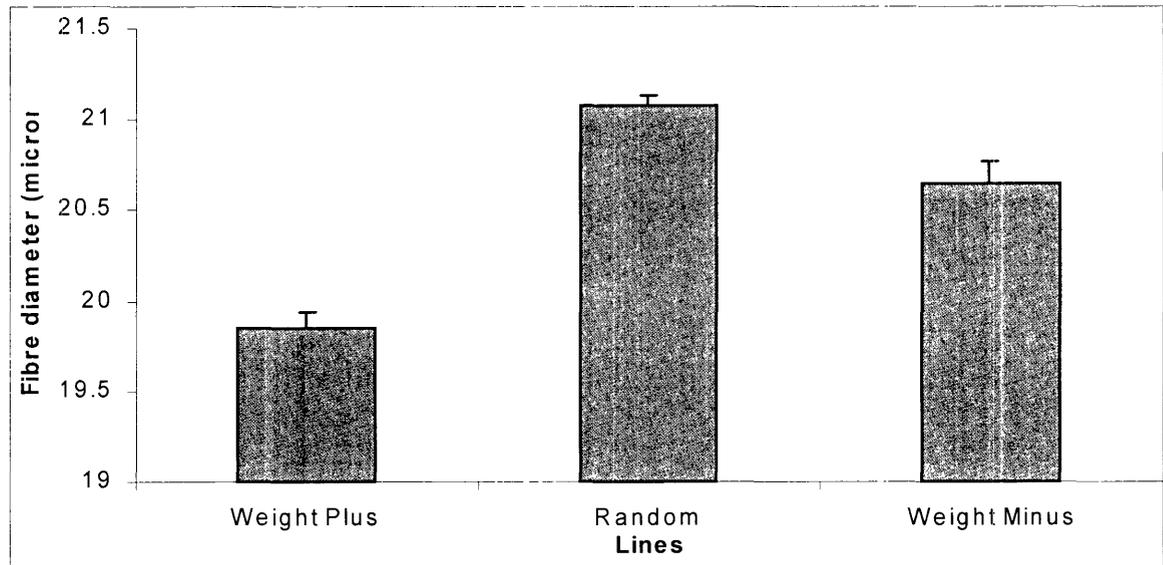


Figure 3.7 Least square means for fibre diameter (microns) of the Weight Plus, Random and Weight Minus lines.

3.4.1.3 Sex effects

3.4.1.3.1 Lamb traits

Figure 3.8 shows the effects of sex on live-weight of lamb and hoggets. Male lambs were significantly (0.2 kg, $P < 0.0001$) heavier than female lambs at birth and at weaning (1.8 kg). They were also heavier at nine months of age (3.8 kg). The male lambs grew significantly faster (14.5 g/day, $P < 0.0001$) from birth to weaning.

Birth-coat score and lamb survivor were significantly higher in female lambs than male lambs by 5.7% and 6.7%, respectively ($P < 0.05$).

3.4.1.3.2 Hogget production traits

Male hoggets outperformed female hoggets in most wool traits. The ram hoggets were significantly superior to the ewe hoggets by 8.5 %, 7.1 % and 5.1 % for greasy, skirted, and clean fleece weights, respectively (Figure 3.9). Ram hoggets had an average weight of 3.9 ± 0.03 for greasy fleece weight, 2.4 ± 0.02 for skirted fleece weight and

2.5±0.02 while the ewe hoggets registered an average of 3.6±0.03, 2.2±0.02 and 2.4±0.02 kg for greasy, skirted and clean fleece weights, respectively.

The males were lower by 3.2 % in yield and 2.0 % (0.41 microns) in fibre diameter. For live weight at 15-16 months, rams were heavier by 23.7 % (10.4 kg) than ewes as shown in Figure 3.8.

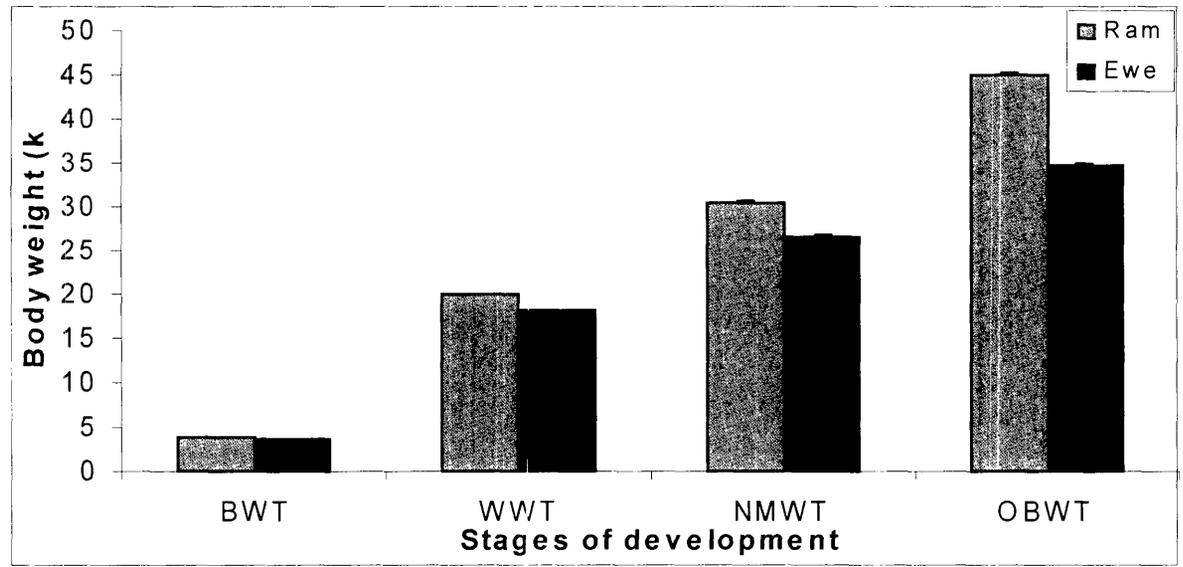


Figure 3.8 Least square means for birth weight, weaning weight, nine-month weight and off-shear weight of rams and ewes at various stages of development.

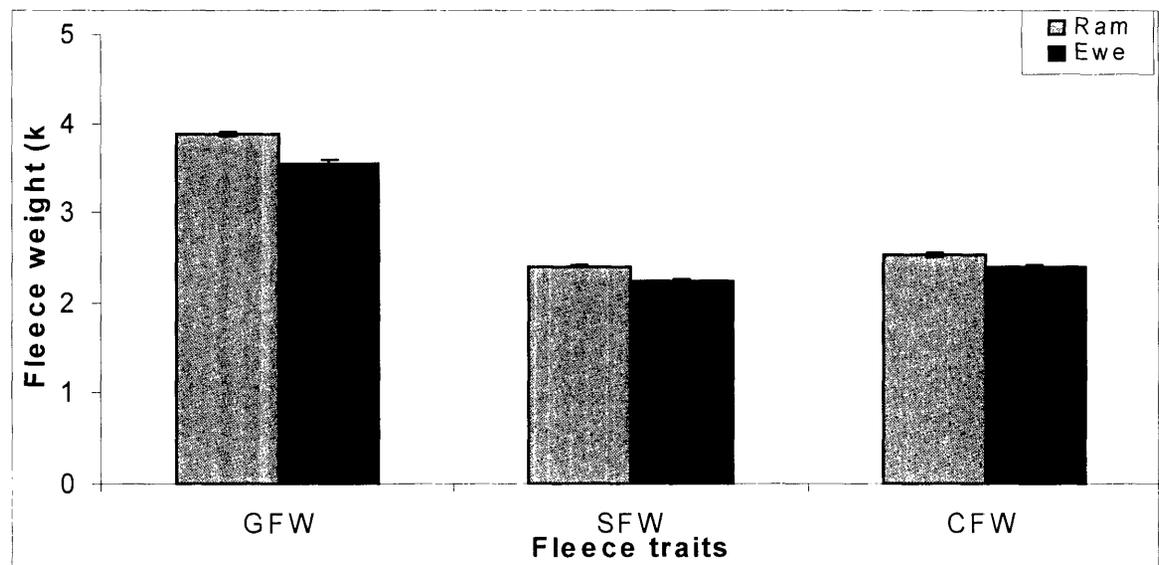


Figure 3.9 Least square means for greasy, skirted and clean fleeced weights (kg) of rams and ewes

3.4.1.4 Birth and birth-rearing type effects

3.4.1.4.1 Lamb traits

Figure 3.10 presents birth and birth-rearing type effects for lamb and hogget live weights. Single-born lambs were significantly (15.9%, $P < 0.0001$) heavier at birth than multiple-born lambs. On the other hand, single-born and-reared lambs grew significantly ($P < 0.0001$) faster to weaning by 4.6% and 16.4% than multiple born/single-reared and multiple born and reared lambs. Weaning weight was 5.9% and 15.8% higher, respectively. The average weaning weight was 20.55 ± 0.14 kg for single-born and-reared lambs, 19.33 ± 0.24 kg for multiple born/single reared lambs and 17.30 ± 0.16 kg for multiple-born and-reared lambs. Nine-month weight was similar for single born/reared and multiple born/single reared lambs but both weights were significantly ($P < 0.0001$) 6.0% more than multiple-born and-reared lambs. The average nine-month weight were 29.33 ± 0.18 kg for single born/reared, 28.86 ± 0.31 kg for multiple-born/single-reared and 27.56 ± 0.19 kg for multiple-born/reared lambs.

Single-born lambs had a significantly ($P < 0.0001$) higher mean birth-coat score (5.1%) and survival rate from birth to weaning (23.2%) compared with the multiple-born lambs.

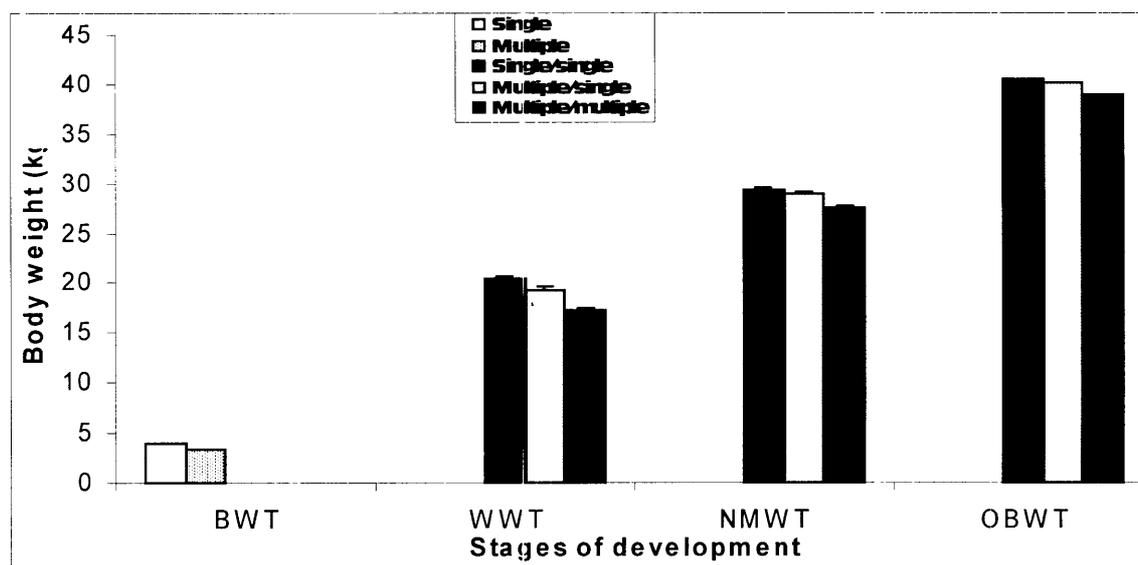


Figure 3.10 Least square means for birth, weaning, nine-month and off-shear body weights (kg) of birth types (single and multiple types) and birth-rearing types (single born/reared, multiple born/single reared and multiple born/reared)

3.4.1.4.2 Hogget production traits

Least square means for birth-rearing type effects on greasy, skirted and clean fleece weights of the three lines are shown in Figure 3.11. Hoggets born and raised as singles had the highest greasy, skirted and clean fleece weights ($P < 0.0001$). Except for greasy fleece weight, no significant differences were observed between single-born and-reared hoggets and multiple-born and single-reared hoggets but both were significantly superior in the fleece weights compared with multiple-born and-reared hoggets.

The average fibre diameter of the single-born and-reared hoggets was 20.4 ± 0.06 microns which was significantly finer than the 20.5 ± 0.11 microns and 20.7 ± 0.06 microns observed for the multiple-born and single-reared and the multiple-born and-reared hoggets, respectively. No significant difference was observed in yield among the three birth and rearing types. For off-shear live weight, multiple born and reared hoggets were significantly inferior to the other groups as shown in Figure 3.10.

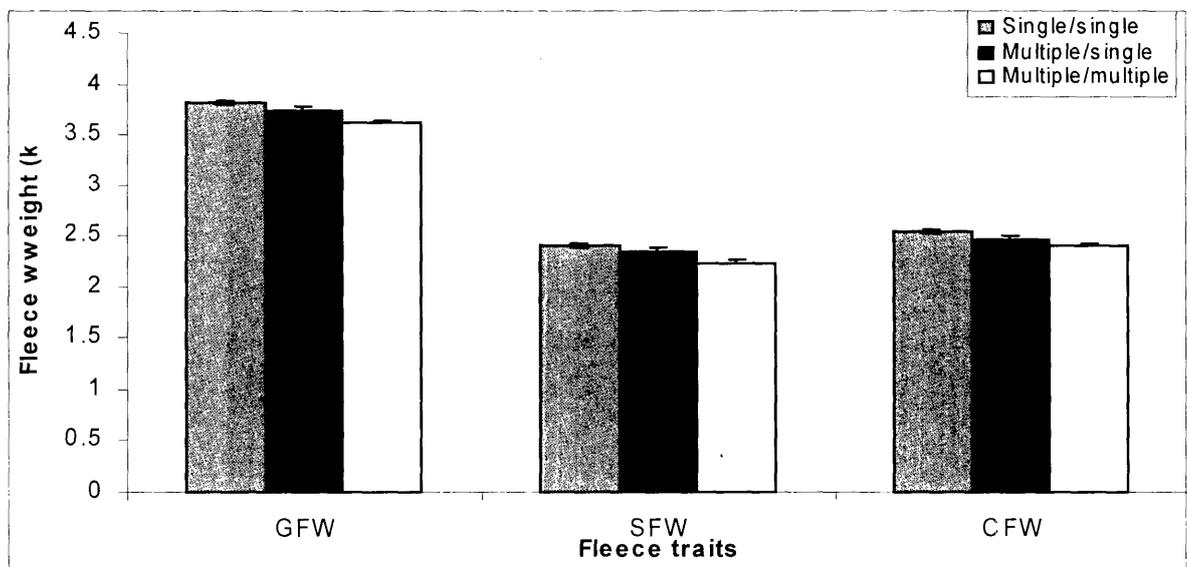


Figure 3.11 Least square means for greasy, skirted and clean fleece weights (kg) of birth types (single and multiple types) and birth-rearing types (single born/reared, multiple born/single reared and multiple born/reared)

3.4.1.5 Year effects

3.4.1.5.1 Lamb traits

Least square means for significant ($P > 0.0001$) year effects on lamb traits are shown in Figures 3.12 and 3.13. Differences between years ranged from 1.0 % to 25.4 % for birth weight, 0.8% to 27.8 % for weaning weight and 0.06% to 18.6 % for nine-month weight.

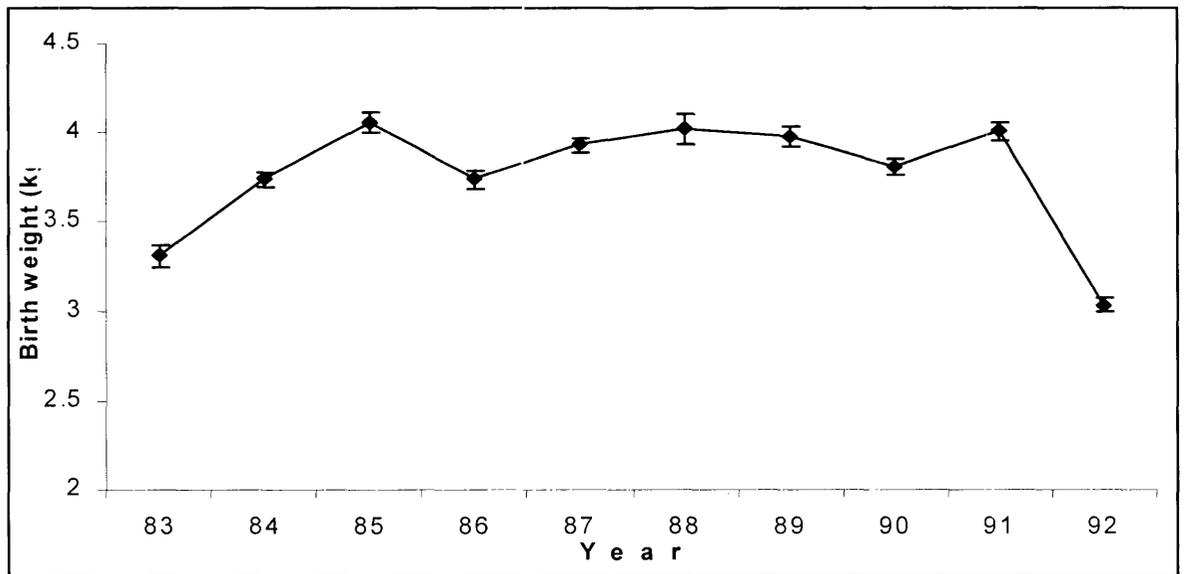


Figure 3.12 Least square means for birth weight as affected by year of birth.

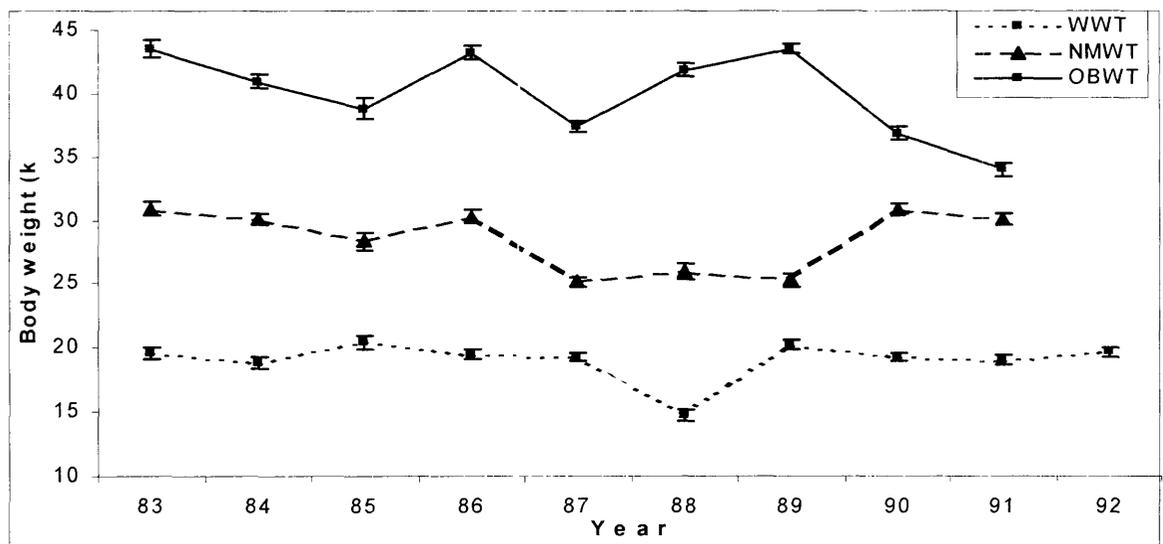


Figure 3.13 Least square means for weaning, nine-month and off-shear live weights as affected by year of birth.

For growth rate to weaning, differences between years ranged from 1.7% to 34.1%. Significant ($P < 0.001$) differences for lamb survival and birth-coat score ranged from 4.9% to 28.4% and 2.6% to 26.8 %, respectively.

3.4.1.5.2 Hogget production traits

Figure 3.14 shows the significant effects of year on fleece traits of hoggets. Differences between years ranged between 2.2% to 28.4 % for greasy fleece weight, 7.8 % to 25.3 % for clean fleece weight and 2.6 % to 25.3 % for skirted fleece weight. Differences between years for yield ranged from 0.4 % to 8.7% and 4.2 % to 12.6 % for fibre diameter. For off-shear live weight, differences between years ranged from 0.73 % to 22.0 % (Figure 3.11).

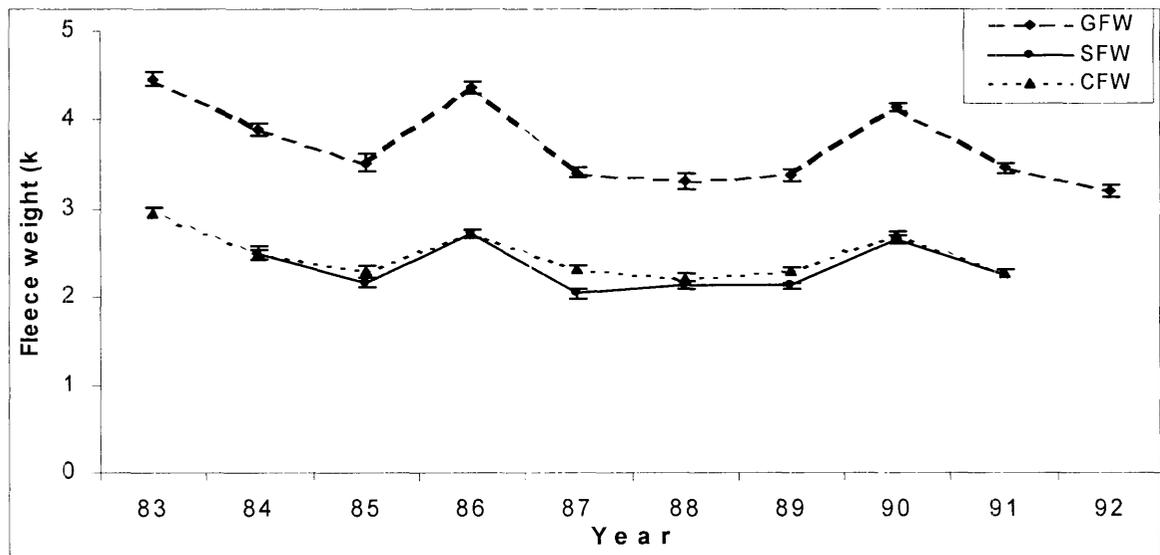


Figure 3.14 Least square means for greasy, skirted and clean fleece weights as affected by year of birth.

3.4.1.6 Age of dam

3.4.1.6.1 Lamb traits

The effect of age of dam in most lamb and hogget traits show the characteristic curvilinear effect (Figures 3.15 and 3.16). Performance of progeny from dams of

intermediate age were higher than the performance of progeny of 2-year old and older ewes.

Older dams produced significantly ($P>0.001$) heavier lambs at birth, weaning and at nine-months than two year old dams. Lambs from older dams also grew faster to weaning. Lamb survival and birth-coat score were also significantly ($P<0.001$) higher for the offspring of older dams. However, the size of the effect of age of dam declined after the ewes reached six years of age.

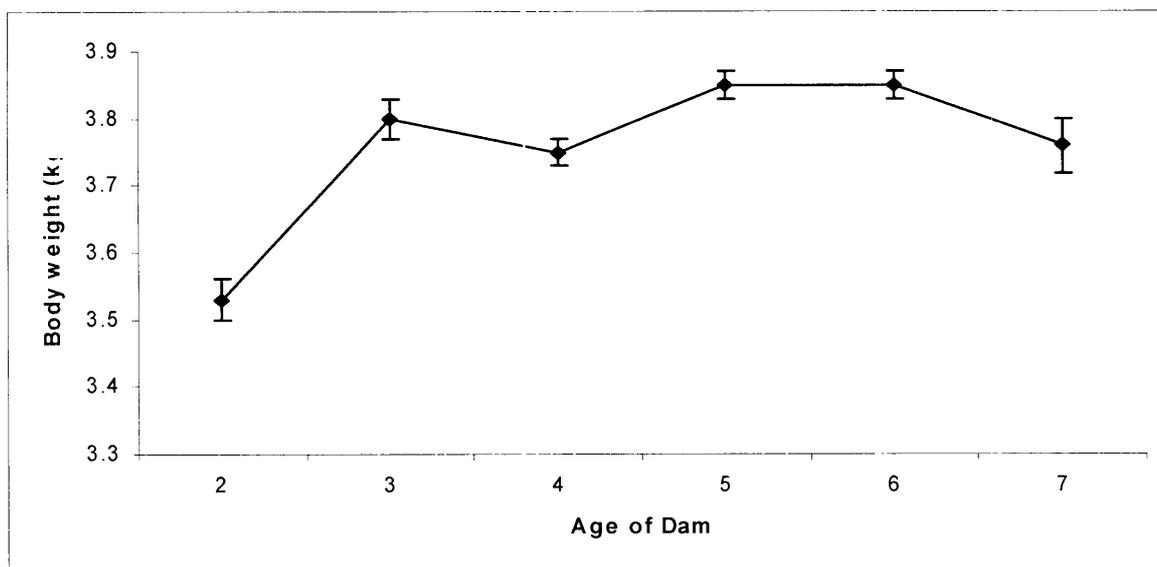


Figure 3.15 Least square means for birth weight as affected by age of dam.

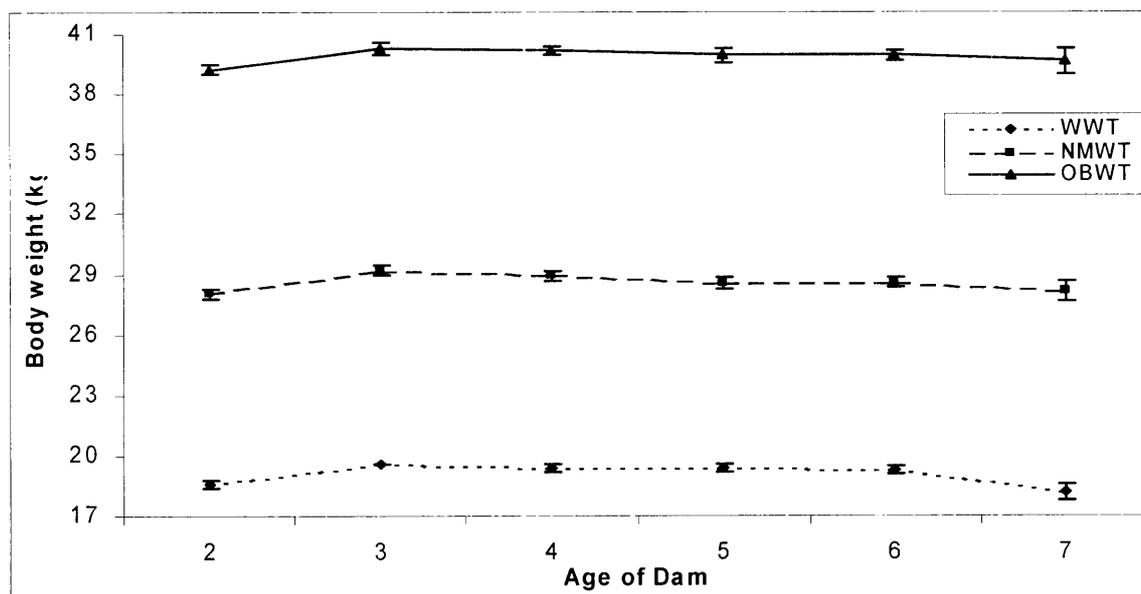


Figure 3.16 Least square means for weaning, nine-month and off-shear live weights as affected by age of dam.

3.4.1.6.2 Hogget production traits

The effect of age of dam on hogget traits show a characteristic curvilinear effect similar to the effect on lamb traits (Figure 3.17). Hoggets from two year old ewes have significantly ($P < 0.001$) lower greasy, skirted and clean weights than hoggets than ewes of intermediate age. Age of dam had no significant effect on fibre diameter, but hoggets of dams seven years or older had significantly ($P < 0.0001$) lower yield compare to hoggets from younger dams. The live-weight of 15-16 month-hoggets from older dams was significantly heavier than hoggets from two-year old dams.

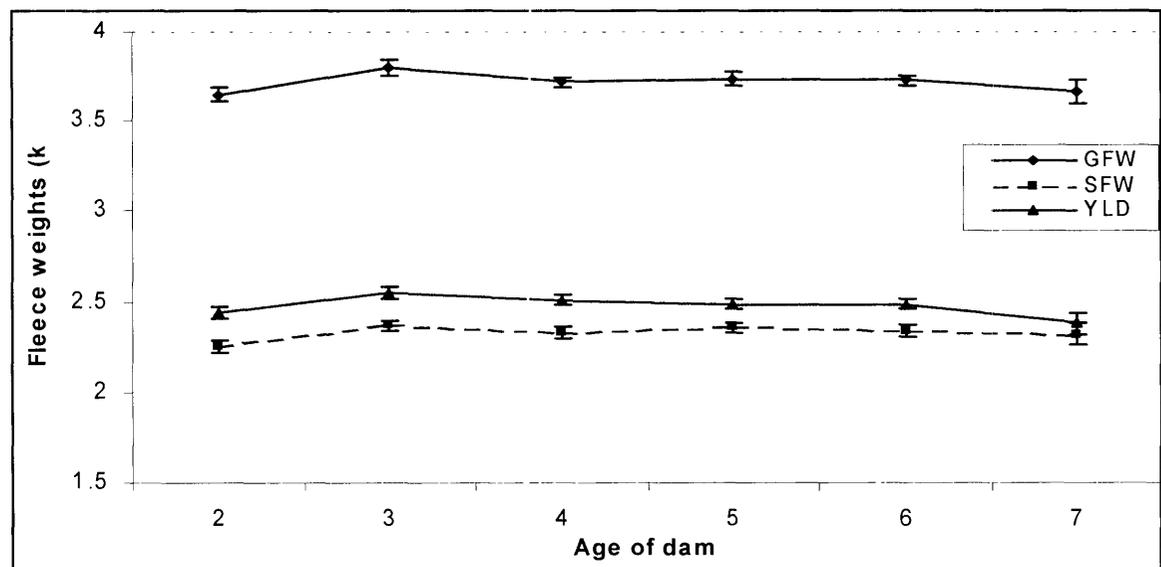


Figure 3.17 Least square means for greasy, skirted and clean fleece weights as affected by age of dam.

3.4.2 Direct additive and maternal genetic effects

3.4.2.1 Variance components

Variance component estimates for lamb and hogget traits calculated in univariate analyses are presented in Table 3.8.

3.4.2.1.1 Lamb traits

The residual variances were larger for most lamb traits compared to direct additive, maternal and permanent maternal environmental variances component. The direct additive variances were also higher than the maternal and permanent environmental variances for most lamb traits except lamb survival. For live weights, the direct additive variance increased from birth weight to off-shear live weight (15-16 months), but at a decreasing rate: 98.0% from birth weight to weaning weight, 51% from weaning weight to nine-month weight and 29.3% from nine-month weight to off-shear live weight. For maternal additive genetic variances, the values increased from birth to weaning and declined thereafter. The permanent maternal environmental variances also showed a similar trend. This could be due to scale effect; mean birth weight is smaller than mean weaning weight, and therefore the variance are expected to increase in magnitude.

3.4.2.1.2 Hogget traits

For wool traits, the direct additive variance were higher for skirted fleece weight, yield, fibre diameter and off-shear live weight while the residual variance was higher in greasy and clean fleece weights compared to other variance components. Maternal additive genetic variances were generally lower compared to the residual and direct additive variances. The correlations between direct additive and maternal variances are mostly negative for wool traits except for fibre diameter.

3.4.2.2 Genetic parameters

Table 3.9 shows the resulting heritability estimates of the direct additive, maternal effect, the estimated genetic correlation between the direct and the maternal effect and the estimated permanent maternal environmental variance as a proportion of the phenotypic variance and their approximate standard errors.

Table 3.8. Variance component estimates from univariate analyses of lamb and hogget production traits.

Traits	Component †					
	σ_P^2	σ_E^2	σ_A^2	σ_M^2	σ_C^2	σ_{AM}^2
<i>Lamb traits</i>						
BWT	0.289	0.143	0.067	0.011	0.036	0.032
BCS	2.551	0.961	1.282	0.080	0.156	0.072
LS	0.147	0.101	0.018	0.003	0.027	-0.002
WWT	14.540	6.910	5.375	1.056	1.791	-0.587
GR	684.000	349.668	299.981	26.851	38.026	-80.523
NMWT	18.600	7.605	11.052	0.492	0.000	-0.500
<i>Hogget traits</i>						
GFW	0.394	0.198	0.196	0.003	0.016	-0.018
SFW	0.218	0.084	0.138	0.008	0.000	-0.012
YLD	28.830	11.185	17.065	0.478	1.169	-1.666
CFW	0.194	0.102	0.096	0.006	0.002	-0.014
FD	1.897	0.722	1.347	0.009	0.000	-0.092
OBWT	26.230	10.360	15.625	0.086	0.000	0.157

† σ_P^2 , phenotypic variance; σ_E^2 , error variance; σ_A^2 , direct additive variance; σ_M^2 , maternal genetic variance; σ_C^2 , permanent maternal environmental; σ_{AM}^2 , direct-maternal genetic co-variance

3.4.2.3 Direct additive heritability

3.4.2.3.1 Lamb traits.

Birth weight and lamb survival from birth to weaning had moderate direct heritability estimates of 0.23 and 0.12, respectively. Weaning weight, birth-coat score, growth rate to weaning and nine-month weight were found to be highly heritable, with estimates of 0.37, 0.53, 0.44 and 0.59, respectively. Heritability estimates of live weights increased with age at weighing from 0.23 at birth to 0.37 at weaning, 0.59 at nine-month old and 0.60 at 15-16 months old (off-shear live-weight weight).

Table 3.9. Genetic parameter estimates and their approximate standard errors for lamb and hogget production traits.

Trait	Parameter [†]			
	h^2	m^2	c^2	r_{AM}
<i>Lamb traits</i>				
BWT	0.230 ± 0.064	0.112 ± 0.011	0.125 ± 0.037	0.238 ± 0.433
BCS	0.502 ± 0.075	0.028 ± 0.024	0.061 ± 0.028	0.264 ± 0.000
LS	0.121 ± 0.054	0.019 ± 0.046	0.187 ± 0.046	-0.264 ± 0.688
WWT	0.370 ± 0.065	0.073 ± 0.096	0.123 ± 0.082	-0.247 ± 0.374
GR	0.439 ± 0.102	0.112 ± 0.067	0.056 ± 0.047	-0.530 ± 0.182
NMWT	0.593 ± 0.865	0.026 ± 0.044	0.000 ± 0.034	-0.214 ± 0.350
<i>Hogget traits</i>				
GFW	0.496 ± 0.085	0.007 ± 0.039	0.043 ± 0.034	-0.248 ± 0.000
SFW	0.632 ± 0.100	0.035 ± 0.042	0.000 ± 0.000	-0.361 ± 0.274
YLD	0.604 ± 0.100	0.017 ± 0.056	0.041 ± 0.040	-0.584 ± 0.751
CFW	0.493 ± 0.097	0.030 ± 0.055	0.011 ± 0.039	-0.480 ± 0.383
FD	0.678 ± 0.080	0.004 ± 0.040	0.000 ± 0.033	-0.831 ± 0.000
BOWT	0.596 ± 0.067	0.003 ± 0.031	0.000 ± 0.000	0.126 ± 1.453

[†] h^2 , direct additive heritability; m^2 , maternal heritability; c^2 , permanent maternal environmental effect; r_{AM} direct-maternal genetic correlation.

3.4.2.3.2 Hogget production traits

All hogget wool traits and 15-16-month live-weight were highly heritable. The wool fleece weights had heritability estimates of 0.49, 0.51 and 0.63 for clean, greasy and skirted fleece weights, respectively. Heritability estimates for yield was 0.60 and 0.68 for fibre diameter. Live-weight had a 0.60 heritability estimate with standard errors of around 0.09.

3.4.2.4 Maternal heritability

3.4.2.4.1 Lamb traits

Most lamb traits showed low levels of maternal heritability. For live weights, birth weight has a moderate estimate of maternal heritability of 0.11, but the values decreased at weaning weight (0.07) and declined further at nine-month old (0.03). Growth rate from birth to weaning registered a moderate estimate of 0.11 maternal heritability while lamb survival and birth-coat score had low maternal heritability estimates of 0.003 and 0.02, respectively.

3.4.2.4.2 Hogget production traits

All wool traits showed very low estimates of heritability: 0.01 for greasy fleece weight, 0.03 for skirted fleece weight, 0.04 for clean fleece weight, 0.02 for yield and 0.004 for fibre diameter. The result shows that maternal effects on wool traits were very minimal. Heritability estimate for off-shear live weight was a low 0.003.

3.4.2.5 Permanent maternal environmental effects

3.4.2.5.1 Lamb traits

Estimates for permanent maternal environmental effects were moderate for birth weight (0.12) and weaning weight (0.12). However, after weaning, the values for other live weight traits, nine-month weight and off-shear live-weight, were very negligible suggesting that permanent maternal environmental effects decreases with age. Birth-coat score and growth rate both registered a permanent environmental effect of 0.06 while lamb survival showed a 0.19 permanent environmental effect.

3.4.2.5.2 Hogget traits

For the wool traits, all traits suggested low permanent environmental estimates. Greasy fleece weight and yield both have an estimate of 0.04 and clean fleece weight had 0.011 estimate. Estimates for yield was 0.04.

3.4.2.6 Direct additive - maternal genetic correlation

3.4.2.6.1 Lamb traits

Direct-maternal genetic correlations for birth weight and birth-coat score were low but positive at 0.24 and 0.26, respectively. Other lamb traits showed low and negative correlation estimates: -0.26 for lamb survival, -0.53 for weaning weight, -0.21 for nine-month weight. A moderate negative direct-maternal genetic correlation estimate was observed for growth rate to weaning.

3.4.2.6.2 Hogget traits

All wool traits showed negative direct-maternal genetic correlations. Greasy fleece weight and skirted fleece weight registered low correlations while yield and clean fleece weight have moderate estimates. Although, in the positive direction, the direct-maternal genetic correlation for off-shear live weight was very low at 0.13.

3.4.3 Bivariate analyses

Estimates of the correlations between the different Merino lamb traits are presented in Table 3.10 while Table 3.11 shows estimates for hogget production traits and between lamb and hogget traits.

3.4.3.1 Phenotypic correlations

3.4.3.1.1 Lamb traits

Phenotypic correlations among lamb live weights were all positive. Correlation between birth weight and weaning weight was 0.19 and 0.24 between birth weight and nine-month weight. Weaning weight correlation to nine-month weight was 0.24. Birth weight has a low and positive correlation to growth rate while weaning weight correlation to growth is high positive.

Birth weight showed a very low but positive phenotypic correlation to birthcoat score, growth rate to weaning and lamb survival. On the other hand, weaning weight phenotypic correlation to birth-coat score is low and negative. Birth-coat score and growth rate and growth rate and lamb survival have negative and negligible correlation while birth-coat score and lamb survival are negligibly correlated in the positive direction.

3.4.3.1.2 Hogget production traits

Phenotypic correlations among the fleece weights are very high and positive in the range of 0.70 to 0.87. Yield showed a negligible and negatively correlation to greasy fleece weight, but positive to skirted fleece weight and a moderate positive correlation to clean fleece weight. Phenotypic correlation of fibre diameter to the fleece weights were 0.22, 0.32 and 0.18 for greasy, skirted and clean fleece weights.

The phenotypic correlations off-shear live weight with fleece weights were moderate and positive (0.42 - 0.43) and with a negligible but positive correlations to yield and fibre diameter.

3.4.3.1.3 Lamb and hogget production traits

The phenotypic correlations of off-shear live weight with the lamb growth traits vary as shown in Table 13. It has a low and positive correlation with BWT (0.22), moderate and

positive correlation (0.43) with weaning weight and a high and positive correlation with nine-month weight (0.68). Birth weight showed a low but positive correlation with fleece weights (0.25 – 0.29) while weaning weight, nine-month weight and off-shear live weight were moderately and positively correlated with the fleece weights (0.41 - 0.56) except for the low positive correlation between nine-month weight and skirted fleece weight (0.37). Yield was negligibly but positively correlated with the growth traits (0.01 – 0.03) while fibre diameter had negligible but positive correlations with weaning weight, nine-month weight and off-shear live weight, but its correlation to birth weight was low and positive.

Table 3.10 Genetic and phenotypic correlation estimates among lamb traits of Merino sheep.

Traits		Correlations †				
1	2	r_{A12}	r_{M12}	r_{AM11}	r_{AM22}	r_{P12}
BWT	BCS	0.291	-0.161	-0.023	0.831	0.074
	GR	0.455	0.243	-0.023	0.831	0.074
	LS	0.222	0.248	-0.048	0.786	0.051
	WWT	0.163	0.236	-0.649	-0.002	0.197
WWT	BWT	0.163	0.236	-0.649	-0.002	0.197
	BCS	0.028	0.300	0.000	0.520	-0.071
	GR	0.560	0.001	0.420	-0.259	0.740
BCS	GR	-0.083	0.001	0.751	-0.603	-0.096
	LS	0.026	0.053	0.014	0.970	0.052
GR	LS	0.000	0.019	-0.001	0.995	-0.051

† r_{A12} , direct genetic correlation; r_{M12} , maternal genetic correlation; r_{AM11} and r_{AM22} , direct-maternal genetic correlations; r_{P12} , phenotypic correlation

3.4.3.2 Direct genetic correlations

3.4.3.2.1 Lamb traits

Birth weight showed a negligible but positive genetic correlation to weaning weight (0.16) and moderate and positive correlations with nine-month weight and growth rate. Likewise, weaning weight was moderately correlated to both growth rate (0.56) and nine-month weight (0.49). Genetic correlation of birth weight to birth-coat score is low but positive and with a negligible but positive association to weaning weight. Birth weight had a moderate and positive correlation to lamb survival. Birth-coat score direct genetic correlation to lamb survival was 0.03 and -0.02 for growth rate

3.4.3.2.2 Hogget production traits

The three fleece weights had very high and positive correlations (0.80 - 0.95) between each other and were all moderately and positively correlated to off-shear live weight (0.43 – 0.55). The genetic correlation between yield and fleece weights were -0.08, 0.05 and 0.41 to greasy, skirted and clean fleece weights, respectively. Fibre diameter, on the other hand, showed a negligible but positive genetic correlation to clean fleece weight and a low and positive correlation to greasy and skirted fleece weights. Correlation between yield and fibre diameter was 0.04 and both were negligibly but positively correlated to off-shear live weight.

3.4.3.2.3 Lamb and hogget production traits

Birth weight and nine-month weight showed moderate and positive genetic correlations to the three fleece weights (0.46 - 0.59) while weaning weight showed a low but positive correlations (0.28 - 0.34). Fibre diameter and yield were both very lowly but positively correlated to the live weights. Direct genetic correlation of off-shear live-weight with other live-weights increased with age from 0.22 for birth weight to 0.66 for nine-month weight.

Table 3.11 Genetic and phenotypic correlation estimates among lamb and hogget traits of Merino sheep.

Traits		Correlations †				
1	2	r_{A12}	r_{M12}	r_{AM11}	r_{AM22}	r_{P12}
BWT	WWT	0.164	0.237	-0.648	-0.002	0.197
	NMMT	0.293	0.571	-0.006	-0.371	0.236
	BOWT	0.244	0.017	-0.034	0.035	0.217
	GFW	0.412	0.976	0.001	0.042	0.267
	SFW	0.425	0.845	-0.063	-0.397	0.261
	CFW	0.374	0.580	-0.043	-0.570	0.243
	YLD	0.050	-0.300	0.006	-0.346	0.219
	FD	0.176	0.446	-0.351	0.562	0.009
WWT	NMWT	0.406	0.222	-0.490	-0.175	0.535
	BOWT	0.490	0.057	-0.000	0.010	0.464
	GFW	0.294	0.683	0.124	0.120	0.375
	SFW	0.351	0.267	-0.120	-0.298	0.416
	CFW	0.395	0.687	-0.119	-0.020	0.403
	YLD	0.004	-0.080	-0.764	-0.421	0.017
	FD	0.128	0.010	-0.655	0.428	0.080
NMWT	BOWT	0.831	0.437	-0.14	0.000	0.660
	GFW	0.557	0.835	0.000	0.001	0.536
	SFW	0.463	0.589	0.006	0.004	0.571
	CFW	0.557	0.392	0.000	0.007	0.516
	YLD	0.064	0.072	-0.455	-0.402	0.027
	FD	0.152	-0.764	-0.315	0.319	0.152
BOWT	GFW	0.485	0.038	0.000	0.001	0.423
	SFW	0.448	0.312	0.125	0.018	0.449
	CFW	0.654	0.214	0.098	0.002	0.437
	YLD	0.034	0.730	0.022	0.009	0.022
	FD	0.060	-0.834	0.031	0.261	0.088
GFW	SFW	0.727	0.987	0.097	0.004	0.776
	CFW	0.938	0.629	0.116	0.100	0.865
	YLD	0.067	0.616	0.139	0.001	-0.081
	FD	0.158	0.001	0.018	0.775	0.217
SFW	CFW	0.810	0.990	0.014	0.001	0.696
	YLD	0.003	0.575	0.088	0.003	0.046
	FD	0.333	0.036	0.007	0.695	0.315
CFW	YLD	0.509	0.709	0.312	0.003	0.408
	FD	0.139	0.102	0.007	0.246	0.183
YLD	FD	0.002	0.041	-0.231	0.075	0.045

† r_{A12} , direct genetic correlation; r_{M12} , maternal genetic correlation; r_{AM11} and r_{AM22} , direct-maternal genetic correlations; r_{P12} , phenotypic correlation

3.4.3.3. Maternal genetic correlations

3.4.3.3.1 Lamb traits

Maternal correlations between lamb traits were all positive except for birth weight and birth-coat score. Birth weight had a low correlation to growth rate, lamb survival and weaning weight. Weaning weight had a low correlation to birth-coat score and a negligible correlation to growth rate. Maternal correlations between birth-coat score, growth rate and lamb survival were all very low.

3.4.3.3.2 Hogget traits

Maternal genetic correlations between fleece weights were very high (0.63 - 0.99). The fleece weights correlations to yield varied from a low correlation for skirted fleece weight to high correlation for clean fleece weight. Fibre diameter had a negligible and low maternal correlation to fleece weight and yield.

Off-shear live-weight had a negligible or low positive correlation to fleece weights, a high positive correlation to yield and a high but negative correlation to fibre diameter.

3.4.3.3.3 Lamb and hogget traits

Birth and weaning weights had a negligible maternal correlation with off-shear live weight while nine-month weight and off-shear live weight were moderately correlated. Live weights generally showed high correlations to fleece weights except for a low correlation between weaning weight and skirted fleece weight and between nine-month weight and clean fleece weight.

Yield showed a decreasing correlation with live weight as the animal aged, from a moderate maternal correlation with birth weight to positive negligible correlation to weaning weight and nine month to a very negative maternal correlation to off-shear live weight. Maternal correlations between fibre diameter and live-weights showed the opposite trend.

3.5 Discussion

3.5.1 Line effects

The superior performance of Weight Plus lambs found in this experiment is consistent with the findings reported by other authors. The results confirmed the conclusion that selection for high weaning weight has led to higher weights at other ages and a faster growth rate (Davis 1987, Hinch *et al.* 1986). Lasslo *et al.* (1985) also found that lines selected for 120-day weight had significantly higher birth weight and weaning weight compared with the unselected controls, with greater difference apparent under dry-lot conditions than under range conditions. Generally, these reports and others have shown that selection for high and low weaning weight in sheep resulted in an increase and decrease in live weights in subsequent generations at weaning (Pattie 1965a) and also at other ages, including maturity (Pattie 1965b, Pattie and Williams 1966 and 1967).

The results of the present study showed that the response in the growth rates in the weaning weight selection lines reported by Pattie (1965b) and Davis (1987, 1987b) were maintained following the suspension of selection. Weaning weights were heavier at weaning and at other ages, including maturity. The suspension of selection within the weaning weight selection lines appears not to have greatly altered the relative performance of the animals in the subsequent generations.

Comparing the three lines under better rainfall conditions, there was an increase in the difference between lines for birth, weaning, nine-month old and off-shear live weights as compared to the difference between lines for the whole duration of the study. However, the difference was non-significant. Further comparison of the performance during better and poorer rainfall conditions showed no significant differences between the lines.

Davis (1987) reported that lamb survival was greatest with lambs selected for high weaning weight which is similar to the present findings although in this case Weight Plus lambs were not significantly different from the Random lambs. In contrast, Lasso *et al.* (1985) found that lamb survival to weaning decreased in positively selected

lines compared with a control line, the reason for which was not given (possibly associated with excessive birth weights and increased proportion of difficult births).

The results for the fleece weight traits in the present study are also in broad agreement with the findings of Davis (1987) that selection for high weaning weight lead to insignificant changes in wool production. He reported that the realised genetic correlation between weaning weight and greasy fleece weight was negligible which indicated that while there was a considerable divergence in mature body size between the selection lines, there was little change in wool production. He also noted negligible changes for yield, clean fleece weight and fibre diameter in mature ewes. The finding of Davis (1987) was in good agreement with the earlier findings of Pattie (1965) that selection for high weaning weight does not increase the value of sheep for wool production. This was also attributed to the negligible and low realised genetic correlations between weaning weight and hogget greasy and clean fleece weight. Pattie (1965) further explained that in the Weight Plus line there was a decrease in follicle density, which resulted to a decrease in the total number of fibres, despite an increase on surface area. In the Weight Minus line, there was a small increase in primary fibre density but its effect on wool production was cancelled by a decrease in surface area and fibre volume. The result implies that selection for weaning weight would result to positive effects on body weights but not to wool production. If a farmer is interested in improving fleece weights only, then selection for body weight traits, weaning weight, specifically, will not significantly improve fleece weights.

3.5.2 Environmental effects

Sex has been widely reported elsewhere to have significant effects on growth and wool production traits. Female lambs have been shown to grow more slowly to weaning than male lambs by between 7.0% (Atkins 1978) and 12.4% (Sidwell and Miller 1971b) which is confirmed in the present study. Likewise, weaning weight has been shown to be significantly greater in male lambs than in female lambs (Sidwell and Miller 1971b), whether castrated or not (Walkley *et al.* 1987). Young *et al.* (1965) and Davis (1987) reported that males were heavier at weaning by 10.24% and 14.25%, respectively, slightly higher than the 8.94% difference reported in this study.

Lamb survival was significantly higher in ewes in this study and is similar to the findings of Lax and Turner (1965) and Mullaney (1969) for other Merino flocks. The 6.7% difference between the sexes is higher than the 4.6% reported by Hight and Jury (1977) but within the 1% - 9% estimates of Gunn and Robinson (1963). In contrast, some other reports have indicated that sex has no influence on lamb survival (Atkins 1978, Davis 1987). For birth-coat score, the present result confirmed the findings of Davis (1987) that ewe lambs had significantly higher birth-coat scores than ram lambs.

Previous findings have shown that ram hoggets are significantly superior to ewe hoggets for fleece weights, other fleece traits and mature live weights (Terril *et al.* 1945, and Jackson and Roberts 1970). The result of this present study is in agreement with other observations. Walkley *et al.* (1987) had similar findings except for yield and crimps while Terril *et al.* (1948b) noted that the greatest differences were found for greasy fleece weight and live weight similar to the findings of the present study. However, Young *et al.* (1965) found that sex differences have negligible effects on fleece weights.

Single-born lambs have been reported to be heavier than multiple-born lambs at birth (Purser and Young 1960, Mullaney 1969, Smith 1977, Hinch *et al.* 1986, Davis, 1987). Differences in birth weight between single and multiple born lambs were in the order of 15-25% (Bogart *et al.* 1957, Starke *et al.* 1958, Turner 1961, Purser and Young 1964, Atkins, 1978) and parallel the 15.9% difference found in this study. The handicap of multiple birth which is presumably due to the competition between foetuses for a limited supply of nutrients could be the main reason for the lower birth weight of multiple-born lambs (Dun and Grewal 1963).

Survival rate of single-born lambs has been shown to be higher than multiple-born lambs in a number of breeds of sheep (Sidwell *et al.* 1962, Sidney and Miller 1971b, Smith 1977 and Dalton *et al.* 1980). Sidwell *et al.* (1962) reported that a higher percentage of single lambs born alive were weaned than of twins. Dalton *et al.* (1980) concluded that the differences in survival between single-born and multiple-born were mainly due to birth weight. Davis (1987) suggested, however, that the major effect was through litter size rather than birth weight directly. As litter size increases from single to twin, there is a corresponding increase in lambs' mortality when lambs are raised by

their dams (Purser and Young 1964, Sidwell *et al.* 1972, Sidwell and Miller 1971a, Hinch *et al.* 1985, and Demiroren *et al.* 1985).

Birth and rearing type effects on weaning weight were significant confirming earlier studies (Hohenboken *et al.* 1976, Walkley 1978, Sidwell and Miller 1971b, Dun and Grewal 1963, Young *et al.* 1965, Davis 1987). Likewise average daily gain was also influenced by birth and rearing type as previously reported by (Sidwell and Miller 1971b, Olson *et al.* 1976, Carter *et al.* 1971, Davis 1987). The post-natal handicap of multiple rearing is linked to the mother's inability to feed and care for several lambs as adequately as she can care for one (Dun and Grewal 1963). This process is critical in the first few weeks of life when the lamb is entirely dependent on the mother (Guyer and Dyer 1954). Although twinning effects were found to be greater at weaning than at other ages, the handicap is evident up to 15-16 months of age (Lax and Brown 1967) and even up to 18 months (Young *et al.* 1965, Lax and Turner 1967). The results of this study agree with these earlier findings

Because of the maternal handicap due to multiple birth, Young *et al.* (1965) concluded that birth and birth/rearing type should not be ignored in any selection program. Davis (1987) agreed, recommending that when selecting on traits such as weaning weight and growth rate a more accurate estimate of breeding value would be obtained by correcting lamb records for both birth and rearing status.

The superiority of the single born and raised hoggets reported in the present study for clean fleece weight and fibre diameter confirmed the previous reports of Dun and Grewal (1963), Lax and Brown (1967), Atkins (1978), Davis (1987), and Walkley *et al.* (1987). The difference in the superiority of single-born and raised hoggets than the multiple born and raised hoggets for clean fleece weight and fibre diameter reported in this study are less than the findings of Mortimer and Atkins (1989) of 8% less wool and and the 5.3% less clean fleece weight reported by Turner (1961) for Merinos at Cunamulla, NSW. On the other hand, the differences are greater than the 0.09 kg less fleece wool of Hight and Terril (1946) and Terril *et al.* (1948b); the 0.03 kg less clean wool reported by Turner (1964) at Trangie; and those reported by Brown *et al.* (1966). Differences in these findings are possibly attributed to the various breeds of sheep used in these studies. Therefore, when selecting for fleece traits and live weight, it is necessary that some corrections should be made for birth/rearing type effects.

The significant findings of the present study on the effects of year of birth on live weights are in agreement with the earlier reports. Year effects were reported to have a significant influence on birth and weaning weights and growth rate to weaning in studies by Sidwell and Miller 1971c, Dun and Grewal 1963, Jackson and Roberts 1970, Walkley *et al.* 1987, Smith, 1977, Atkins 1978, and Davis 1987. The present results for wool traits are also similar to the findings of Mortimer and Atkins (1989) for GFW (4.0 to 4.7 kg), and FD (19.5 to 21.9 microns). Year differences in live weight were larger (27.9 to 43.8 kg) but confirmed the reports of Terilli *et al.* (1948b) and Brash *et al.* (1997) that year was a significant source of variation for most hogget fleece traits and live weight. Year effects were also observed on lamb survival/livability (Sidwell *et al.* 1962; and Dalton *et al.* 1979) which suggested that there are environmental and/or management influences over and above nutritional differences associated with varying lamb birth weights (Hinch *et al.* 1985).

The present results on the effect of age of dam confirmed the findings of Atkins (1978) and Davis (1987) that the age of dam is a significant source of variation for birth weight. The progeny of two-year old ewes were lighter and grew more slowly than lambs born to older ewes. Atkins (1978) argued that birth weight increased progressively with increasing dam age up to five years and that the difference in growth rate between lambs born to ewes which were older than two years of age was less marked. Weaning weight and growth rate were also influenced by age of dam and the result of the study showed that the weaning weights of lambs of 4-year old ewes were 5.6% heavier than those of 2-year old ewes. The lambs of 7-year or older ewes were 1.99% lower than those of 2-year old ewes. Although, slightly higher, the findings are similar to those of Vesely *et al.* (1965, 1967). In both instances, the curvilinear effect of age of dam on growth rates are confirmed.

The pattern of increasing birth weight with increasing age of dam is associated with a progressive improvement in the pre-natal environment with age (Blackwell and Henderson 1955, Dickerson *et al.* 1955, Hight and Jury 1970b). On the other hand, the effect of the dam's age on growth rate of lambs is a manifestation of a relatively poorer post-natal maternal environment of maiden ewes as compared to older ones which is mainly due to the lower milk production of younger ewes (Owen, 1957).

Lamb survival was also shown to increase with age in agreement with published reports (Bowman 1966, Lax and Turner 1965, Sidwell and Miller 1971b). The lower survival rate of lambs from younger ewes means that 2-year old ewes require better management than older group of ewes as suggested by Dalton *et al.* 1980).

Walkley *et al.* (1987) reported that age of dam did not significantly affect most fleece traits such as greasy fleece weight, clean fleece weight, yield, fibre diameter. However, a tendency for offspring of 2 year-old ewes to have lower greasy and clean fleece weight was apparent. The present study which showed significant effects of the age of dam for fleece traits with the exception of fibre diameter is in agreement to the findings of Terril (1965) that offspring from mature dams produced 0.3 lbs more clean fleece weight than those for 2 year-old dams.

3.5.3 Genetic and phenotypic parameters

3.5.3.1 Direct additive heritability

The direct heritabilities and standard errors estimated for lamb and hogget production traits in the present study are in general agreement with the early estimates as presented in Section 3.4.1.2.1.

Several published reports on genetic parameters of direct and maternal effects on lamb weights reported varied estimates between studies. However, most results showed that direct heritabilities increased with age (Mavrogenis *et al.* 1980, Nasholm and Dannel 1996, Notter and Hough 1997). from birth weight to mature age, and the results presented here agree reasonably well with the previous investigations.

Birth weight is shown in the present study to be within the ranges of the estimates reported. The estimate is similar to the reports of Mortimer and Atkins (1995) and Larsgard (1998). However, the estimate is higher than the estimates of Maria *et al.* (1993), Nasholm and Dannel (1996), Van Wyk *et al.* (1993) but lower than the high heritability reports of Olivier *et al.* (1994), Pitono and James (1995) and Vaez Torshizi *et al.* (1995). The high direct heritability of weaning weight found in this study was higher than most estimates but within the same level of the estimates of Maria *et al.*

(1994). The same was true with growth rate, which was higher than the low and moderate estimates of the previous reports (Van Wyk *et al.* 1993, Larsgard and Olesen 1998).

The direct heritability estimates for nine-month weight and off-shear live weight are generally higher than the estimates for birth and weaning weights which agrees to the finding that direct heritabilities increase with age. Due to the higher heritability of hogget live-weight, Young *et al.* (1965) suggested that faster genetic gains in WWT could be achieved by selecting on hogget weight rather than on weaning weight as the need to adjust for environmental effects would be less critical at the later age. Compared to previous reports, the estimates reported here are generally higher (Notter and Hough 1993, Mortimer and Atkins 1995, Vaez Torshizi *et al.* 1995, and Lewis and Beatson 1999). It was, however, similar to one of the estimates reported by Hickson *et al.* (1995).

The high heritability estimates for birth-coat score is lower than findings of Davis (1987) who used both REML and GLS methods. It was also lower to that obtained by Morley (1955) and Gregory (1982b) using paternal half-sib methods of estimation. The high heritability of birth-coat score is typical of wool production traits which are relatively free from maternal effects according to Black and Reis (1978), who suggested that nutritional requirements of follicle development are minor compared to those of growth. Schinkel (1955) suggested that the pregnant ewe needs to experience extremes of nutritional environment before there is an effect on follicle membrane and primary-secondary follicle ratios in the lamb; it is a difference in primary to secondary follicle ratio that changes BCS. The lamb survival heritability estimate of the present study was lower than those reported by Davis (1987) using both GLS and REML methods. Bindon and Piper (1977) also found a low heritability for lamb survival in Merinos. Lamb survival as with other production traits is likely to be lowly heritable according to Falconer (1981) due to the influence of natural selection which causes fixation of desirable genes and thus reduces additive genetic variance. The lower lamb survival and birth-coat score reported here could be attributed to the fact that maternal effects were not accounted for in the previously mentioned reports. Nasholm and Danell (1996) explained that estimates of direct heritability will decrease when maternal effects are included and if the direct-maternal genetic correlation is positive.

The heritabilities of greasy and clean fleece weights estimated in the present study are in general agreement with the earlier estimates of Hickson *et al.* (1995). However, both estimates are higher than values previously reported (Mortimer and Atkins 1994, Swan and Hickson 1994, Olivier 1994, Lewis and Beatson 1999). The heritability estimates for fibre diameter, on the other hand, were generally in agreement with the estimates of the previously mentioned reports. Yield also showed a very high heritability level which confirms previous reports.

3.5.3.2 Maternal heritability

Maternal heritability for the various live weights was smaller than direct heritability. Similar to previous reports, the finding of the present study showed maternal heritability estimates decrease in importance with increasing age for growth traits (Tosh and Kemp 1994, Mortimer and Atkins 1995, Van Wyk 1995, Hickson *et al.* 1995, Nashol and Dannel 1996). Robison (1981) also reported that maternal effects in mammals are important to young animals but diminish with age. This suggests that the influence of maternal effects are significant to lamb weights and is strongest and of substance on birth weight (Nasholm and Dannel 1996).

The maternal heritabilities reported in the present study largely agree with the estimates previously reported for birth weight (Olivier *et al.* 1993, Mortimer and Atkins 1994, Pitono and James 1995), for weaning weight (Pitono and James 1995, Notter and Hough 1997, Lewis and Beatson 1999), for the nine-month weight and for off-shears live weight (Hickson *et al.* 1995, Mortimer and Atkins 1995).

Maternal heritability estimates for the wool traits were generally lower compared to the estimates of Mortimer and Atkins (1994), but higher than the report of Hickson *et al.* (1995). Mortimer and Atkins (1994) found significant maternal effects for greasy and clean fleece weights shorn at 12 months but not for fibre diameter, staple length and follicle density. They recommended extending estimates of maternal effects to a wider range of ages. Swan and Hickson (1994) observed significant maternal effects for greasy fleece weight at weaning but there was no carry-over effect when measured at 12 months and for fibre diameter, unlike for live weights. Hickson *et al.* (1995) found quite small maternal effects for fleece weight traits, in particular clean fleece weight, from 10

month of age onwards and therefore has limited influence on lifetime production. He suggested that genetic evaluation for fleece traits will not be greatly biased by ignoring maternal effects at the ages at which selection occurs. Based on these reports and on the result of the study, no immediate need to consider maternal effects on fleece traits in breeding programs.

3.5.3.3 Permanent maternal environmental effects

Effects of permanent maternal environment, which were moderate for birth weight, weaning weight and lamb survival was in agreement with most published estimates. The result indicates that the permanent maternal environmental effect is substantial for birth weight (Maria *et al.* 1994, Mortimer and Atkins 1995) and weaning weight (Mortimer and Atkins 1995, Tosh and Kemp 1995). Post-weaning daily gain was also influenced by permanent maternal environmental effects as well as birth and weaning weights, which was attributed to uterine capacity and maternal behaviour of the dams (Pitono and James 1995). The estimates for nine-month old and off-shear live-weights were found to be very small that it has no possible influence on the traits. This confirms the reports of Tosh and Kemp (1995) on 10-16 months of age and Mortimer and Atkins (1994) on 9 and 16 months of age Merinos. The findings of Hickson *et al.* (1995) also showed significant permanent effects for live weight at 10 months of age but not older ages.

For the wool traits, the effect found in this report was too small, which indicates that its influence on fleece traits can be ignored. Swan and Hickson. (1994) reported a permanent maternal environmental effect of 0.1 for greasy fleece weight at weaning and 0.05 at 12 months of age, which are greater than the findings of the present study.

3.5.3.4 Direct-maternal genetic correlations

Direct-maternal correlation on birth weight was low and positive and low negative for weaning weight and nine-month weight. Estimates from most studies have tended to be negative for birth and weaning weights (Maria *et al.* 1993, Mortimer and Atkins 1994, Van Wyk *et al.* 1994, Tosh and Kemp 1994, Lasgard and Olesen 1998).

Olivier *et al.* (1993) positive correlation for birth weight while find Nasholm and Dannel (1994, 1995) showed that direct-maternal correlations were positive and increased with age, from 0.105 at birth to 0.638 at slaughter age. Pitono and James (1995), however, reported a reverse trend with direct-maternal correlations decreasing as the age of the offspring decreases with positive correlations for birth weight and weaning weight and negative for 6 month-age. He reasoned that the result was in accordance with Bradford (1972), who reviewed some selection experiments in sheep and found that about half of the response to selection for weaning weight was due to milk yield of the dam. The finding suggests that there is a positive or at least a lowly negative genetic correlation between the direct and maternal effects. Koch *et al.* (1982) also reported that birth weight for cattle was more strongly influenced by direct variation than by maternal genetic effects, with a small positive or negative correlation between them.

For wool traits, the correlations were from low to moderate and were similar to the results of previous estimates.

3.5.3.5 Phenotypic correlations

The negligible but positive phenotypic correlation of birth weight with birth-coat score and lamb survival in the present study agreed with the findings of Davis (1987), who found the low association quite surprising because of the important environmental association between the two traits. However, Piper and Bindon (1977) showed a curvilinear relationship between birth weight and lamb survival and concluded that a low phenotypic correlation is expected. The low association between birth-coat score with other lamb traits is expected because the follicle number and primary: secondary follicle ratio, which determines birth-coat score, are established early in foetal life relative to other traits and are thus less influenced by pre and post-natal effects (Davis 1987).

Phenotypic association between birth weight and growth rate and between weaning weight and growth rate confirmed the findings of Davis (1987) for Merinos and of Vesely *et al.* (1967) and Ercanbrack and Price (1972) for other breeds.

The very high correlation between greasy fleece weight and clean fleece weight estimated in the present study confirms previously well documented findings (Mullaney *et al.* 1970, Gunawan *et al.* 1985, Gunawan and James 1986, James *et al.* 1987, Lewer *et*

al. 1994). The correlations between greasy fleece and skirted fleece and between clean fleece weight and skirted fleece weight also agreed with the report of Mortimer and Atkins (1989).

The correlations between the fleece weights and yield, between fleece weights and fibre diameter and between yield and fibre diameter in the present study confirmed most published reports. The results agreed with the findings of Lewer *et al.* (1994) that retention of sheep with high greasy fleece weight will lead to increased fibre diameter and decreased yield. The same result will occur if clean fleece weight is used as a selection criterion except that yield and fibre diameter should increase.

The result of phenotypic correlations between various live weights follow the trend observed by Lewer *et al.* (1994) that there is a significant trend for the correlations to increase as the sheep aged, and to decrease as the records become more widely separated in time. Mortimer and Atkins (1996) found birth weight to have low positive phenotypic correlation with various live weights and a strong positive correlation among weaning, 9 months and 15 months weights. The weighted average direct phenotypic correlation between the live weights ranged from 0.20 to 0.66 which agrees to literature estimates for Merino sheep (Davis 1987, Vaez Torshizi 1995, Mortimer and Atkins 1996) and have been reviewed for wool sheep breeds by Fogarty (1985).

The correlations between growth traits (birth weight, weaning weight, nine-month weight and off-shear live weight) and wool traits (greasy fleece weight, clean fleece weight, skirted fleece weight, yield and fibre diameter) agreed with literature estimates and suggest that growth traits contribute to increases in fleece weight performance in hoggets.

3.5.3.6 Genetic correlations

The low positive genetic correlation between birth weight and lamb survival found in the present study and the negligible association between birth-coat score and lamb survival is in agreement with published reports. Davis (1987), however, showed a higher genetic correlation between birth weight and birth-coat score than found in this report. The genetic correlation between birth weight and growth rate and weaning

weight and growth rate confirmed published reports (Vogt *et al.* 1967, Ercanbrack and Price 1972, Davis 1987). Davis (1987) which found the genetic correlation between weaning weight and growth rate not to be significantly different from unity and suggested that the genetic control of weaning weight is largely determined by growth rate to weaning and that birth weight is relatively unimportant as a component of weaning weight.

The positive genetic correlations among all the live weight traits indicated that genetic potential for weight is exhibited early in life. It also confirmed well the suggestion that growth at all ages is under the same genetic control (Taylor 1980, Atchley 1984). Mortimer and Atkins (1996) reported those genetic correlations among live weight increased with age. Birth weight had low positive direct genetic correlations with all later live weights. Strong, positive genetic correlations occurred among weaning and post-weaning weights, which the result of the study is in complete agreement. The low to high and positive correlations between growth traits also indicated that selection for any one weight would result in considerable positive change in all weights at all ages. In order to minimise the effect of selection for weight on birth weight and possible increased frequency of dystocia, Martin *et al.* (1980) suggested that selection would be best directed towards weight at later ages although selection for weight at later ages would lead to increased mature weights and greater maintenance costs.

The very high genetic correlations observed in this study between greasy fleece weight, off-shear live weight and clean fleece weight were generally within the range of those previously published. The high genetic correlations between greasy fleece weight and clean fleece weight indicate the usefulness of greasy fleece weight as an indirect but very precise selection criterion for improving clean fleece weight. On the other hand, the lower correlation between skirted fleece weight and clean fleece weight suggests no advantage in using off-shear live weight over greasy fleece weight as an indirect selection criterion to improve clean fleece weight (Mortimer and Atkins 1989).

The negligible and moderate genetic correlations reported in the present study of greasy fleece weight and clean fleece weight with fleece weight, a component of the traits, was lower than many estimates (Mullaney *et al.* 1970, Jackson and James 1970, Davis and Kinghorn 1986, Davis 1987 and Mortimer and Atkins 1989). However, they

were similar to those reported by Beattie (1962), Brown and Turner (1968) and Gregory (1982b). The result may suggest that selection for fleece weights may result in coarser wool.

Except for clean fleece weight, genetic correlations of yield with other wool traits were negligible and negative, which generally are in agreement with most published reports.

The four lamb and hogget growth traits (birth weight, weaning weight, nine-month weight and off-shear live weight) have low to moderate and positive correlations to the fleece weights (greasy fleece weight, clean fleece weight and skirted fleece weight). This is in full agreement with the reports of Young *et al.* (1965), Walkely *et al.* (1987), Lewer *et al.* (1994) and Brash *et al.* (1997). The positive genetic correlations suggest that selection for increased live weight at any age up to 16 months should result in increased fleece weights. By including any live weight in a breeding plan, as a selection criterion will therefore provide additional information, which will increase the accuracy of selection for fleece weight (Lewer *et al.* 1994). Davis and Kinghorn (1986) also reported that selection for larger animals would give sheep with heavier fleeces. Robertson (1987) also noted that although increases in wool weights have been observed due to selection for increased weight at various ages, the increases have been more in line with expectations based on genetic correlations between fleece weights and hogget live weights than with the higher correlation with weaning weight

The negligible and positive genetic correlation between the growth traits and fibre diameter compared well with the estimates of Lewer *et al.* (1994), Beattie (1962), Hancock *et al.* (1979), but were lower compared to the findings of Davis and Kinghorn (1986), and Davis (1987). Likewise, the genetic correlations between the growth traits and yield agreed well with most reported experiments.

3.5 Conclusion

Lines previously selected for high and low weaning weights were different in lamb and hogget production traits following the suspension of selection. The Weight Plus lambs were heavier by at birth, at weaning and at nine months old and grew faster from birth to weaning than the Weight Minus and Random lambs. For hogget

production traits, the Random line significantly performed better in greasy, clean and skirted fleece weights and yield than the lines selected for high and low weaning weights. The Weight Plus hoggets, however, had the heaviest live weight at 15-16 months and finest wool. The results of this study showed that the responses in growth traits observed in the weaning weight selection lines in the previous experiments of Davis (1986) and Pattie (1965ab) were maintained following the suspension of selection. Similar conclusion is made for the wool traits except for fibre diameter. Apparently, the suspension of selection within the weaning weight lines did not greatly alter the performance of the animals in the subsequent 5-6 generations. Effects which could change responses in the lines appear not to have been operating greatly during the short period of study.

Sex, birth and birth rearing types, year and age of dam are environmental factors that significantly influence most lamb and hogget traits. Single born and reared rams and born to an intermediate age dam are heavier at various ages and produce more wool. Year was a significant source of variation for all traits. To increase the accuracy of selection and efficiency of production, considerable attention needs to be paid to account for environmental factors.

Direct additive and maternal heritability, phenotypic and genetic correlation estimates were in general agreement with previously published studies. Maternal effects have substantial influence on growth of younger animals but less on wool traits. The high positive phenotypic and genetic correlations between growth traits and fleece traits suggest that selection for any one live weight and fleece weight would result in a positive change in all weights at various ages and in fleece weights.

Chapter 4

Genotype x environment interactions for lamb traits

4.1 Introduction

The phenotype of an animal is determined by its genotype and the environment in which it is found; while the relative merit of various genotypes depends on the environmental conditions to which the animals are exposed. The existence of genotype and environment (G x E) interactions may mean that the best genotype in one environment is not the best in another environment or simply that the genotype performance in one environment is different in terms of magnitude in another environment. Therefore, genotype and environment interactions can involve changes in rank order for genotypes between environments as well as changes in the absolute and relative magnitude of genetic and environmental sources of variation between environments.

Genotype and environment interactions have important implications for the design and efficiency of selection programs. The interactions resulting from changes in magnitude may be of low significance, but genotype and environment interactions that alter the phenotypic ranking of a series of genotypes between environments can considerably hamper a selection program. The presence of a substantial interaction means that selection should be carried out in the environment in which the animals will be kept provided that the environment is fairly predictable. If the environmental

variation is likely to be unpredictable in time or degree, then the breeder has little choice but to aim at general adaptability over a range of conditions.

Genotype and environment interactions have been observed in growth studies in mice (Falconer 1960, Dalton 1967) and for several traits in chicken (Dickerson 1962) where effects appear to be more pronounced for egg production rather than for growth of broiler stock (Hartman 1990). Many researchers have reported differential responses of Zebu and European breeds of cattle to tropical and temperate environments (Cartwright 1955, Miller *et al.* 1963, Butts *et al.* 1971, and Gregory 1979). In sheep, Dunlop (1962 and 1963), Carter *et al.* (1971 and 1973) and Hohenboken *et al.* (1976, 1981, 1984 and 1988) have focused their studies of genotype x environment interactions on traits of economic importance such as growth, wool production, reproduction and carcass traits. They reported that significant and real interactions were observed for many traits but these were generally of moderate to small size accounting for only a minor fraction of the variance. Lasslo *et al.* (1985) examined genotype x environment interactions in sheep selected for weaning weight and concluded that selection under better feed conditions resulted in equivalent improvement in growth rate in a dry lot conditions as that attained by animals selected under range conditions.

Sheep in Australia are raised in a wide variety of environments. These locations show considerable variation in climate (temperature, rainfall, humidity and solar radiation), geography (soil quality and altitude), systems of management (extensive or intensive grazing and natural or improved pasture) and feed quality and availability (total and seasonal). These environmental variations are considerable and consequently genotype x environment interactions are likely to exist, and are of more considerable importance in sheep and cattle managed under extensive conditions than in housed species where these environmental variables are more closely controlled.

The main objective of this study was to determine if genotype x environment interactions influenced performance in lambs. Using two lines of Merino sheep selected for and against weaning weight and a randomly selected control group, comparisons were made of performances in two grazing environments. Traits evaluated in this study included birth weight, birth-coat score, lamb-survival to weaning, weaning weight and growth rate to weaning.

4.2 Review of Literature

4.2.1 Genotype x environment interactions

Genotype x environment interactions may be defined as the varying response of genotypes in various environments (Pani and Lasley 1972). Its genotype and environment determine the phenotype of an animal. In equation form it can be written as:

$$P = G + E \quad (\text{Equation 1})$$

where

P = phenotype of an individual,

G = genotype of an individual and

E = environment provided to an individual.

The equation is true when genotype and environment are not dependent in each other. When interaction between genotypes and environments exists, the equation 1 becomes:

$$P = G + E + I_{GE} \quad (\text{Equation 2})$$

where

I_{GE} = interaction between genotype and environment.

Kearsey and Pooni (1996) illustrated the nature and causes of genotype x environment (G x E) interactions. Theoretically, G x E may be recognised in at least three forms:

- In a given environment, the environmental variation for a particular trait may vary with the genotype,
- The environment variance exhibited by a particular genotype may alter with the environment, and

Genotype x environment interactions

- The genetic variance among a collection of genotypes may alter with the environment, that is the effects of given allele substitutions may be quite different in one environment than in the other environment.

Type effects may be created by differences in single gene or genotypes of families, strain, breeds or species, while environmental differences may be either macro (such as climates, management practices, nutritional regimes, hygiene situation, type of housing) or micro such as presence of subclinical infections, differences between age groups, sexes). Thus a manifold combination of effects between genotype and environment can be imagined, which can also influence phenotypic expressions to a significant degree in practice (Barlow 1981). If macro environmental variables are controllable and measurable, one can explore the situation by plotting the phenotypic score against the level of the variable. Uncontrolled macro environments, like locations and seasons, complicate the statistical analysis, exploitation of G x E and interpretation of the results (Kearsey and Pooni 1996). If genotypes x environment interactions are ignored, this will cause bias in estimating the genetic parameters and predicting the breeding values. However, often researchers ignore G x E when planning experiments with different locations or seasons. So when analysing such type of data, genotype x environment interactions should be taken into consideration.

Dunlop (1962) classified genetic differences as either large or small. He defined small genetic differences as those occurring among individuals of a single population such as single flock, or the related flocks of a breed or strain, and large genetic differences as those between strains, breeds, species or even wider genetic divisions. Similarly, environment differences were either large or small. Small environmental differences are those occurring from individual to individual in a single general environment where differences are due to such definable elements in the environment as field, age, sex, etc, are either non-existent or have been corrected for, and large environmental differences as those between different districts or regions, or widely different husbandry or nutritional regimes.

4.2.2 Genotype x environment interactions for sheep

Experiments to estimate the importance of G x E interactions for a number of economically important traits of sheep have been conducted, but still relatively little critical information is available. The static experimental approach, where relative performances of different genotypes are measured under different environments in factorially designed experiments and interaction variance estimated, have long been applied in most studies conducted in sheep. The choice of genotypes and treatments has created a body of literature with a wide range of genotype and treatment combinations. A review of the reports on G x E interactions, specific interactions between genotype x location and genotype x year on various traits of economic importance in sheep is presented below.

4.2.2.1 Genotype x location interactions

4.2.2.1.1 Growth traits

An experiment to estimate the importance of genotype x environment interactions for a number of economically important characters in sheep was conducted from 1959 to 1965 by the Canada Department of Agriculture and the Virginia Agricultural Experiment Station (Carter *et al.* 1971a, 1971b, 1973). The two breed crosses used were North Country Cheviot x grade Canadian Leicester crossbreds (NC x L) and Hampshire x (Hampshire x Rambouillet) backcrosses (H x HR). Samples of each ewe breed cross were kept to five lamb crops at two locations: Glade Springs, Virginia, U.S.A. and Ottawa, Ontario, Canada. Both locations are in the humid temperate regions of Eastern North America with a continental climate. They have a difference from each other of 9 degrees of latitude or approximately 966 kilometres (north-south) with Ottawa having a colder and longer winter. The station at Glade Spring is approximately 627.9 meters above sea level, while elevation at Ottawa is 85.3 meters. Summer temperatures average a little lower at Glade Spring than Ottawa due presumably to differences in elevation and summer day length.

The researchers reported some ewe breed x location interactions for live weight of ewes. Both breeds were heavier at Glade Spring than at Ottawa. The breed x location interaction was significant suggesting that NC x L ewes responded more favourably to the environment in Canada than did the Hampshire cross ewes. In a second experiment (Carter *et al.* 1971b), significant ewe breed x location interactions were evident for birth weight with NC x L ewes being heavier at both locations, but more so at Ottawa than at Glade Springs. The situation was similar with respect to the 120-day weight. However, there was no significant evidence for a breed x location interaction on average daily gain. The researchers reported that while ewe x breed interactions were present for birth and 120-day weight, the differences involved were relatively small and could not be seen as important enough to seriously affect choice of a ewe breed or breed cross in terms of commercial production. However, they concluded, that when the differential responses in lamb performance are added to the ewe productivity, the local adaptation of ewe breeds or ewe crosses is of considerable importance with respect to total production.

Osman and Bradford (1965) studied genotype x location interactions at two locations in California using whiteface Targhee-type sheep. At Davis, the ewes and the lambs were grazed on irrigated pastures and at Hopland, the flocks were run on semi-arid range. They reported significant sire x location interactions for 120-day weight and body conformation but concluded that the interaction effects were small. In another study, Redomska (1965) investigated sire x flock (confounded with location) interactions in the progeny of Merino lambs and found interactions negligible for birth weight, but noted the presence of sire x station interactions for weaning weight.

Dunlop (1963) found significant interactions of strain x location for most body attributes of adult Merino sheep raised in three locations in eastern Australia. For live weight, 6 out of 13 interactions tested were significant, 9/12 for body length, 5/10 for width of hips, 3/12 for width of shoulders, 5/12 for depth of chests, 5/12 for length of forelegs, 3/10 for sire index, 1/13 for weight of lamb born, 2/13 for number of lambs weaned and 2/13 for weight of lambs weaned. This is similar to the findings of Carter *et al.* (1971a, 1971b, 1973) and Osman and Bradford (1965), with the interactions observed being moderate to small in size and accounting for only a minor fraction of the variance. Dunlop (1963) concluded that since the strain and location interactions

were generally small to moderate in size and accounted for only a small fraction of the variance, specific adaptations were not important in the choice of the strain of sheep to be used in a particular area.

Selection for 120-day weight was conducted in two flocks from a common base population of grade Targhee sheep by Lasslo *et al.* (1985). At Davis, the sheep were maintained on a good plane of nutrition, on irrigated pasture or in a drylot while at Hopland, the sheep grazed annual grassland range, with supplementary feeding only at mating and lambing. Results showed that in both environments, selection increased weaning weight compared with unselected controls, with more improvement made in the better drylot environment. The improvement in 120-day weight made at Davis was expressed at Hopland, but not to the same degree.

Eady *et al.* (1990) ran seven groups of Merino wethers in two locations in Queensland and found large differences in the mean live weight between locations. Within each location, the proportion of live weight lost or gained by the sheep over a certain period was similar for all groups. Live weight ranking of groups was consistent, and no significant group x location interaction occurred. Hohenboken *et al.* (1976) also examined genotype x environment interaction effects on three breeds of sheep raised in two management system environments for three years. They reported no significant sire or dam breed x environment interactions for birth weight.

4.2.2.1.2 Wool traits

Significant strain x location interactions were found for twelve wool traits of the Australian Merinos examined by Dunlop (1962), but these generally accounted for only a small fraction of the variance. Dunlop (1962) concluded that specific adaptation in these characteristics should not be an important reason for the choice of the strain of sheep to be used in particular areas. In another experiment, Dunlop and Young (1966) estimated the interactions between sire and year (age), sire and drop (year) and sire x station in clean wool weight from five Merino strains at three locations. Sire and year (age) and sire and drop (year) interactions were found to be small and non-significant while the sire x station interactions were of appreciable size. They concluded that interactions will seldom appreciably hinder genetic progress from individual selection.

In contrast, Eady *et al.* (1990) showed significant group x location interactions on clean fleece weight and fibre diameter among seven groups of Merino ewes run in two locations. However, there were no significant interactions for the mean scoured yield and commercial value of fleece wool. Carter *et al.* (1971a) also found a breed cross x location interaction for greasy fleece weight for two breed crosses of ewes reared in two locations which approached significance. However, they concluded that the interaction component for the trait was small and not considered of great importance. In contrast, Vouchenko (1992) found no line x location interaction for fleece weight or wool length among four lines of Askanian sheep at two locations: breeding farm and production complex.

Staple length was the only trait for which a significant sire x location interaction was found in the study of Osman and Bradford (1965). This study conducted at Davis and Hopland in California with Targhee sheep identified no significant sire x location interactions for greasy fleece weight, fleece grade or face score. The authors concluded that the interactions, at least the kind leading to reversal of rank of genotypes between environments, were not of major importance confirming the earlier conclusions of Dunlop (1962).

4.2.2.1.3 Reproductive traits

Carter *et al.* (1971a) identified a ewe- breed x location interaction for number of ewe lambing and average lambing date. The significant breed x location interaction for weight of lamb weaned per ewe mated was explained by the different fertility of the two breed crosses of ewes at the two locations. However, there was no evidence of a breed cross x location interaction for lambs born, lambs weaned per ewe mated or lamb weaned per ewe lambing. This finding was in agreement with the earlier findings of Lax and Turner (1968) who reported no significant strain x location interaction for survival of single lambs from birth to weaning in a study of five strains of Australian Merino at three locations.

Dunlop (1963) concluded that for reproductive characteristics of Merino ewes, most differences between strains were small. The lack of large and consistent strain x location interaction was explained by the non-uniformity of individual environments

from year to year. This was demonstrated by the presence of year x station interactions which were occasionally significant and which accounted for more of the variation in reproductive traits than did strain x station interactions. It was presumed that local and temporary climatic variability was responsible for these interactions. De Hass and Dunlop (1969) also suggested that strain x location interactions were not large enough to suggest any difference in the adaptations of strains to particular locations.

4.2.4.1.4 Carcass traits

In crossbred lambs evaluated by Carter *et al.* (1973), there was a significant ewe breed x location interaction for weight carcass of loin. However, there was no evidence of a breed x location interactions in any linear carcass measurement (carcass length, carcass depth, cross-sectional area of loin eye-longissimus muscle) or fat thickness of the 12th to 13th rib were observed when carcass weight was held constant. The significant ewe breed x location interaction appeared to be a reflection of differential response to the environment in growth rate and general size and not to differential skeletal or muscle growth.

4.2.2.2 Genotype x year interaction

4.2.2.2.1 Growth traits

Atkins (1978) studied five breeds of sheep to estimate possible importance of genotype x environment interaction in production and reported that significant breed x year interactions were detected in growth rate mainly due to the differential response of the breeds to changes in environment caused by the variation between years. He further reported that differences between breeds increased with improving environmental conditions.

Hohenboken *et al.* (1988) reported some significant ewe genotype x year interactions for birth weight and weaning weight of three breeds of sheep (Coopworth, Industry Romney and Waihora Romney). However, they concluded that the

unconventional cross-classified analyses of variance did not reveal large, consistent nor economically important ewe genotype x nutritional treatment or year interactions.

In an earlier study, Hohenboken *et al.* (1976b) found no significant interactions between sire breed x year, dam breed x year, sire breed x dam breed x year and sire breed x dam breed x management system x year for birth weight, weaning weight and carcass weight gain per day. These authors used Hampshire, Suffolk and Willamette breeds of sheep run under two management systems. Interactions between ewe breed and year were not significant for birth weight, average daily gain and 120-day weight in the study of Carter *et al.* (1971b).

4.2.2.2 Wool traits and reproductive traits

Atkins (1978) observed a significant breed x year interactions for both greasy and clean fleece weights in an experiment involving five breeds of sheep. He suggested that the interaction was due to the differential responses of the breeds to variations in environment between years. In another experiment, Atkins (1980) reported that between-bred differences in the slope regressions accounted for 50% of the total interaction variation. The fitted regressions clearly showed that some breeds (eg. Corriedale) respond to more changes in the environment than others (eg. Peppin Merino), and in this instance differences in slope were sufficient for breed rankings to change. Jackson and Roberts (1970) explained that strain x year interaction for fibre diameter and stud within-strain x year interactions in greasy fleece weight, clean fleece weight and yield reflected variations between the strains in their response to changes in environment. In Peru, significant interactions between genetic origin and age in Corriedales were observed for fleece-weight, fibre diameter and staple length in a study involving three different genetic origins (Diez *et al.* 1974).

In the study of Dunlop (1962), no significant strain x year interactions were observed in all wool traits observed: greasy fleece weight, clean scour yield, crimps per inch, fibre diameter, staple length, count, character, soundness and handle. However, second order interactions of station x strain x year interaction were significant for the different traits assessed.

Dunlop (1962) found that strain x location x year interactions were mostly insignificant for most wool traits such as clean fleece weight, greasy fleece weight, yield, fibre per mm of skin, crimps per inch, fibre diameter and staple length. However, traits that are subjectively assessed like count, character, colour and handle were significant. The interactions account for a very small fraction of the variance through they may be real on some occasions (Dunlop 1962). In a related experiment, strain x location x year interactions were absent for most body traits and reproductive traits but were significant on face cover and weight of lamb weaned (Dunlop 1963).

4.2.2.4 Interaction between selection lines and environment

Woolaston (1987) reported that one of the features of long-term experiments with Merinos is that differences in wool production between selected and control flocks appear to be related to the level of performance of the control flock. Significant flock x nutrition interactions for wool growth and efficiency of conversion were observed in a pen-feeding studies utilising the Trangie fleece-weight selection lines (Williams 1966). As intakes were increased, differences in wool production between the lines increased. A similar effect was found at pasture by Hamilton and Langlands (1969), indicating that the Fleece Plus sheep were less effective in increasing wool production when pasture availability was low. In the studies of Seville and Robards (1977), the efficiency of selected sheep relative to unselected sheep increased with increasing intake, then decreased again at high intakes. The interaction observed did not result in rank changes between selected and unselected lines, merely a change in the magnitude of their difference.

4.2.3 Conclusion

The greater the difference in genotype and /or environment, the more likely that genotype x environment interaction will be important. When the two environments differ widely, breed rankings can change. However, when the environments are less diverse, the relative performance of breeds should be more predictable. Genotype x environment interaction can have an important impact on a breeding program, but the magnitude of interaction is not always known.

diverse, the relative performance of breeds should be more predictable. Genotype x environment interaction can have an important impact on a breeding program, but the magnitude of interaction is not always known.

Genotype x environment interactions, specifically line x location and line x year influence different economically important trait groups in sheep such as growth, reproduction, wool and carcass. Significant and real interactions were observed in many traits studied. However, they were generally of moderate to small size and accounted for only a minor fraction of the variance. Hence, they may not be considered of any practical importance in terms of commercial production, except when a very large difference between environments exists.

4.3 Materials and Methods

4.3.1 Source of data

The data used in this study were recorded at the Agricultural Research Centre, Trangie and the University of New England, Armidale. The study used animals from the Trangie Weight Selection Experiment which was conducted by NSW Agriculture between 1951 and 1995. The environment, management and data recorded on the three lines involved on the three lines in this experiment are described in detail in Chapter 2.

4.3.2 Experimental animals and observations

In this study, data on animals born between 1983 and 1987 at the two locations were used. From Trangie, records were available from a total of 1519 sheep: 444 from the Weight Plus line (progeny of 26 sires), 209 from the Weight Minus line (progeny of 26 sires) and 866 from the Random line (progeny of 47 sires). From Armidale, 929 sheep records were available: 354 from the Weight Plus line (progeny of 26 sires), 163 from the Weight Minus line (progeny of 26 sires) and 391 from the Random line (progeny of 46 sires).

During the period of the study, joinings were conducted using rams selected randomly within lines after selection was suspended from Trangie-bred rams. Five to

ten rams were used each year and these rams were used in Trangie for joining in February to March and transported to Armidale for an April joining. Table 1 shows the percentage linkage of sires of the three lines at the two locations. On the average, 93.12 % of Random rams used for joining in Trangie were also used in Armidale, 92% for Weight Plus and 92.76% for Weight Minus rams.

Within the five-year period, animals were born during July and August at Trangie and August and September at Armidale. Weaning was in the months of November to December at Trangie and December to January at Armidale.

Table 4.1. Percentage linkage of sires of the three lines within the five-year period at the two locations.

Year	Line		
	Random	Weight Plus	Weight Minus
1983	88.89	100.00	83.33
1984	100.00	60.00	80.00
1985	95.46	100.00	100.00
1986	93.75	100.00	100.00
1987	87.50	100.00	100.00
Mean	93.12	92.00	92.67

The traits observed on animals included birth weight, weaning weight, growth rate to weaning, lamb survival to weaning and birth-coat score. Data for birth weight and birth-coat score were recorded for five years (1983-87) and only four years (1983-86) of recording occurred for growth rate, lamb survival and weaning weight. Descriptions of the various lamb traits are given in Chapter 2.

4.3.3 Statistical Analyses

Least squares analyses of variance was used to estimate the effects of environmental sources of variation on the data for the lamb traits, as well as testing genotype x environment interactions. The general linear model procedure (GLM) of the Statistical Analysis System (1990) program was used for all analyses. The linear

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model (Model 1) fitted for lamb traits birth weight, birth-coat score and lamb survival was:

$$y_{ijklm} = \mu + l_i + p_j + y_k + s_l(l_i p_j y_k) + l_i p_j + l_i y_k + p_j y_k + l_i p_j y_k + b_1 \text{dob}_{ijklm} + b_2 \text{dob}_{ijklm} + e_{ijklm} \quad (\text{Model 1})$$

where

$$\begin{aligned}
 y_{ijklm} &= \text{individual observation,} \\
 \mu &= \text{overall mean,} \\
 l_i &= \text{effect of the } i\text{th line (} i = 1,2,3; 1 = \text{Random, } 2 = \text{Weight Plus, } 3 = \text{Weight Minus),} \\
 p_j &= \text{effect of the } j\text{th location (} j = 1 \text{ and } 2; 1 = \text{Trangie, } 2 = \text{Armidale),} \\
 y_k &= \text{effect of the } k\text{th year (} k = 1,2, \dots 5; 1 = 1983, 2 = 1984, 3 = 1985, 4 = 1986, 5 = 1987), \\
 s_l(l_i p_j y_k) &= \text{effect of the } l\text{th sire within } i\text{th line, } j\text{th location and } k\text{th year,} \\
 l_i p_j &= \text{interaction effect between line and location,} \\
 l_i y_k &= \text{interaction effect between line and year,} \\
 p_j y_k &= \text{interaction effect between location and year,} \\
 l_i p_j y_k &= \text{interaction effect between line, location and year,} \\
 b_1 \text{dob}_{ijklm} &= \text{linear regression effect due to the day of birth,} \\
 b_2 \text{dob}_{ijklm} &= \text{quadratic regression effect due to the day of birth,} \\
 e_{ijklm} &= \text{random error effect assumed NID } \sim(0, \sigma_e^2).
 \end{aligned}$$

A linear model (Model 2) was fitted to weaning weight and growth rate as follows;

$$y_{ijklm} = \mu + l_i + p_j + y_k + s_l(l_i p_j y_k) + l_i p_j + l_i y_k + p_j y_k + l_i p_j y_k + b_1 \text{wage}_{ijklm} + b_2 \text{wage}_{ijklm} + e_{ijklm} \quad (\text{Model 2})$$

where y_{ijklm} , μ , l_i , p_j , y_k , $s_l(l_i p_j y_k)$, $l_i p_j$, $l_i y_k$, $p_j y_k$, $l_i p_j y_k$ and e_{ijklm} are as for Model 1 and

$$\begin{aligned}
 b_1 \text{wage}_{ijklm} &= \text{linear regression effect due to the weaning age of lamb,} \\
 b_2 \text{wage}_{ijklm} &= \text{quadratic regression effect due to the weaning age of lamb.}
 \end{aligned}$$

The linear model fitted included fixed effects of line, location, year and line x location, line x year, location x year and line x location and year interactions. Sire nested within line x location x year was fitted as a random effect. Day of birth was fitted as a covariate for birth weight, birth-coat score and lamb survival and lamb age at weaning was fitted as a covariate for weaning weight and growth rate to weaning. The covariates were first fitted within location, but since the result showed non-significant effects, they were later fitted within cohorts.

4.3 Results

4.4.1 Analyses of variance

Table 4.2 shows the analyses of variance for the various lamb traits. The model accounted for 35%, 25%, 13%, 58% and 45% of the total variation in birth weight, birth-coat scores, lamb survival to weaning, weaning weight and growth rate to weaning, respectively. The main effects of line, location and year had significant influence ($P < 0.05$) for most traits except lamb survival. Line x location interaction ($P < 0.001$) were significant for birth weight, weaning weights and growth rate. Line by year interactions were significant for birth weight and birth-coat score and non-significant for lamb survival, weaning weight and growth rate. Location x year interactions were significant effects ($P < 0.001$) for birth weight, birth-coat score, weaning weight and growth rate but non-significant for lamb survival. The second order line x location x year interactions were significant for birth-coat score, lamb survival and growth rate.

Sire nested within line, location and year had a significant effect for all lamb traits. Day of birth, fitted as linear and quadratic regressions within cohort, had no significant effect in any lamb trait while weaning age, fitted as linear and quadratic regressions within cohort, significantly influenced growth rate. When fitted in a linear regression model it significantly influenced weaning weight.

4.4.2 Genotype effects

The least square means for the selection and control lines are shown in Table 4.3. The Weight Plus lambs were significantly ($P < 0.001$) heavier at birth (11.7%) and at weaning (12.7%) and grew faster to weaning (13.3%) than the Random lambs. In turn, Random lambs performed better than the Weight Minus lambs in the three traits by 16.1%, 24.92 % and 29.47%, respectively. Comparing the selection lines, the Weight Plus line was heavier than the Weight Minus line by 29.8% for birth weight, 40.7% for weaning weight and 50.0% for growth rate. However, the Weight Minus lambs scored 15.3% higher in birth-coat score than the Weight Plus lambs. Random lambs had significantly higher birth-coat scores than Weight Plus lambs by 35.3% and 17.4% higher than Weight Minus lambs. Lamb survival rates between lines were not significantly different.

4.4.3 Location effects

Lambs raised in Trangie performed significantly better than lambs raised in Armidale (Table 4.4). The Trangie lambs were heavier at birth by 14.1%, at weaning by 7.3% and higher growth rate (7.3%) than Armidale-born lambs. The birth-coat score of Trangie lambs were also higher (17.2%) while lamb survival showed no significant difference between the two locations.

Table 4.2. Analyses of variance for birth weight (BWT), birthcoat score (BCS), lamb survival to weaning (LS), weaning weight (WWT) and growth rate to weaning (GR).

Sources of variation	d.f.	F-values				
		Birth weight (kg)	Birthcoat scores	Lamb survival rate	Weaning weight (kg)	Growth rate (g/day)
<i>Main Effects</i>						
Line	2	208.96 ^{***}	69.05 ^{***}	2.42 ^{ns}	155.41 ^{***}	142.90 ^{***}
Location	1	32.05 ^{***}	6.33 [*]	3.07 ^{ns}	5.59 [*]	7.23 ^{***}
Year	4	4.10 ^{**}	8.30 ^{***}	2.23 ^{ns}	12.97 ^{***}	16.06 ^{***}
Sire(loc*line*year)	164 ^a	1.53 ^{***}	2.46 ^{***}	1.38 ^{***}	1.48 ^{***}	1.67 ^{***}
<i>Interactions</i>						
Location x line	2	7.80 ^{***}	0.32 ^{ns}	2.20 ^{ns}	20.90 ^{***}	10.79 ^{***}
Line x year	8	3.59 ^{***}	2.93 ^{**}	0.84 ^{ns}	0.86 ^{ns}	1.78 ^{ns}
Location x year	4	20.15 ^{***}	8.49 ^{***}	0.70 ^{ns}	22.30 ^{***}	42.01 ^{***}
Location x line x year	8	1.41 ^{ns}	2.55 ^{**}	2.54 ^{**}	1.53 ^{ns}	3.61 ^{***}
<i>Regressions</i>						
Day of birth (L)	1	0.01 ^{ns}	0.00 ^{ns}			
Day of birth (Q)	1	0.45 ^{ns}	0.00 ^{ns}			
Weaning age (L)	1			3.29 ^{ns}	0.00 ^{ns}	7.09 ^{**}
Weaning age (Q)	1			2.82 ^{ns}	4.65 [*]	8.39 ^{**}
Residual	2204 ^b	0.42	1.97	0.15	12.26	795.10
Coefficient of determination		0.35	0.25	0.13	0.58	0.45

*** P<0.001, ** P<0.01, * P<0.05, ^{ns} not significant.

^a 164 for BWT and BCS, 134 for LS, and 133 for WWT and GR.

^b 2204 for BWT, 2180 for BCS, 1680 for LS, 1273 for WWT, and 1266 for GR.

Table 4.3 Least square means and standard errors for genotype effects on the different lamb traits.

Lamb traits	Genotype		
	Random	Weight Plus	Weight Minus
Birth weight (kg)	3.67 ± 0.02 ^b	4.10 ± 0.03 ^a	3.16 ± 0.04 ^c
Birthcoat score	3.37 ± 0.06 ^a	2.49 ± 0.06 ^c	2.87 ± 0.09 ^b
Lamb survival rate	0.77 ± 0.02	0.74 ± 0.02	0.70 ± 0.03
Weaning weight (kg)	19.75 ± 0.16 ^b	22.25 ± 0.22 ^a	15.81 ± 0.32 ^c
Growth rate (g/day)	138.65 ± 1.30 ^b	157.11 ± 1.66 ^a	107.09 ± 2.61 ^c

*Means within rows having the same superscript did not differ significantly at P<0.05.

Table 4.4 Least square means and standard errors for location effects on the different lamb traits.

Lamb traits	Location	
	Trangie	Armidale
Birth weight (kg)	3.88 ± 0.04 ^a	3.40 ± 0.06 ^b
Birth-coat score	3.14 ± 0.08 ^a	2.68 ± 0.12 ^b
Lamb survival rate	0.79 ± 0.03	0.68 ± 0.04
Weaning weight (kg)	19.79 ± 0.21 ^a	18.75 ± 0.31 ^b
Growth rate (g/day)	139.03 ± 1.69 ^a	129.54 ± 2.50 ^b

*Means between lines having the same superscript did not differ significantly at P<0.05.

Table 4.5 Least square means and standard errors for year effects on the different lamb traits.

Lamb traits	Year				
	1983	1984	1985	1986	1987
Birth weight (kg)	3.54 ± 0.05 ^a	3.63 ± 0.04 ^{ab}	3.78 ± 0.05 ^a	3.61 ± 0.04 ^b	3.65 ± 0.03 ^{ab}
Birthcoat score	2.96 ± 0.10 ^{ab}	2.50 ± 0.09 ^c	3.06 ± 0.10 ^{ab}	3.13 ± 0.09 ^a	2.89 ± 0.07 ^b
Lamb survival rate	0.71 ± 0.03	0.73 ± 0.02	0.79 ± 0.03	0.71 ± 0.03	-
Weaning weight (kg)	18.69 ± 0.31 ^b	19.78 ± 0.31 ^b	20.48 ± 0.30 ^a	18.12 ± 0.28 ^b	-
Growth rate (g/day)	126.86 ± 2.48 ^b	142.73 ± 0.44 ^a	142.49 ± 2.41 ^a	125.06 ± 2.28 ^b	-

*Means between lines having the same superscript did not differ significantly at P<0.05.

4.4.4 Year effects

Year means were significantly different ($P < 0.05$) for all traits except for lamb survival (Table 4.5). Differences between traits varied from 3.6% to 6.8% in birth weight, 2.3% to 25.2% in birth-coat score, 3.5% to 13.0% in weaning weight and 0.17% to 14.1% in growth rate. The highest mean birth weight (3.78 kg), weaning weight (20.48 kg) and lamb survival (0.79) were observed in 1985, the highest birth-coat score (3.13 score units) in 1986 and the fastest growth rate (142.73 g/day) in 1984.

4.4.5 Genotype x location interaction

The genotype x location interaction was significant for most lamb traits except lamb survival. For all traits, no changes in rank were involved.

Genotype x location was significant ($P < 0.001$) for birth weight as shown in Figure 4.1. At Trangie, the Weight Plus lambs were heavier at birth than the Random lambs by 13.3% and 34.2% heavier than the Weight Minus lambs. The same result was observed in Armidale with the Weight Plus lambs heavier by 9.9% and 25.2% than the Random and Weight Minus lambs, respectively. The mean birth weight of Weight Plus was 4.43 ± 0.04 kg at Trangie and 3.77 ± 0.06 kg at Armidale. Similarly, the average birth weight of Weight Minus lambs were 3.30 ± 0.06 kg at Trangie and 3.01 ± 0.08 at Armidale while the Random lambs had an average birth weight of 3.91 ± 0.04 and 3.43 ± 0.06 kg for Trangie and Armidale, respectively.

Genotype x location interaction was significant ($P < 0.001$) for weaning weight (Fig. 4.2). The weaning weight of Weight Plus lambs at Trangie was significantly heavier compared to the Random (19.1%) and Weight Minus lambs (54.9%). At Armidale, the Weight Plus lambs were also heavier by 6.6% than Random lambs and 27.2% heavier than Weight Minus lambs. The mean weaning weight of Weight Plus lambs was 23.88 ± 0.28 kg at Trangie and 20.61 ± 0.37 kg at Armidale. On the other hand, Weight Minus and Random lambs had an average weaning weight of 15.42 ± 0.05 and 20.05 ± 0.03 kg at Trangie and 16.20 ± 4.53 and 19.44 ± 0.34 kg at Armidale, respectively.

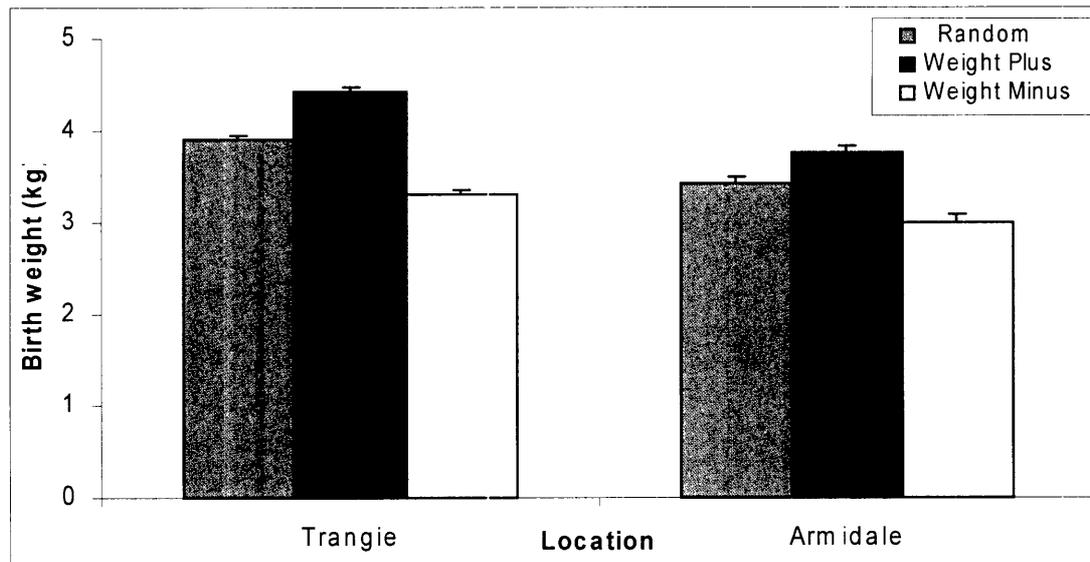


Figure 4.1 Genotype x location interaction for birth weight

For growth rate to weaning, the genotype x location interaction was significant ($P < 0.001$). At Trangie, the Weight Plus lambs grew significantly faster to weaning by 19.3% and 54.8% than the Random and Weight Minus lambs, respectively (Figure 4.3). At Armidale, although the growth rate of the Weight Plus line was higher than

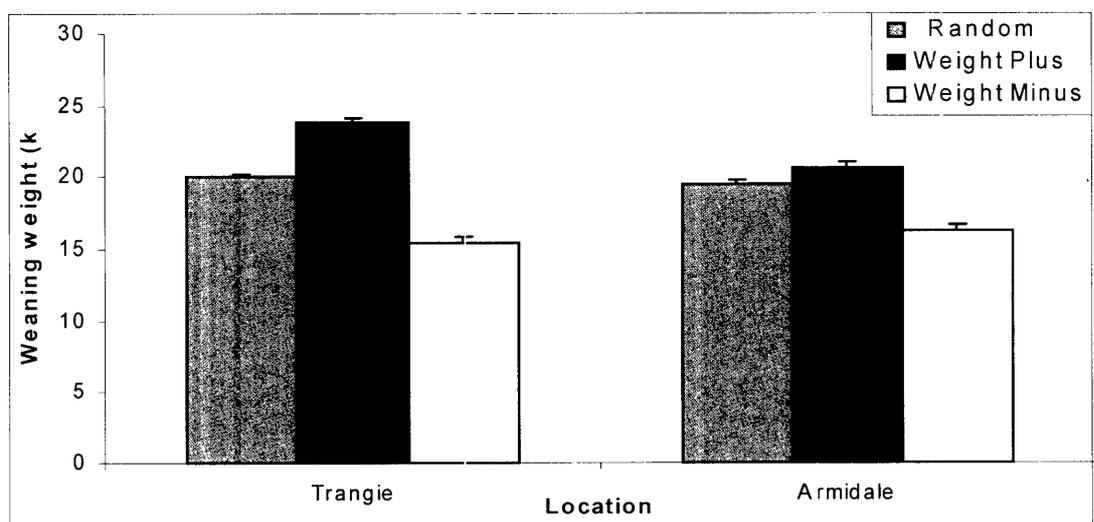


Figure 4.2 Genotype x location interaction for weaning weight.

the Random line, the difference between the two lines was not significant. However, lambs in both lines grew significantly faster by 7.1% to 38.4% than the Weight Minus line. The Weight Plus, Weight Minus and Random lines registered an average growth rate to weaning of 167.91 ± 3.59 , 140.70 ± 1.68 and 108.48 ± 3.59 at Trangie and 146.31 ± 3.02 , 136.61 ± 2.76 and 105.72 ± 4.23 at Armidale, respectively.

The genotype x location interaction was not significant for the two other lamb traits of survival and birth-coat score. Although differences between lines were not significant, the Random line showed the highest birth-coat scores at the two locations while the highest lamb survival rate was registered by the Weight Plus line at Trangie and by the Random line at Armidale.

4.4.6 Genotype x year interaction

Significant ($P < 0.001$) line x year interactions were observed ($P < 0.01$) for birth weight and birth-coat score. This interaction was non-significant for lamb survival, weaning weight and growth rate. Both significant interactions were small in size and involved no changes in rank between lines in each year of observation.

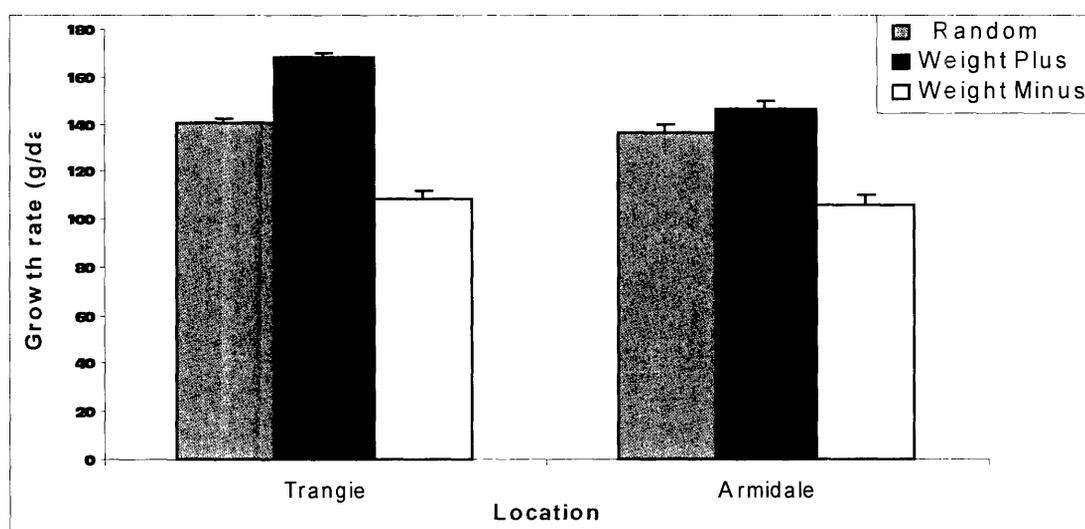


Figure 4.3. Genotype x location interaction for growth rate to weaning

For birth weight, the Weight Plus were the heaviest, followed by the Random line and then the Weight Minus line in the period from 1983 to 1987. The Weight Plus lambs were significantly ($P < 0.001$) heavier than the Weight Minus

lambs by 43.6 % in 1983, 26.8% in 1984, 27.2% in 1985, 27.7% in 1986 and 25.4% in 1987 (Figure 4.4). On the other hand, the Random line was also significantly ($P<0.001$) heavier than the Weight Mirus line by 21.3%, 9.3%, 16.0%, 21.3 % and 13.6% for the years from 1983 to 1987, respectively.

The Random line was significantly higher in birth-coat score than the Weight Plus line. In 1983, the difference between the two lines was 51.9%, 16.8% in 1984, 46.5% in 1985, 26.2% in 1986 and 32.1% in 1987. The birth-coat score of the Random line was also significantly higher than the Weight Minus lambs in the years 1983 (33.7%), 1985 (33.6 %) and 1987 (14.2%), but non-significant in 1984 and 1986. Between the selection lines, no significant difference was observed except in 1986 when the Weight Minus line scored 20.7% significantly higher than the Weight Plus line (Figure 4.5).

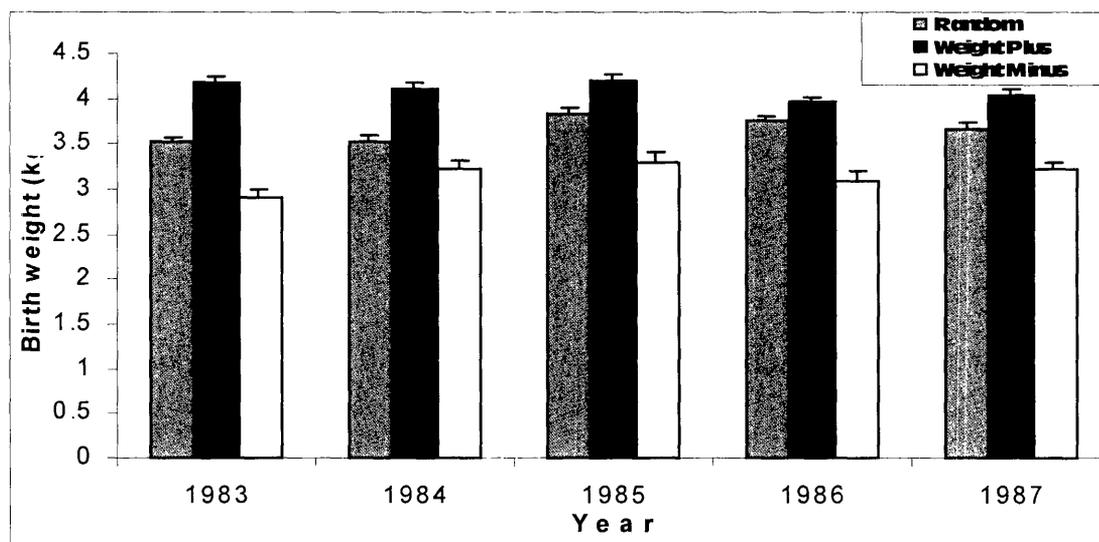


Fig. 4.4. Genotype x year interactions for birth weight

4.4.7 Location x year interaction

Location x year interactions were large and significant ($P<0.001$) for most lamb traits except lamb survival. Changes in ranking between location occurred in weaning weight and growth rate. Trangie lambs were significantly heavier at birth than the Armidale lambs in most years of the study, except in 1983. Trangie lambs were heavier by 13.5% in 1984, 22.0% in 1985, 11.4% in 1986 and 26.3% in 1987 as shown in Figure 4.6. No rank changes between locations occurred for birth weight during the four-year period mentioned. For birth-coat score, location x year

interaction was found significant in 1984, 1986 and 1987 and non-significant in 1983 and 1985. Trangie lambs showed higher birth-coat score units than Armidale lambs by 63.2% in 1984, 22.3% in 1986 and 15.7% in 1987 (Figure 4.7).

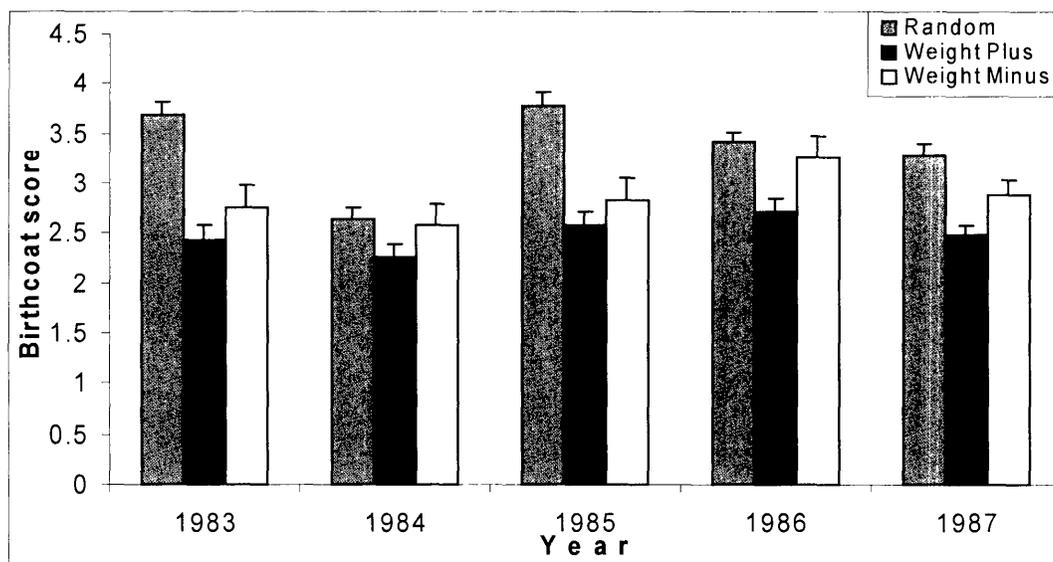


Fig. 4.5. Genotype x year interactions for birthcoat score

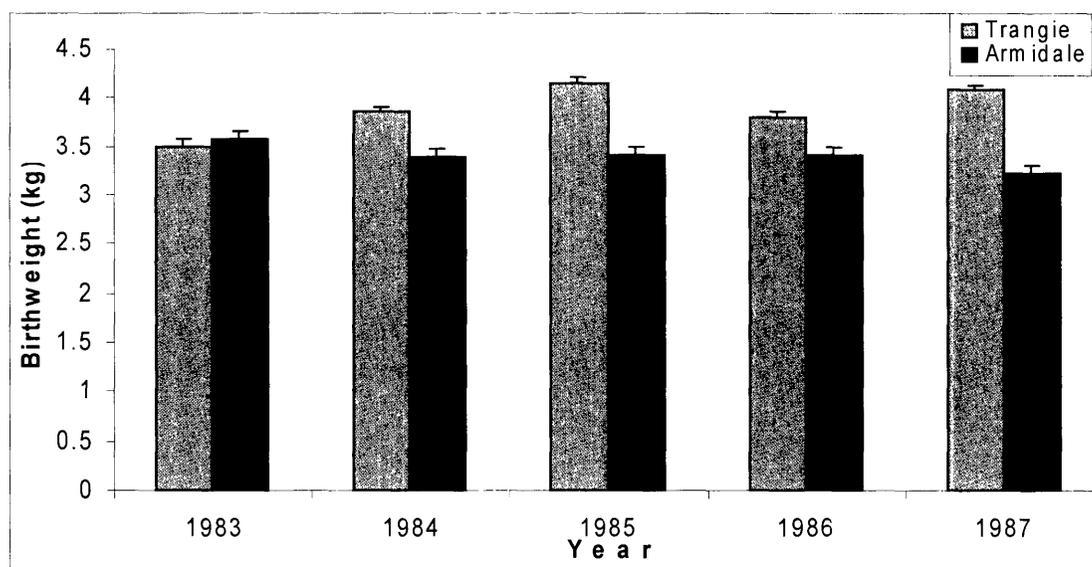


Fig. 4.6. Location x year interactions for birth weight

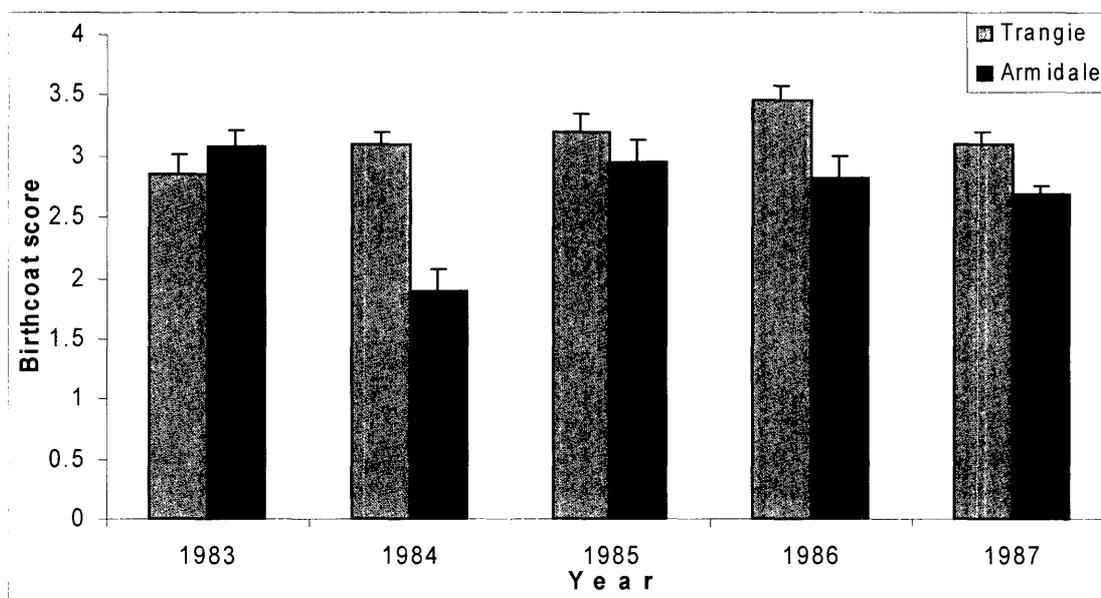


Fig. 4.7. Location x year interactions for birthcoat score

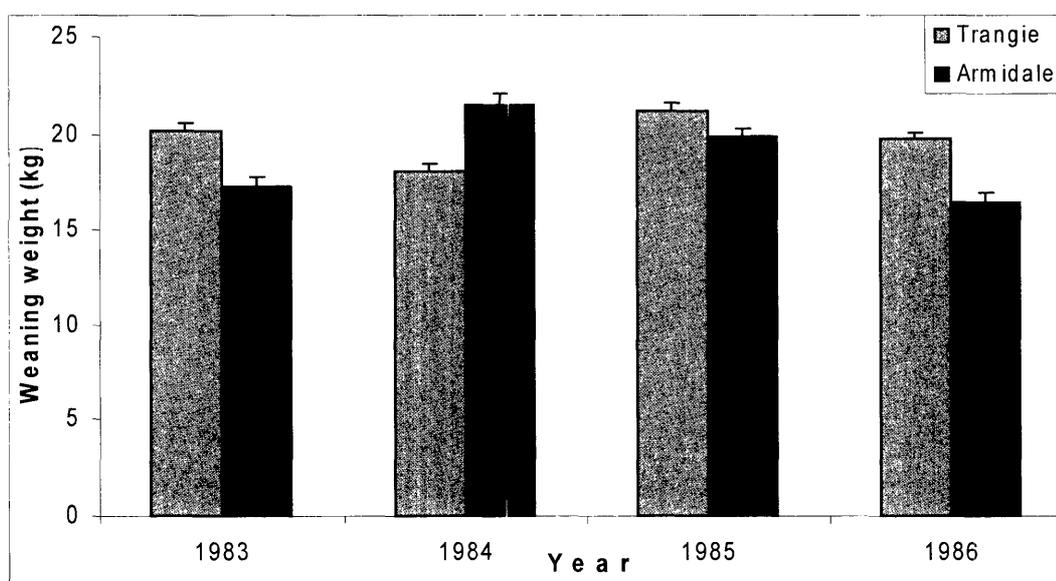


Fig. 4.8. Location x year interactions for weaning weight

For weaning weight, the location x year interaction was significant ($P < 0.001$). The Trangie lambs were significantly heavier at weaning than the Armidale lambs in 1983 by 16.9%, 6.8% in 1985 and 20.1% in 1986. However, in 1984, the Armidale lambs were heavier by 19.0% (Figure 4.8). For growth rate to weaning the lines in the two locations were significantly ($P < 0.001$) different each year, except for 1985. In 1983, the Trangie lambs grew faster by 33.3% and 24.8%

in 1986. Armidale lambs, on the other hand, grew faster than the Trangie lambs in 1984 by 29.8% (Figure 4.9).

4.4.8 Genotype x location x year interactions

The second order interactions of line x location x year were significant ($P < 0.001$) for birth-coat score and growth rate to weaning while birth weight, weaning weight and lamb survival were found to be not significant.

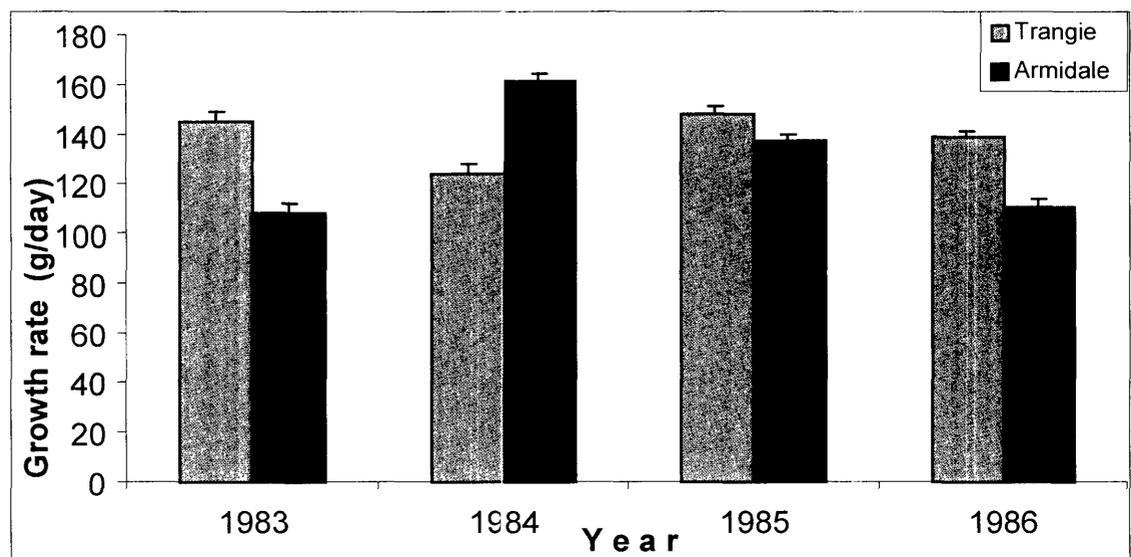


Fig. 4.9. Location x year interactions for growth rate to weaning

4.5 Discussion

4.5.1 Genotype effects

The result of the present study is consistent with the result in previous experiments of Pattie (1965a) and Davis (1987) and the result in Chapter 3. With the performance of the lines combined in two locations, the Weight Plus line still showed higher weaning weight, birth weight and grew faster from birth to weaning compared to the Weight Minus and Random lines.

4.5.2 Location and year effects

Differences between location for birth and weaning weights, growth rate and birth-coat score were significant and these could be attributed to several factors such as climatic conditions, type of pasture, stocking rate and other management practices of the two locations. Birth-coat score was shown not to differ significantly between locations in the previous chapter but the difference was significant in this chapter. A systematic measurement difference cannot be ruled out since scores were made by different persons at the two locations.

Based on the results, Trangie is considered a more favourable environment since for many traits mean levels of performance were significantly higher at Trangie than at Armidale.

Dunlop (1963) studied genotype x environment interactions that involved examination of five strains of Australian Merinos managed as breeding groups in three wool growing areas, including Armidale. He reported that for adult body size traits, location was of moderate importance with body size being generally lower at Armidale compared to the two other stations at Deniliquin and Cunnamulla. He noted that the climatic features of Armidale were not typical of those normally suited to medium wool Merinos. In contrast the Cunnamulla and Deniliquin environments were typical of environments suited to medium wool Merino sheep.

Differences among years are usually highly significant due to large yearly fluctuations common of most grazing or rangeland environments in Australia. The findings of the present study are in agreement with the findings reported in Chapter 3 and with published reports. Year has a significant influence on birth weight, weaning weight and growth rate (Sidwell and Miller 1971c, Dun and Grewal 1963, Jackson and Roberts 1970, Walkley *et al.* 1987, Smith 1977, Atkins 1978 and Davis 1987).

4.5.3 Genotype x location interactions

Birth weight, weaning weight and growth rate of the Weight Plus lambs were highest at both locations and the differences were much larger at Trangie resulting in significant line x location interactions. The interaction is a measure of

the differential response of the three lines of Merino to the environment at the two locations. The findings are similar to those findings of Carter *et al.* (1971a) of genotype x environment interactions for lamb performance traits involving two breed crosses raised in two locations in North America. The ewe breed x location interaction was found to be significant for birth weight and 120-day weight with one cross at both locations but with the difference being much larger at Ottawa than at Glade Springs. However, there was little evidence for a breed x location interaction in average daily gain. Dunlop *et al.* (1963) in his study of five strains of the Australian Merino at three locations, with contrasting environment which included Armidale, also reported significant strain x location interactions for adult live weight, weight of lambs born, weight of lambs weaned and other body traits. Although, the interactions were significant, they were generally of moderate to small in size and accounted for only a small fraction of the variance. Carter *et al.* (1971) also concluded that while the breed x location interaction was significant, the differences involved were relatively small in magnitude and of no great importance in terms of commercial productions.

It was observed that differences between lines at Trangie were greater than those at Armidale. This suggests that differences between genotypes will vary depending on the environmental conditions under which the animals are raised. Consequently, selecting genotypes in one environment may not result in similar performance differences at another site. Lasslo *et al.* (1985) reported on genotype x environment interactions of Targhee sheep selected for high weaning weight and noted that genetic improvements due to selection made under feedlot conditions was greater than the responses to selection made under range conditions.

Interactions in the traits involved no rank changes. This could be attributed to the fact most genotype x location interactions were relatively small. Dunlop *et al.* (1965) also concluded that although interactions were significant, they were generally of moderate to small in size and accounted for only a small fraction of variance. Similarly, Carter *et al.* (1971a) also found that the differences involved were relatively small in magnitude.

The line x location interaction was non-significant for lamb survival, a finding that confirms the report of Lax and Turner (1965). In a study of five strains of the Australian Merino at three locations the latter authors found no significant

strain x location interactions for survival of single lambs from birth to weaning. This confirms that lamb survival is not only influenced by extrinsic factors such as climatic conditions but more of intrinsic factors such as birth-coat, birth weight, mothering ability, age of dam and more importantly of improved management practices.

4.5.4 Genotype x year interactions

Chapter 3 showed significant line x year interaction for most lamb traits including birth weight, weaning weight, growth rate to weaning and birth weight. However, in the present study significant line x year interactions were observed only in birth weight and birth-coat score. This difference could be attributed to the longer observation period (10 years) evaluated in Chapter 3 compared to four-to-five years of observations in this study. In addition, the data used in the longer study came from Trangie only while the latter experiment included the data from both Trangie and Armidale.

This result of the present study is in agreement with the findings of Hohenboken *et al.* (1988) who reported significant ewe genotype x year interactions for birth weight and weaning weight of the three breeds of sheep (Coopworth, Industry Romney and Waihora Romney). However, they concluded that the unconventional cross-classified analyses of variance did not reveal large, consistent nor economically important ewe genotype x nutritional treatment or year interactions. In another related study, Atkins (1978) reported significant ewe breed x year interactions for growth rate of Romney sheep that he ascribed mainly to the differential response of the lines to the changes in the environment. However, the interaction observed was found to be small in size accounting for a very small fraction of variance.

4.6.5 Location x year interactions

Location x year interaction was significant for birth weight, weaning weight, growth rate to weaning and birth-coat score that indicated the presence of large yearly differences in environmental factors at the two locations. However, no interaction was observed for lamb survival. The result of the present study is in

agreement with the findings of Carter *et al.* (1971b) who reported large and highly significant location x year interactions for average daily gain and 120-day weight of two breed crosses. They attributed the interaction to large yearly fluctuations in environmental factors between the two stations. Similar effects were also reported for ewe productivity traits (Carter *et al.* 1971) and sheep carcass traits (Carter *et al.* 1973). The moderate interactions observed in this experiment are also in agreement with the findings of Dunlop (1962, 1963) who found the significant location x year interactions for live weight, weight of lambs born and weight of lambs weaned of five strains of Australian Merino at three locations.

4.7 Conclusion

Lines of Australian Merino sheep previously selected for weaning weight and a randomly selected control line were significantly different in lamb traits. This indicated that the suspension of selection within lines has appeared not to have greatly altered the relative performance of the animals in the subsequent generations. Effects that could change responses in the lines appear not to have been operating greatly during the short period of the study. Differences between location for the various lamb traits could be attributed to several factors but Trangie is considered a more favourable environment since for many traits mean levels of performance were significantly higher at Trangie than at Armidale. Differences among years are expected to be highly significant due to large yearly fluctuations common of most grazing or rangeland environments in Australia.

The significant line x location interactions for birth weight, weaning weight and growth rate to weaning show the differential response of the three lines of Merino to the environment in two locations. The differences between lines at Trangie were found to be greater than those at Armidale and this suggests that differences between genotypes will vary depending on the environmental conditions under which the animals are raised. Thus when selecting genotypes in one environment the outcome may not be similar performance at another site.

Line x year interactions were also found significant for birth weight and birth-coat scores but interactions were found to be relatively small. The location x year interactions were also found to be significant for most lamb traits indicating the

presence of large yearly differences in environmental factors in the two locations. Most interactions involved no rank changes which suggests that most interactions were too small in magnitude to eventually affect the ranking of the lines.

Overall the results suggested that genotype x environment interactions do exist for Merino sheep in Australian environments. However, the two environments of Armidale and Trangie do not differ widely enough to result in changes in rank between lines.

Chapter 5

Direct and Correlated Responses after the Suspension of Selection

5.1 Introduction

Sheep selection experiments have been used for a number of reasons (Hill 1980). One reason is to provide an experimental check on theoretical predictions of the responses to selection progress in selected and correlated traits and determines how long predicted or initial rates of responses are maintained. The selection experiments also allowed the examination of the symmetry of direct and correlated responses as studies included to divergent lines as well as a control group.

The majority of selection experiments in beef cattle and sheep have focused on growth rate with weaning and yearling weights as the common selection criteria. The use of weaning weight, as a selection criterion, is common as it is a common measurement taken in most performance recording schemes or it is easy to measure and has been positively correlated with efficiency of food utilisation. It is also important to select on weaning weight because it is a measure of both growth and dam's ability to raise heavier lambs. Numerous studies have been conducted to examine the effect of selection for weaning on sheep growth and efficiency (Pattie 1965a, Lasslo *et al.* 1985b, Hinch *et al.* 1986 and Herd *et al.* 1993), reproduction (Pattie 1965b, Bradford *et al.* 1986) and wool production (Pattie 1965b, Davies *et al.* 1987, Herd *et al.* 1993).

The Trangie Weight Selection experiment has provided data for direct and correlated responses to selection on weaning weight (Pattie 1965a and 1965b, McGuirk 1973, Davis 1987). The experiment included approximately ten generations of selection

breeding in different lines that extended over 33 years from 1951 to 1983. Davis (1987) analysed the Trangie data from 1951 to 1983 and concluded that selection for weaning weight lead to higher birth weight, weaning weight and pre-mating live weight and growth rates. Earlier reports had also shown that selection for high and low weaning weight in sheep resulted in an increase and decrease in live weights in subsequent generations at weaning (Pattie 1965a) and other ages including maturity (Pattie 1965b, Pattie and Williams 1966 and 1867). However, Pattie (1965) reported that selection for increased weaning weight does not appeared to have increased the value of sheep as wool producers. Likewise, Davis (1987) concluded that longer-term selection for high weaning weight in the same flock lead to an insignificant change in wool production.

The primary objective of this study was to determine the direct and correlated responses of lines selected for high and low weaning weights after the suspension of selection and replacement rams and dams chosen at random from within each line. Selection differential, cumulative response, realised heritabilities for weaning weight, genetic trends, and realised genetic correlations between weaning weight and other growth and wool traits were calculated. Correlated responses were estimated for lamb traits: birth weight, birth-coat score, lamb survival, growth rate and nine-month weight; and for hogget traits: greasy fleece weight, clean fleece weight, skirted fleece weight, fibre diameter and off-shear live weight.

5.2 Review of Literature

5.2.1 Response to selection

Response to selection (R) is the difference of mean phenotypic value between the offspring of the selected parents and the whole of the parental generation before selection. The measure of selection applied is the average superiority of the selected parents known as *selection differential (S)*. It is the mean phenotypic value of the individuals selected as parents expressed as a deviation from the population mean, that is from the mean phenotypic value of all the individuals in the parental generation before selection was made (Falconer 1993). Each sex is equally important in contributing genes to the next generation, so selection differential is calculated separately for each sex then average:

$$S = (S_m + S_f)/2$$

where S_m = selection differential for males and S_f = selection differential for females

The regression of offspring on mid-parent is equal to the heritability, provided there is no non-genetic cause of resemblance between offspring and parents. If these conditions are true, then, the ratio of response to selection differential is equal to the heritability, and the response is given by

$$R = h^2 S$$

where h^2 is the heritability and S is the selection differential.

The response to selection could be predicted without having to actually measure selection differential. This is made possible by predicting S from a knowledge of the proportion of animals retained for breeding (p) and assuming normality. The standardised selection differential is called *selection intensity*, symbolised by i . The selection differential then is

$$S = i \sigma_p$$

where i = is the selection intensity, σ_p is the standard deviation of phenotypic values. Similar to selection differential, selection intensity is calculated for each sex and then average:

$$i = (i_m + i_f) / 2$$

where i_m is the selection intensity for males and i_f is the selection intensity of females.

The predicted response per generation then is;

$$R = i h^2 \sigma_p$$

where i is the selection intensity, h^2 is the heritability and σ_p is the standard deviation of phenotypic values.

Since $h = \sigma_A / \sigma_p$, where σ_A is the standard deviation of breeding values, the equation is then is;

$$R = i h \sigma_A$$

5.2.2 Selection for growth in sheep

Growth rate is an important selection criterion because of the ease with which it can be measured and the accumulation of evidence that is closely related to efficiency of production. Selection for weaning weight or average daily gain to weaning will increase live weight at all ages from birth to maturity. If slaughtered at a fixed live weight, efficiency of growth should be improved by selection of weaning weight (Barlow, 1978) which should also allow genetic progress towards a leaner and larger carcass (Thompson, 1990). Selection for growth is a much-researched topic in both laboratory and domestic animals. A number of reviews of growth selection experiments have been reported for mice (Roberts 1974 and 1979, McCarthy 1980 and 1982), poultry (McCarthy and Siegel 1982); swine (Glodek, 1982), and cattle (Barlow 1978, Dalton and Baker 1980, Baker and Morris 1984, Mrode 1988a and 1988b and Baker *et al.* 1991). Clarke (1986) and Robertson (1987) have both reviewed the literature for sheep.

Selection for live weight has been conducted in a number of sheep experiments for a variety of breeds and in different countries including New Zealand, the U.S., and Australia. Pattie (1965a, 1965b), McGuirk (1973) and Davis (1987) studied direct and correlated responses to selection for high and low weaning weight in the Trangie selection lines using data from the first 4, 6 and 10 generations, respectively. The same selection lines of Merinos are examined in this thesis although the present data includes ten years after the suspension of selection.

Lasslo *et al.* (1985) reported an experiment where selection for 120-day weight in two flocks was conducted from a common base population of grade Targhee sheep. At Davis, California, sheep were maintained on a good plane of nutrition on irrigated-pasture or in a dry-lot. At Hopland, sheep grazed annual grassland range with supplementary feeding only at mating and lambing. A selected line, replicate control lines and a line mated to the Davis' selected line were maintained at Hopland from 1961 through 1980 with early results reported by Osman and Bradfield. (1965).

Johnson *et al.* (1995) studied the responses to selection for yearling fleece and live weight in Romney sheep in New Zealand. Two selection lines were selected for fleece weight and the other for live weight and a control line were maintained. In Spain, Jurado *et al.* (1994) examined the selection response for growth in a Spanish Merino flock selected for high weaning weight.

5.2.2.1 Direct responses

In the ten generations of selection for high and low weaning weight in the Trangie experiment, Davis (1987) reported a divergence between the selected lines which was in broad agreement with theoretical expectations based on previous experiments. Earlier reports had shown that selection for high and low weaning weight in sheep resulted in an increase and decrease in live weight in subsequent generations at weaning (Pattie 1965a) and at other ages, including maturity (Pattie 1965b, Pattie and Williams 1966 and 1967). In a summary of weight selection lines for which results have been reported, selection for live weight has resulted in divergent direct responses ranging between 0.5 and 1% from the control line mean per year (Davis, 1987).

Pattie (1965a) reported that the realised heritability for the Weight Plus flock was significantly greater for ewes than for rams ($P < 0.05$). No other differences between the realised heritabilities were significant and there was no significant asymmetry of response. On the pooled estimate of realised heritability for each sex obtained from the divergence between the two selection flocks, the difference between ewes and rams was not significant. McGuirk (1973) also found no difference between realised heritability estimates from rams and ewes after six generations of selection in the same line. In contrast, Davis (1987) reported that realised heritabilities from the upward and downward lines were generally inconsistent and different to the Divergence estimates except over the full duration of the experiment. Estimates for the upward, downward and divergent comparison for the full experiment were 0.146 ± 0.029 , 0.158 ± 0.035 and 0.159 ± 0.017 , respectively. Realised heritabilities estimated over the different periods were asymmetric, as were the least squares genetic trends suggesting that the Random line may have been a less suitable control.

Positive genetic improvement was noted in Targhee sheep selected for 120-day weight and raised in two environments. In both environments, selection increased weaning weight compared with unselected controls, with more improvements made in the drylot environment at Davis than in the range conditions at Hopland. Direct response for the selected lines at Davis was 0.524 ± 0.073 kg/yr and 0.151 ± 0.034 kg/yr at Hopland with corresponding realized heritabilities of 0.17 and 0.06 (Lasslo *et al.* 1985). Purser (1982) reported a 0.24 ± 0.11 realised heritability for Cheviot sheep selected for weaning weight.

Johnson *et al.* (1995) evaluated single trait selection for yearling live weight in Romney sheep and reported realised heritabilities of 0.36 ± 0.03 . These estimates were calculated from the regression of response on selection differential with the direct response to selection, derived from deviation from a control line, as at 11.9 kg or 28% per year and the corresponding annual rate of response was 0.53 kg/year or 1.2% per year.

The response to selection for growth in a Spanish Merino flock experiment was reported by Jurado *et al.* (1994). The phenotypic weaning weight was 2.4 kg higher than the initial values, with the estimated and theoretical responses similar in the sire population. At the 13th lambing season, average breeding value of 30-day weight of the ram population was 600 grams higher than the mean initial breeding value in the base population. Projected average breeding value of the lamb population under random mating at the 23rd lambing season was equal to 404 grams.

5.2.2.2 Correlated responses

5.2.2.2.1 Growth

Davis (1987) reported a high correlation between weaning weight and various growth traits in both realised and half-sib estimates. Realised genetic correlation estimates calculated from the divergence of Weight Plus and Weight Minus lines were 0.811 ± 1.33 , 0.752 ± 0.104 and 0.645 ± 0.078 for birth weight, growth rate and live weight, respectively. Pattie (1965b) also found a high realised genetic correlation between weaning weight and hogget live weight of 0.72.

The results in the single trait selection for weaning weight in Targhee sheep indicate lambs with heavier birth weights in the three selected lines (Lasslo *et al.* 1985). Clarke (1986) reported the same result for Romney sheep. The findings of the various experiments supports the theory of Atchley (1984) which describes how selection on one part of the growth curve causes correlated responses in other sections of the growth curve resulting in 'overscaling' of the curve with little change in its shape.

5.2.2.2 Wool production

Except for folds and crimps per inch, Pattie (1965b) reported that selection for weaning weight resulted in positive correlated responses in most wool production traits; greasy fleece weight (0.08), yield (0.22), clean fleece weight (0.24) and staple length (0.17). Turner *et al.* (1970) experiment on selection on weight at 10-11 months and the weight selection experiments reviewed by Clarke (1986) came up with similar results. The responses were generally small but positive and in good agreement with the low to negligible correlations between the selection criterion and the hogget wool production traits.

Davis (1987) reported a moderate realised genetic correlation (0.13 ± 0.04) between weaning weight and greasy fleece weight which was much higher than the half-sib estimates of 0.48 ± 0.12 . He explained that the low correlation indicates that while there is a considerable divergence in mature body size between the selection lines, there was little change in wool production. Similarly, flocks selected for increased fleece weight have produced little if any increase in live weights (Davis and McGuirk 1987). Barlow (1974) reported a realised genetic correlation between clean fleece weight and live weight at 15 to 17 months of 0.16 ± 0.08 in Merino sheep selected for clean fleece weight

5.2.2.3 Reproduction

Davis (1987) reported that realised genetic correlations between weaning weight and the reproductive traits were variable, but all were found to be positive. However, the realised genetic correlation between weaning weight and lamb survival was very high and slightly above the theoretical limit for a genetic correlation of 1.0 indicating a close relationship between the two traits. Realised genetic correlations between weaning weight and other traits were; 1.061 ± 3.537 with lamb survival, 0.277 ± 0.088 with fertility, 0.136 ± 0.034 with prolificacy, 0.413 ± 0.152 with lamb survival, and 0.546 ± 0.269 with rearing ability. Land *et al.* (1982) also concluded that the correlation between reproductive rate and live weight is generally considered to be positive, but realised responses to selection on weight were inconsistent between studies. In contrast, Pattie (1965b) reported that there were no significant differences between the flocks selected for and against weaning weight in any measures of reproductive performance.

Selection for growth rate to weaning results in heavier lambs but does not generally indicate an increase, and may even result in a decrease in total lamb production per ewe (Lasslo *et al.* 1985). Results from the experiment showed that the proportion of ewes lambing decreased significantly in the selected line at Davis and the trend was negative but non-significant at Hopland. The differences in litter size between lines within location were not significant. Lamb survival to weaning decreased in the selection lines compared to their respective controls but the trend in the Hopland line was negative and non-significant. As a result of the decreases in lamb survival and fertility, none of the selected lines produced more total lamb weight weaned per ewe than the controls, in spite of the significant direct response to selection and increased growth rate. Mature ewes of the selected lines in both locations produced less total lamb weight weaned per ewe than their respective controls. The result indicate that single trait selection for growth rate to weaning weight resulted in heavier lambs but did not increase and may even result in a decrease in total lamb production per ewe.

In the three Romney weight selected lines reviewed by Clarke (1986), prolificacy increased at a rate of approximately 0.7% per year relative to their controls.

5.2.3 Responses to relaxed selection

There is little published research on responses occurring after selection is relaxed in ruminant species. In studies using *Drosophila melanogaster*, Yoo (1980) reported an increased abdominal bristle number due to selection in six replicate lines of *Drosophila melanogaster*. Each line was selected for 86-89 generations and subsequently maintained for 32-35 generations without selection. Response was apparent for at least 75 generations and average total response was in excess of 36 additive genetic standard deviations of the base population or 51 times the response in the first generation. The pattern of long-term response was diverse and unpredictable, typically with one or more accelerated responses in later generations. At termination of the selection, most of the replicate lines were extremely unstable with high phenotypic variability, and lost much of their genetic gains rapidly upon relaxation of selection.

Roberts (1966) studied large and small lines of mice that were first described and studied by Falconer (1960). Selection was continued in both lines, but from generation 32 onwards, the selected character was changed from growth between 3 and 6 weeks to 6-week weight. Two 'offshoots' were taken from each of the small and large lines, and in one case, selection was relaxed and in the second pair of 'offshoots', the direction of the selection was reversed. The results showed that in the large line, over the early generations, the superiority in fertility for both relaxed and reversed selections was unquestionable. However, in later generations the superiority in litter size was not apparent. In the small line, when selection for low live weight was relaxed, the effects on the fertility of mice on the parental line were again beneficial. The number of sterile matings fell, the reduction being more noticeable in the back selected line than in the relaxed line. This was slightly different from the large lines where the ranking of the relaxed and back-selected lines were reversed. For the six-week live weight, reversed and relaxed selection from the large line at the selection limit failed to yield any response. This indicated that, effectively, the additive genetic variance in this line had been exhausted. In contrast, the small line at the selection limit regressed slightly towards the base population when selection was relaxed. Reversed selection yielded a ready response until a new selection limit was apparently reached. Loci affecting live weight in this line had therefore not been fixed by selection.

Falconer (1955) reported some short-term studies of a similar kind on two lines studied by Roberts (1966). Reversed selection was carried out from the small (NS) line on two separate occasions. The first (from generation 12) was at a time when the line was still responding to selection, but by the second time (from generation 20) the line was approaching its ultimate limit. Over four generations, the response to the reversed selection was unmistakable. The other study described by Falconer was the relaxation of selection from the 24th generation of the large (NF) line, after the line had reached its selection limit to artificial selection. Over six generations, there was no indication that the relaxation of selection resulted in any separation from the line under continued selection.

5.2.4 Conclusion

Selection for weaning weight results to divergence between the lines studied with the response being observed in the direction of selection. Selection for high and low weaning weight in sheep resulted to an increase and decrease in live weight at weaning in subsequent generations, and at other ages. On the other hand, responses for selection for growth are affected by the animal's environment. Realised heritabilities were asymmetric and differences between sexes were not significant.

Weaning weight as a selection criterion has a high and positive realised genetic correlation with other growth traits. Although positive, its correlation with most wool production traits is from small to negligible. Correlation between live weight and reproductive traits are also positive, but differences between flocks selected for growth rate are inconsistent.

5.3 Materials and Methods

5.3.1 Data source

The data of the present study were from the Trangie Weight Selection Experiment. The environment, management, selection procedures, description of the experimental animals and data recorded on the three lines are discussed in detail in Chapter 2.

The Trangie Weight Selection Experiment commenced in 1951 and selection for high and low weaning weight was continued for 32 years until it was suspended in 1983. Between 1983 to 1992, when selection ceased, replacement rams and ewes were chosen at

random within each line. Pattie (1965a, 1965b) and Davis (1987) described and reported the responses to selection of the selection lines and the random line. For this chapter, the focus of the study is the period between 1983 and 1992 when selection for weaning weight was suspended. To provide a comparison of the two periods, analyses of the data from 1951 to 1982 were also included.

5.3.2 Lamb traits

Data for a total of 3104 lambs collected between 1983 and 1992 were used. There were 838 records for the Weight Plus line, 430 the Weight Minus line and 1836 for the Random line. Lamb traits include birth weight, birth-coat score, lamb survival and growth-rate to weaning. Most traits were measured in the 10-year period except for NMWT in 1992. Table 5.1 shows the number of lambs in the selection lines for which each of the recorded traits in each year and Table 5.2 for the random line.

5.3.3 Hogget traits

Hogget production traits were recorded for the selection and random lines between 1983 and 1992 include greasy fleece weight, clean fleece weight, yield, skirted fleece weight, fibre diameter and of-shear live weight. No records were available for yield, clean fleece weight, skirted fleece weight and fibre diameter in 1992. Table 5.3 shows the number of hoggets in the selection lines for which each of the traits was recorded in each year. The number of hoggets in the random line are shown in Table 5.4.

Table 5.1 Number of lamb records for each trait in the Weight Plus and Weight Minus line

Year	Weight Plus						Weight Minus					
	BWT	BCS	LS	GR	WWT	NMWT	BWT	BCS	LS	GR	WWT	NMWT
1983	46	46	46	35	35	33	26	26	26	19	19	18
1984	102	102	102	88	88	88	48	49	49	28	28	28
1985	81	81	81	73	73	73	27	27	27	23	23	21
1986	87	87	87	66	66	64	51	51	51	37	37	35
1987	128	128	128	104	105	99	56	56	56	38	38	33
1988	141	141	141	101	101	100	39	39	39	21	21	21
1989	48	49	49	38	39	38	38	38	38	26	26	24
1990	82	78	82	65	63	60	50	50	50	39	39	38
1991	52	52	51	38	38	37	41	41	41	28	28	29
1992	71	71	71	42	42	-	50	51	50	29	30	-
Total	837	835	838	650	650	592	426	798	431	288	289	247

Table 5.2 Number of lamb records for each trait in the Random line.

Year	Lamb traits					
	BWT	BCS	LS	GR	WWT	NMWT
1983	123	124	124	93	94	92
1984	195	195	195	168	168	163
1985	157	158	158	134	135	131
1986	210	210	210	176	176	170
1987	179	180	179	147	147	141
1988	200	202	202	156	159	157
1989	207	205	211	154	156	151
1990	222	223	228	181	183	171
1991	217	218	218	177	177	173
1992	109	109	109	80	80	-
Total	1819	1824	1834	1466	1475	1349

Table 5.3 Number of hogget records for each trait in the Weight Plus and Weight Minus lines.

Year	Weight Plus						Weight Minus					
	GFW	YLD	CFW	SFW	FD	OBWT	GFW	YLD	CFW	SFW	FD	OBWT
1983	31	30	30	16	30	30	18	18	18	11	18	18
1984	87	86	86	87	86	84	25	25	25	25	25	22
1985	73	73	73	71	73	72	19	19	19	17	19	19
1986	62	59	59	56	59	59	34	33	33	32	33	33
1987	101	101	101	95	101	101	33	32	32	31	32	30
1988	100	99	99	100	99	99	20	20	20	20	20	19
1989	39	39	39	38	39	39	23	23	23	23	23	23
1990	60	59	48	59	59	58	38	37	33	38	37	38
1991	36	36	36	36	36	36	29	29	29	29	29	29
1992	38	-	-	-	-	39	27	-	-	-	-	27
Total	627	582	570	558	582	617	266	236	232	226	236	258

Table 5.4 Number of hogget records for each trait in the Random line.

Year	Random line					
	GFW	YLD	CFW	SFW	FD	BOWT
1983	86	84	84	45	84	88
1984	163	161	161	161	161	162
1985	132	131	131	107	161	130
1986	168	160	160	158	160	168
1987	143	143	143	128	143	142
1988	156	155	155	155	155	152
1989	151	151	151	150	151	150
1990	168	165	149	169	165	160
1991	173	100	100	173	100	173
1992	78	-	-	-	-	75
Total	1418	1250	1234	1246	1250	1400

5.3.4 Statistical Methods

5.3.4.1 Direct response

Direct response in weaning weight was estimated by calculating genetic trends for upward, downward and divergent selection. and realised heritabilities To calculate realised heritabilities, cumulative selection differentials and cumulative responses were first estimated.

5.3.4.1.1 Phenotypic trends

Cohort means for phenotypic response were calculated from weaning weight data corrected for significant environment effects ($P < 0.05$). The significance of the effects of sex, year of birth, birth/rearing type, and age of dam were estimated by fitting Model 5.1 within lines and reducing the model until only significant effects remained.

Model 5.1 was as follows:

$$y_{ijklmno} = \mu + y_j + s_k(y_j) + m_l + t_m + d_n + b_1dob_{ijklmno} + b_2dob_{ijklmno}^2 + y_j m_l + y_l t_m + y_l d_n + e_{ijklmno} \quad (5.1)$$

where

- y_{ijklmn} = individual observation,
- μ = overall mean,
- y_j = effect of the j th year of recording ($j = 1, 2, \dots, 10$; 1 = 1983, 2 = 1984, 3 = 1985 . . . 10 = 1992),
- $s_k(l, y_j)$ = effect of the k th sire within l th line and j th year,
- m_l = effect of l th sex ($l = 1, 2$; 1 = male, 2 = female),
- t_m = effect of m th type of birth/rearing ($m = 1, 2, 3$; 1 = single/single, 2 = multiple/single, 3 = multiple/multiple),
- d_n = effect of the n th age of dam ($n = 2, \dots, 7$; 2 = 2 years old, 3 = 3 years old, 4 = 4 years old, 5 = 5 years old, 6 = 6 years old, 7 = 7 years old and up),
- b_1wage_{ijklmn} = linear regression effect due to the age at weaning,
- $b_2wage_{ijklmn}^2$ = quadratic regression effect due to the age at weaning,

$$\begin{aligned}
 y_j m_l &= \text{interaction effect between year and sex,} \\
 y_j t_m &= \text{interaction effect between year and birth type,} \\
 e_{ijklmno} &= \text{random error effect assumed NID } \sim (0, \sigma^2 e).
 \end{aligned}$$

5.3.4.1.2 Genetic trends

Phenotypic responses were determined but the genetic responses are of more important and interest. Genetic responses were calculated by two ways; as deviation of selection lines from control means, and through estimated breeding values. These were regressed on year of birth to determine the annual genetic response and on generation number to get the genetic response per generation.

5.3.4.1.2.1 Deviation from control

Direct cumulative genetic responses for weaning weight were estimated as the deviation of the mean phenotypic performance of each selection line from that of the Random line in each year. In this way, environmental effects were removed. This assumes also that genetic drift was absent in the Random line, with all fluctuations in the means being attributed to non-genetic factors such as year. Further, it is also assumed that errors due to environmental fluctuations are common to all individuals in all lines. An estimate of genetic divergence between the high and low lines was obtained by the difference between the responses of the two lines.

The genetic responses calculated are as follows;

$$\begin{aligned}
 \text{Upward Response} & \quad - \quad C_{W^-} - C_R \\
 \text{Downward Response} & \quad - \quad C_R - W_{W^-} \\
 \text{Divergence} & \quad - \quad C_{W^+} - C_{W^-}
 \end{aligned}$$

where;

$$\begin{aligned}
 C_{W^+} & \quad - \quad \text{cohort means for Weight Plus line} \\
 C_{W^-} & \quad - \quad \text{cohort means for Weight Minus line} \\
 C_R & \quad - \quad \text{cohort means for Random line}
 \end{aligned}$$

Average annual genetic responses were estimated for upward, downward and divergent responses by linear regression on year of birth to obtain measures of the average annual genetic responses. The year 1951 was designated as year 1. The regressions were

constrained to pass through the origin as all lines were derived from the same base population (Smith 1988).

5.3.4.1.2.2 Estimated breeding values

The mixed model methodology of Henderson (1973) can be used to estimate genetic and environmental trends. A general mixed model is described as one where both fixed and random effects are fitted in the same model and estimated simultaneously in the same analysis. The mixed model is shown below;

$$Y = Xb + Zu + e$$

where

Y = vector of weaning weight

X = incidence matrix relating records to fixed effects

b = vector of fixed effects

Z = incidence of matrix relating to random effects

u = vector of random effects

e = vector of random residual errors

From this model, breeding values can be obtained by best linear unbiased prediction (BLUP) for weaning weight in the selection lines. BLUP is the method that is used worldwide to give estimated breeding values (EBV's) for commercially important traits. BLUP uses all available information to estimate an animal EBV's, such as information from all genetically related animals, and possibly from correlated traits if multi-trait BLUP is used. Furthermore, BLUP corrects fixed effects such as herd, year-season of production, etc., it accounts for unequal use of best sires in different herds, for selection and non-random mating (Van der Werf 1999).

Data were analyzed for estimated breeding values based on a univariate animal model using the program ASREML developed by Gilmour *et al.* (1999). The model fitted year, sex, birth/rearing type and age of dam as fixed effect.

All annual genetic responses were regressed on year of birth (1951 as year 1) to obtain measures of the average annual genetic response in weaning weight. The

regressions were forced through the origin as all lines were derived from the same population (Smith 1988).

5.3.4.2 Generations of selection and generation interval

The generation coefficient of an individual (GC_i) indicates the average number of selections in the pedigree back to the ancestor parents in the foundation population. The generation coefficient was calculated for each individual born within the selection lines according to the following (Brinks *et al.* 1961):

$$GC_i = 1 + 0.5(GC_S + GC_D)$$

Where: GC_S and GC_D are the respective generation coefficients for the sire and dam of the i th individual. Sires (s) and dams (s) used in the foundation population were given a generation coefficient of zero.

The number of generations of selection corresponding to an individual (GS_i) can then be calculated as:

$$GS_i = 0.5(GC_S + GC_D).$$

Averaged over all lambs born within a particular year gives the generations of selection for that drop.

The generation interval (L) is defined as the average age of the parents at the birth of their selected offspring. It is a useful measure that reflects selection response and can be used to express on an annual basis. Generation interval was calculated within each selection-line by determining the average age of parents when their progenies are born separately for each sex, then the two results are averaged to get the overall interval as shown;

$$L_{overall} = \frac{L_m + L_f}{2}$$

where L_m is the generation interval for males and L_f is the generation interval for females.

5.3.4.3 Selection differential

Cumulative selection differentials are calculated by two commonly used methods; (1) the technique used by Pattie (1965) and described by Turner and Young (1969) and (2) the method of Newman, Rahnefeld and Fredeen (1973) which was used in this experiment. The method used involved the following factors;

- Contemporary Group (CG) - a group of lambs of the same sex born in the same line, season, and herd;
- Individual deviation (ID) - the individual's deviation in performance from the mean of his contemporary group;
- Individual's Accumulated Selection Differential (IAS) - the individual's ID plus the mean accumulated selection differential (MAS) of the parents of his contemporary group;
- Mean Accumulated Selection Differential (MAS) - the weighted mean IAS of the parents of the CG – weighted by the number of progeny each parent contributed to the CG.

The method is almost identical to the method used by Pattie (1965a) but differs because the value of an individual's IAS (Turner's individual cumulated selection differential) is computed. This was done by adding his own deviation from the mean performance of his contemporary group to the MAS of all parents contributing progeny to that group, rather than to the average IAS of the individual's parents.

In determining the cumulative selection differential, all foundation animals were arbitrarily assigned an IAS of zero. Each animal born subsequently in either the selected or control line was assigned an IAS as defined above. This IAS value was then considered to be the accumulated selection differential applicable to that animal wherever it subsequently appeared as a parent.

5.3.4.4 Realised heritabilities

Realised heritability estimates were obtained from the linear regression of direct response on cumulative selection differential (Falconer, 1981), with regression constrained to pass through the origin. For comparison, realised heritabilities were calculated using responses estimated in two ways; as deviation from control and as means of annual estimated breeding values.

Standard errors from the realised heritability estimates were calculated accounting for drift variances (Hill 1972). The standard error of regression coefficient calculated from the usual regression analysis assumes that the individual year observations are independent and have equal variances, which is not true. The genetic sampling of parent each year increases the variance of the successive yearly means and gives rise to a covariance between means at different times which result to an underestimation of the sampling variances of the regression coefficient. Drift variance can be accounted for in the variance estimator according to the following (Hill 1972);

$$V(b_c) = S'CS(S'S)^{-2}$$

Where $V(b_c)$ is the sampling variance of the realised heritability, S is the vector of cumulative selection differentials and C is the variance-covariance matrix of cumulative response.

5.3.4.5 Correlated responses

To measure correlated responses, realised genetic correlation between weaning weight and various lamb and hogget traits were evaluated. Annual genetic responses and responses per generation were also estimated for each trait.

5.3.4.5.1 Responses

Responses were estimated by fitting models, which accounted for significant sources of variation and estimating cohort means. The models fitted to account for significant effects were as follows:

For the trait growth rate:

Model 5.1

For lamb traits birth-coat score, birth weight and lamb survival:

Model 5.2:

$$y_{ijklmno} = \mu + y_j + s_k(y_j) + m_l + t_m + d_n + b_1dob_{ijklmno} + b_2dob^2_{ijklmno} + y_jm_l + y_it_m + y_id_n + e_{ijklmno} \quad (5.2)$$

where

Y , μ , y_j , $s_k(y_j)$, m_l , t_m and d_n are as for Model 5.1

$b_1dob_{ijklmno}$ = linear regression due to day of birth.

$b_2dob^2_{ijklmno}$ = quadratic regression due to day of birth

Model 5.3 was fitted to nine-month weight;

$$y_{ijklmno} = \mu + y_j + s_k(y_j) + m_l + t_m + d_n + b_1nmage_{ijklmno} + b_2nmage^2_{ijklmno} + y_jm_l + y_it_m + y_id_n + e_{ijklmno} \quad (5.3)$$

where

Y , μ , y_j , $s_k(y_j)$, m_l , t_m and d_n are as for Model 5.1

$b_1nmage_{ijklmno}$ = linear regression due to age at weighing.

$b_2nmage^2_{ijklmno}$ = quadratic regression due to age at weighing.

For off-shear live weight, Model 5.4 was fitted:

$$y_{ijklmno} = \mu + y_j + s_k(y_j) + m_l + t_m + d_n + b_1osbage_{ijklmno} + b_2osbage^2_{ijklmno} + y_jm_l + y_it_m + y_id_n + e_{ijklmno} \quad (5.4)$$

where

Y , μ , y_j , $s_k(y_j)$, m_l , t_m and d_n are as for Model 5.1

$b_1osbage_{ijklmno}$ = linear regression due to age at weighing.

$b_2osbage^2_{ijklmno}$ = quadratic regression due to age at weighing.

Model 5.5 was fitted for the various wool traits of greasy, skirted and clean fleece weights, yield and fibre diameter:

$$y_{ijklmno} = \mu + y_j + s_k(y_j) + m_l + t_m + d_n + b_1sage_{ijklmno} + b_2sage^2_{ijklmno} + y_jm_l + y_it_m + y_id_n + e_{ijklmno} \quad (5.5)$$

where

$Y, \mu, y_j, s_k(y_j), m_l, t_m$ and d_n are as for Model 5.1

$b_1sage_{ijklmno}$ = linear regression due to age at shearing.

$b_2sage^2_{ijklmno}$ = quadratic regression due to age at shearing.

5.3.4.5.2 Genetic responses

Cumulative correlated responses for weaning weight in the three lines were estimated as the deviation of the mean phenotypic performance of each selection line from the Random line. This procedure assumes that random genetic drift was absent in the Random line, with all fluctuations in the means attributed to non-genetic factors such as year. It was also assumed that errors due to environmental fluctuations are common to all individuals in all lines. Divergent correlated response was also calculated between the two lines. The divergence would be expected to be greater than either upward or downward response and that estimate of this response would be expected to be more precise.

Annual genetic responses in the lamb and hogget traits were estimated from the regression of correlated response on year of birth. The regressions were forced through origin as all three lines were derived from the same population (Smith 1988).

5.3.4.5.3 Realised genetic correlations

The regression of correlated response on cumulative selection differential was estimated for each of the correlated traits with the regression being forced to pass through the origin. The regression of correlated response on cumulative selection differential for weaning

weight, denoted as b , from which the realised genetic correlation was obtained, has the following expectation:

$$b = r_G \cdot h_1 \cdot h_2 \cdot \sigma_2 / \sigma_1$$

where;

r_G = realised genetic correlation

h_1 = realised heritability of weaning weight

h_2 = realised heritability of correlated trait

σ_1 = phenotypic standard deviation of weaning weight

σ_2 = phenotypic standard deviation of the correlated trait

Since the realised heritabilities of the correlated traits are unknown, the estimated heritability of the various traits calculated in Chapter 3 were used. The phenotypic standard deviations for weaning weight and the correlated traits were obtained from estimates within each line.

The approximate standard error for the realised genetic correlation was calculated using the following formula (Atkins and Thompson 1986b);

$$V(r_G) = \frac{V(b)}{h_1^2 h_2^2} + \frac{V(h_1^2) b^2}{4 h_2^2 (h_1^2)^3} + \frac{V(h_2^2) b^2}{4 h_1^2 (h_2^2)^3}$$

where $V(r_G)$ and $V(b)$ are the respective variances of the realised genetic correlation and the correlated regression, and all other parameters are as defined previously.

5.4 Results

5.4.1 Generation coefficients and generation intervals

From 1951 to 1992, approximately there were 13.51 generations studied, with the three lines having similar changes in the generation coefficient. The Weight Plus line has a generation coefficient of 13.80, 13.47 for Weight Minus and 13.26 for the Random line. Between 1983 to 1992, the three lines had an average of 2.93 generations. The generation coefficients for the three lines were 3.09, 2.91 and 2.8 for the Weight Plus, Weight Minus and Random lines, respectively.

The generation interval during the suspension of selection remained relatively constant with an average of 2.91, 3.13 and 2.97 years and in the Weight Plus, Weight Minus and Random lines, respectively, and a mean of 2.87 for the three lines. The average age of dam was 3.81, 4.26 and 3.95 years for the Weight Plus, Weight Minus and Random lines, respectively. The average age of sire in all lines was 2.0 years.

5.4.2 Direct responses

5.4.2.1 Phenotypic trends

The phenotypic responses in weaning weight for the two selected lines and the control line shows the large variability from year to year, which tended to be parallel for all lines suggesting environmental effects peculiar to each year (Figure 5.1). Analysis showed that year effects were important, but appeared random and with no obvious trends associated with between-years variations. From 1983 to 1992, the Weight Plus line showed the highest weaning weight followed by the Random and the Weight Minus lines, respectively. The average weaning weight per year ranged from 18.2 to 25.6 kg in the Weight Plus line, 13.5 to 17.2 kg in the Weight Minus line and 14.7 to 23.2 kg in the Random line. For the ten-year period, Weight Plus line had an average of 22.7 kg which

was 30.1% significantly ($P>0.01$) greater than the Weight Minus line and 16.7% greater than the Random line.

5.4.2.2 Genetic trends

5.4.2.2.1 Deviation from Control line

Genetic trends were estimated as deviations from the control line means. These are plotted in Figures 5.2 for upward and downward responses and in Figure 5.3. for the divergent response. In Figure 5.2, the variations from year to year in the two lines tend to be parallel with large fluctuations in responses when selection for weaning weight was relaxed. Both lines showed an upward trend but declined sharply in 1990 and rose slightly in the last two years. The Divergent response rose to its highest response in 1985 when selection was relaxed followed by a declining trend until 1992 suggesting a decrease in the difference between the selected lines.

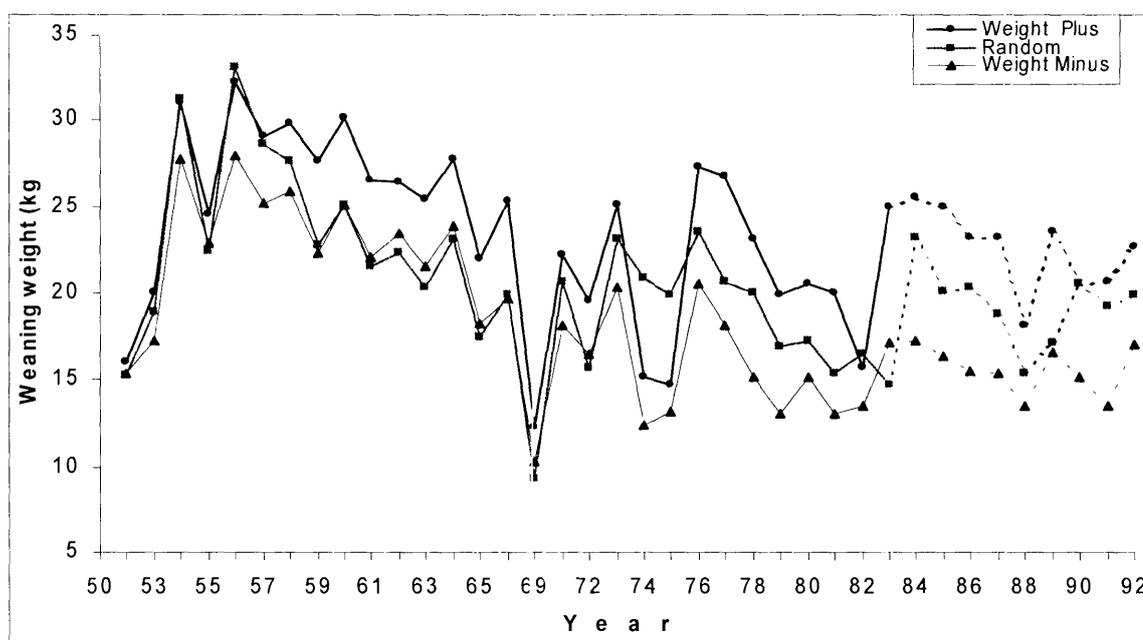


Figure 5.1 Weaning weight of the Weight plus, Weight Minus and Random lines (1975- 1992). Dotted lines – selection relaxed; solid lines – selected for weaning weight for comparison.

The regression coefficients for the genetic responses in terms of actual annual genetic deviations between 1983 and 1992 are shown in Table 5.5. As expected, both the Divergent and Upward selections showed positive genetic changes while the Downward selection was negative. For the Divergent selection, the annual genetic change was 0.18 kg/year. Comparing the two selection lines, the result shows that the annual genetic change in Weight Minus line was greater than that observed in the Weight Plus line.

Regressions are also reported where genetic responses were regressed on generation number. For the divergence in weaning weight, the change per generation was 0.56 kg per generation. As in annual genetic changes, the Weight Minus line showed a higher genetic change per generation of -0.31 kg/generation compared to the 0.25 kg/generation for the Weight Plus line.

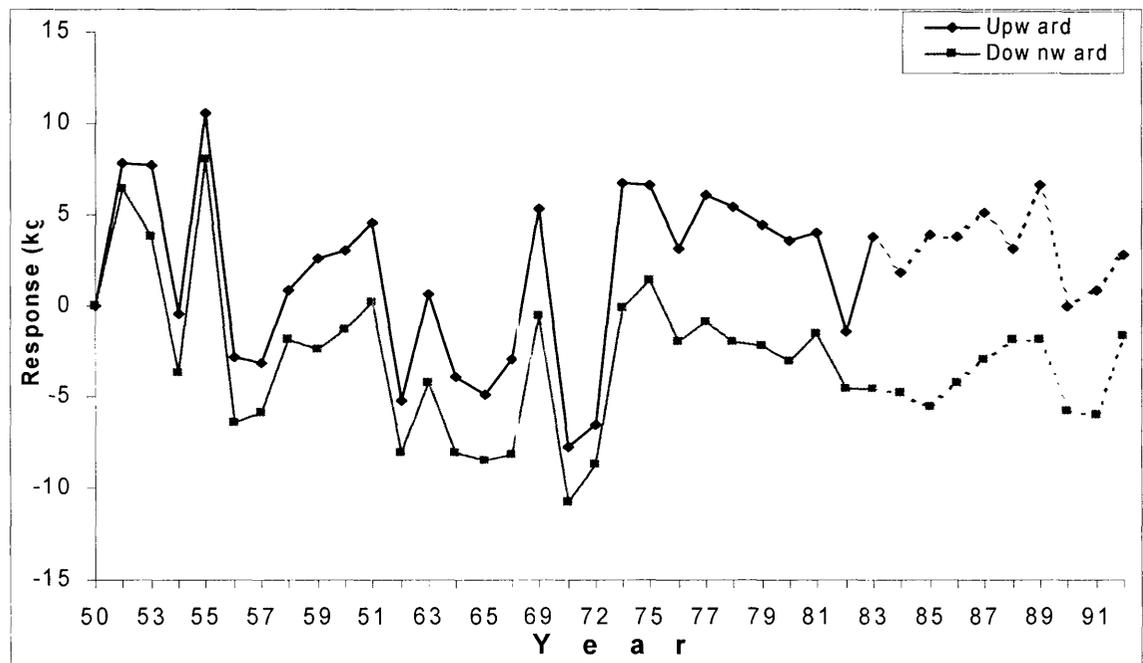


Figure 5.2. Response to upward (Weight Plus - Random) and downward (Weight Minus - Random) selections, measured as deviations from the control line (1975-1992). Dotted lines – selection relaxed; solid lines – selected for weaning weight for comparison.

Table 5.5 Genetic responses and standard errors from the regression of response to Divergent, Upward and Downward selection on year of birth (b , kg/yr) and generation number (b , kg/generation).

Responses	Annual		Generation	
	b (kg/yr)	s.e	b (kg/generation)	s.e.
Divergent	0.179	0.014	0.563	0.043
Upward	0.081	0.014	0.248	0.043
Downward	-0.097	0.012	-0.305	0.038

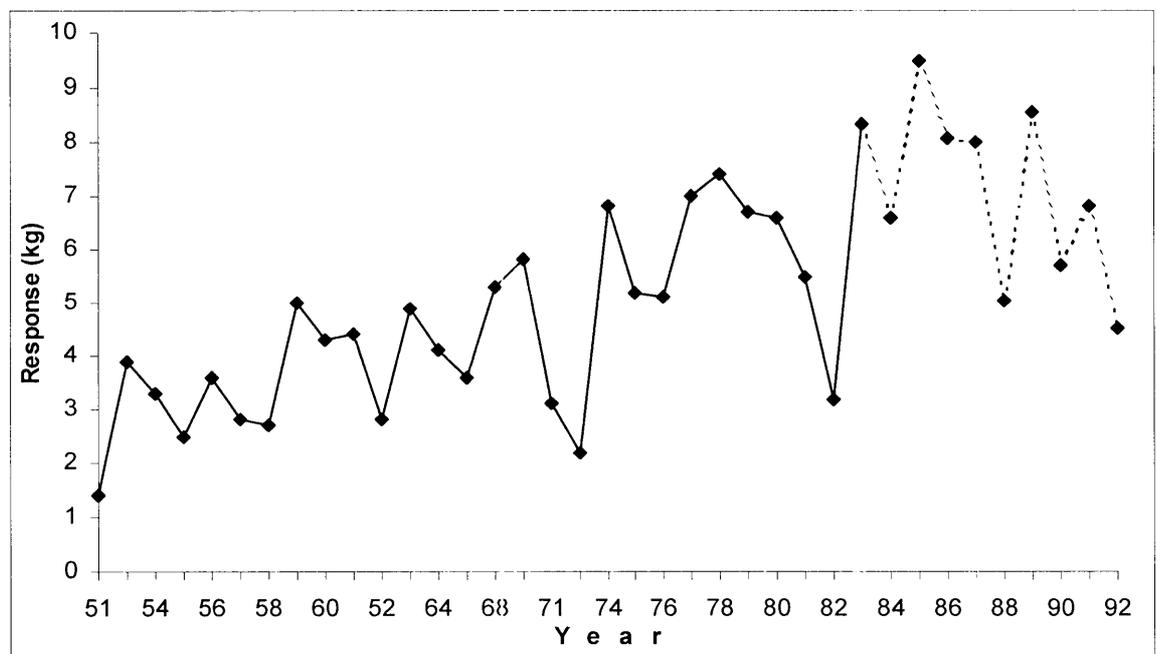


Figure 5.3. Response to divergent selection (Weight Plus – Weight Plus). Dotted lines – selection relaxed; solid lines - selected for weaning weight for comparison.

5.4.2.2.2 Estimated breeding values

The mean estimated breeding for direct, maternal and total of direct and maternal effects are shown in Figures 5.4, 5.5, and 5.6. The regression coefficients of average estimated breeding values on year and on generation number for the three lines are given in Table 5.6. For the direct effects, the Weight Plus line showed a decreasing trend upon the suspension of selection for weaning weight but an upward trend was observed in the

later years while the Weight Minus line responded positively with an upward trend when selection was relaxed. The annual genetic change was 0.18 kg/year for the Divergence selection and with the Upward selection registering higher genetic change of 0.11 kg/year than the Weight Minus line of -0.07 kg/year. Regression for the average estimated genetic breeding values on generation number was similarly greatest with the Divergence selection with 0.58 kg/generation compared to the 0.34 and -0.23 kg/year for the Upward and Downward selections, respectively.

Table 5.6 Mixed model genetic trends and standard errors from the regression of average estimated breeding values of Divergent, Upward and Downward selection on year of birth (b , kg/year) and generation number (b , kg/generation)

Response	Annual		Generation Number	
	b (kg/year)	$s.e.$	b (kg/generation)	$s.e.$
<i>Direct effects</i>				
Divergent	0.185	0.009	0.584	0.027
Upward	0.113	0.011	0.344	0.033
Downward	-0.075	0.011	-0.230	0.027
<i>Maternal effects</i>				
Divergent	0.039	0.003	0.124	0.008
Upward	0.016	0.002	0.047	0.006
Downward	-0.024	0.002	-0.075	0.008
<i>Direct and Maternal effects</i>				
Divergent	0.117	0.006	0.368	0.019
Upward	0.069	0.007	0.212	0.021
Downward	-0.048	0.006	-0.150	0.021

For the maternal effects, the breeding values were less variable as compared to the direct effects but showing a similar genetic trend for the three lines when selection for weaning weight was suspended. The annual genetic changes were 0.04, 0.02 and -0.02 kg/yr for the Divergence, Upward and Downward selections, respectively. The average genetic changes per generation were 0.12 kg for the Divergent selection, 0.05 kg for Upward selection and -0.08 kg for the Downward selection. For the total of direct and

maternal effects, the genetic trends of the three lines were similar to that of the direct effects and maternal effects. The Divergence selection showed the greatest genetic changes both on yearly (0.12 kg) and on per generation (0.37 kg) basis with Upward selection showing greater genetic changes than Downward selection.

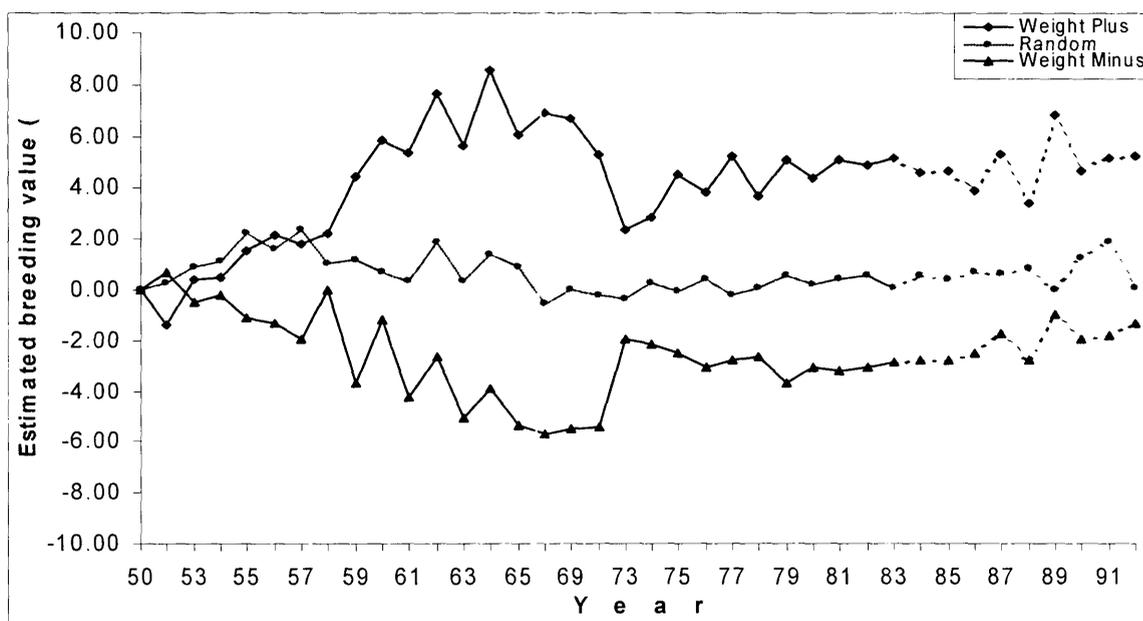


Figure 5.4 Genetic trends in estimated average breeding values for the direct component of weaning weight for the Weight Plus, Weight Minus and Random lines. Dotted lines – selection relaxed; Solid lines – selection for weaning weight.

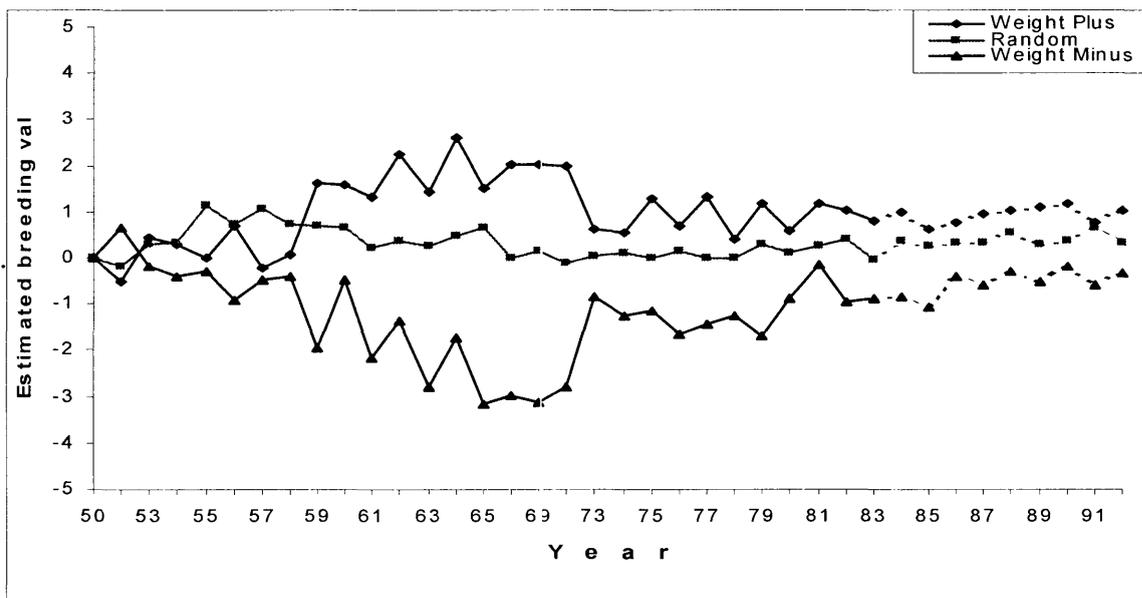


Figure 5.5 Genetic trends in estimated average breeding values for the maternal component of weaning weight for the Weight Plus, Weight Minus and Random lines. Dotted lines – selection relaxed; solid lines – selection for weaning.

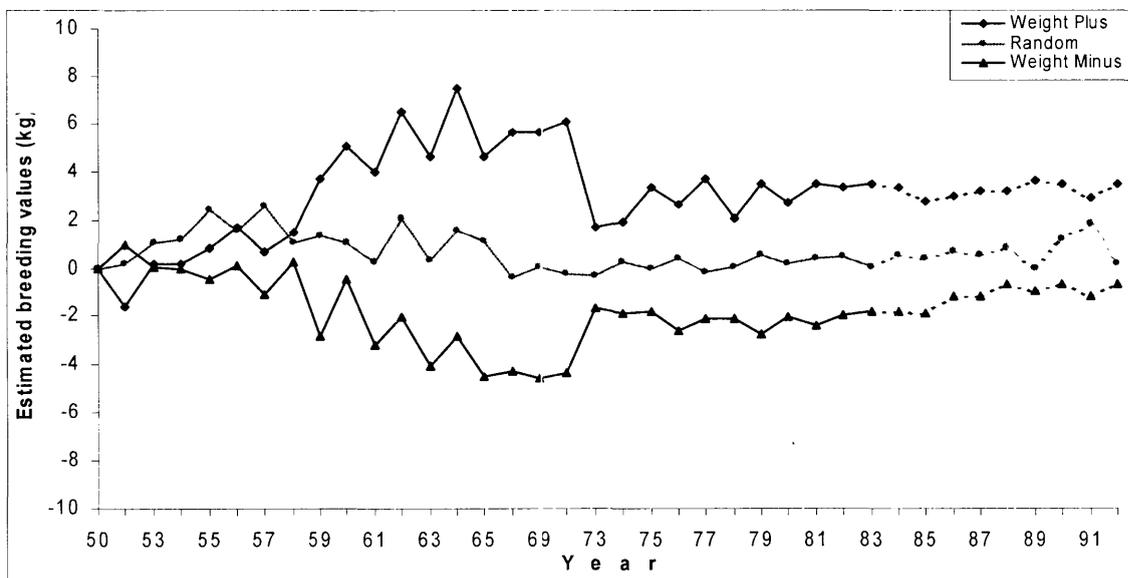


Figure 5.6 Genetic trends in estimated average breeding values for the total of the direct and maternal effects of weaning weight for the Weight Plus, Weight Minus and Random lines. Dotted lines – selection relaxed; solid lines – selection for weaning weight.

5.4.3 Selection differentials

The cumulative selection differentials for the selected lines maintained their levels when selection was relaxed in 1983 until 1992 as shown in Figure 5.7. The Random line, on the other hand, maintained a low near zero level for the whole period of relaxed selection. The total cumulative selection differential for the Weight Plus line was 22.91 kilograms. It increased by only 0.85 kilograms between 1983 and 1992 or 0.085 kilograms per year. For the Weight Minus lines, the total cumulative differential at the end of the experiment was -16.63 kilograms. Between 1983 and 1993, it decreased by -1.32 kilograms or with an annual decrease of -0.132 kilograms. The cumulative selection differential for the Random line maintained a low level even during the suspension of selection, not changing appreciably with time even until the last year of the experiment. The cumulative selection differential was obtained for the Random line to indicate occurrence of any inadvertent selection pressure. The results showed no evidence of such changes.

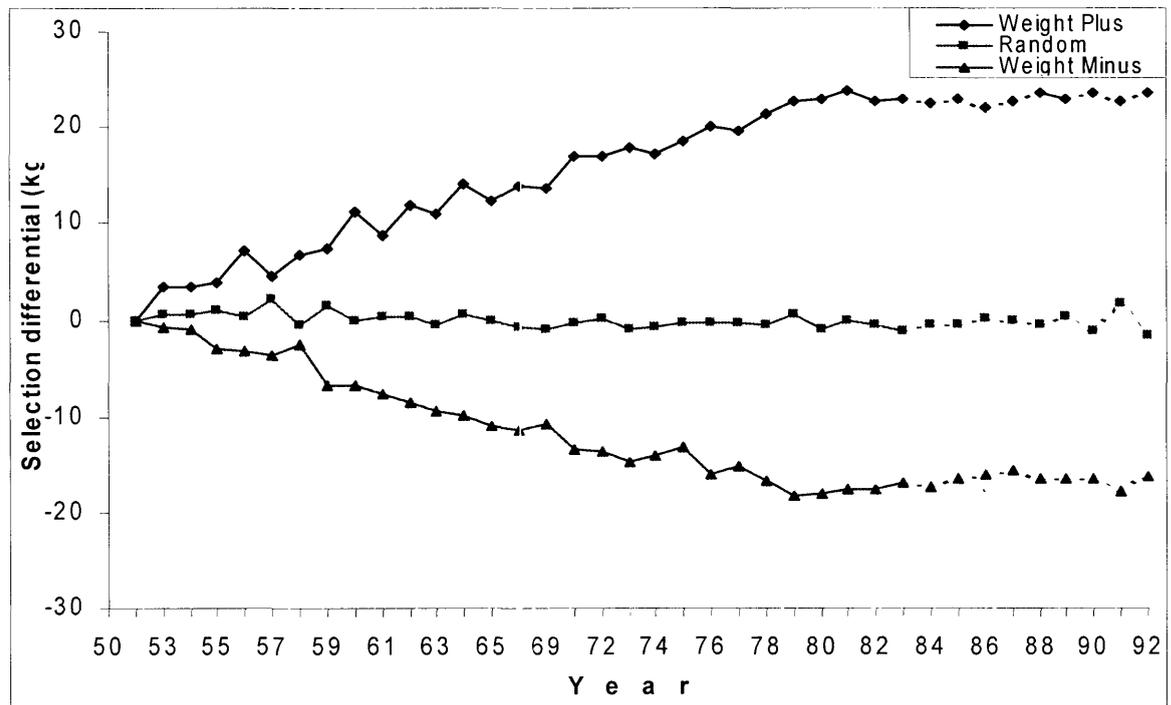


Figure 5.7 Cumulative selection differentials of the Weight Plus, Weight Minus and Random lines. Dotted lines – selection relaxed; solid lines – selected for weaning weight.

5.4.4 Realised heritabilities

Realised heritabilities (h^2) and standard errors for the period when selection was suspended for Upward, Downward and Divergent selections are shown in Table 5.7. Scatter plots of cumulative response versus cumulative selection differential are shown in Figure 5.8 for Upward selection, Figure 5.9 for Downward selection and Figure 5.10 for Divergent selection. Regression lines depicting the estimated realised heritability are also shown.

Table 5.7 Realised heritabilities (h^2) and their standard errors (s.e) calculated as regression of cumulative response on cumulative selection response and average estimated breeding values for Upward, Downward and Divergent selections calculated

Response	Annual genetic trends		Estimated breeding values	
	h^2	s.e.	h^2	s.e.
Divergent	0.171	0.011	0.18	0.005
Upward	0.134	0.021	0.18	0.017
Downward	0.226	0.025	0.17	0.017

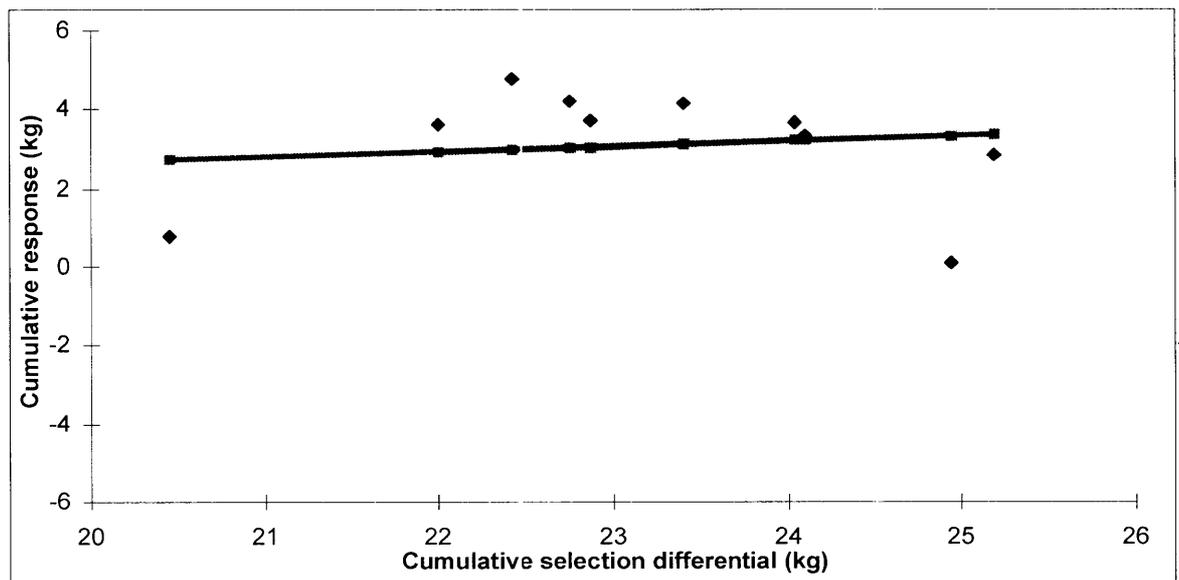


Figure 5.8 Cumulative response versus cumulative selection differential and heritability for upward ($h^2 = 0.18$) selection

Realised heritability of weaning weight estimated from regression of cumulative response of the selection lines as a deviation from the control line was 0.17 ± 0.01 for the Divergence of Weight Plus and Weight Minus lines. Realised heritabilities in the Upward selection of 0.13 ± 0.021 was significantly lower than the Divergence estimates. The heritability estimates of 0.23 ± 0.025 for the Downward selection was greater than the estimates of the two lines mentioned above. These regression estimates which were forced through the origin were found to be significantly ($P < 0.05$) different between lines.

On the other hand, the realised heritability for weaning weight derived from regressing mean estimated breeding values on cumulative selection differential did not significantly different from each other. The Divergent selection has a realised heritability of 0.18 ± 0.005 , 18 ± 0.017 for Upward selection and 0.17 ± 0.017 for the Downward selection. These estimates were significantly different from the estimates derived from regressing cumulative response on cumulative selection differential.

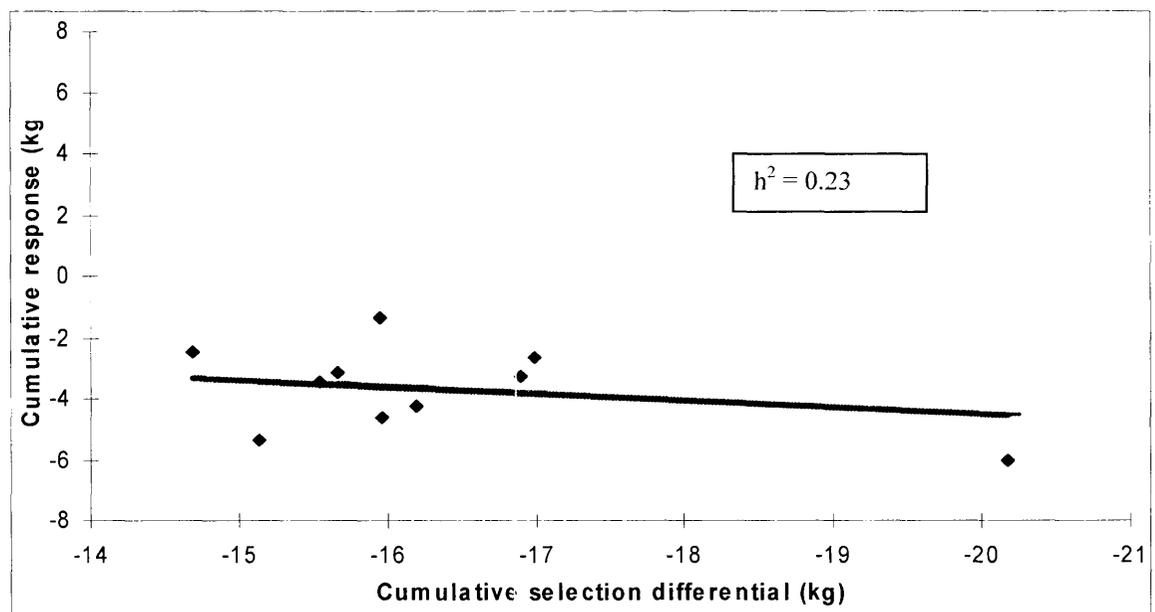


Figure 5.9 Cumulative response versus cumulative selection differential and heritability for downward ($h^2 = 0.17$) selection

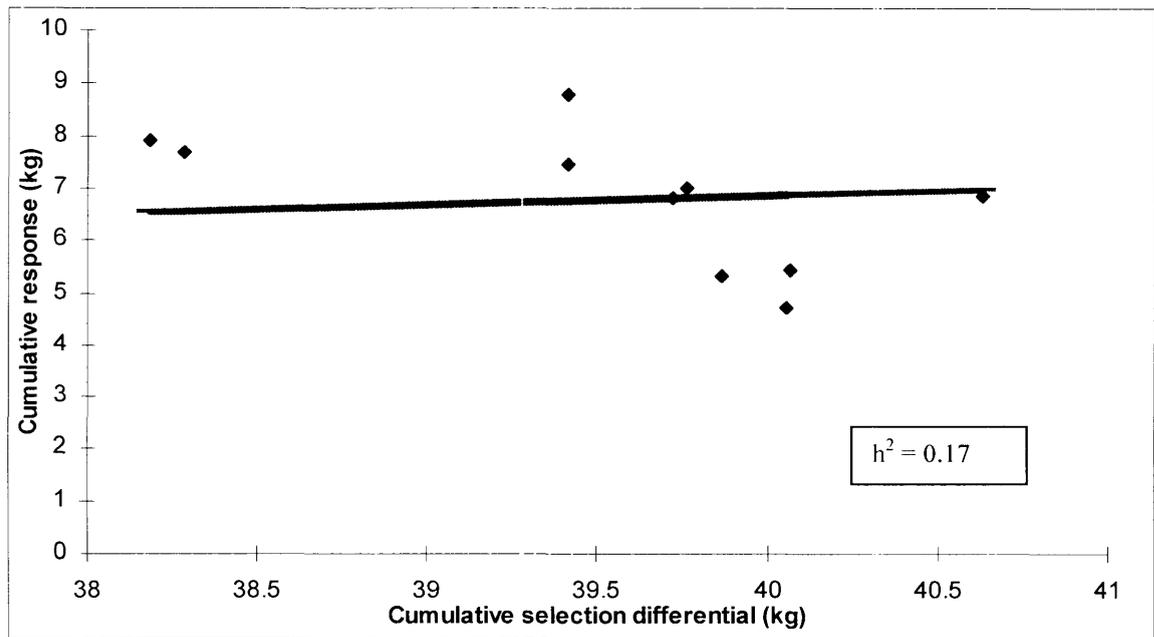


Figure 5.10 Cumulative response versus cumulative selection differential and heritability for divergent ($h^2 = 0.18$) selection

5.4.5 Genetic correlations

5.4.5.1 Genetic response

The regression coefficients for the annual changes in correlated traits for Upward, Downward and Divergent response after the suspension of selection in terms of actual deviations are given in Table 5.8. For the Upward selection, there was a significant increase ($P < 0.01$) in live weights at various ages. Birth weight significantly increased by an average of 0.02 kg/year while nine-month weight and off-shear live weight increased by 0.12 kg/year and 0.16 kg/year, respectively. For the wool traits, all traits except for yield significantly ($P < 0.01$) declined; 0.003 kg/year for greasy, clean, and skirted fleece weights and 0.016 scores/year for birth-coat score. Fibre diameter, on the other hand, decreased significantly ($P < 0.01$) making it thicker by 0.03 microns per year.

The regression coefficients for annual genetic changes in correlated traits for downward response showed significant but negative annual genetic changes except for

birth-coat score, yield and fibre diameter. A decline of 0.02 kg per year was observed for greasy fleece weight, while skirted fleece and clean fleece weights declined by 0.1 kg/year. For the divergent selection, all live weights showed significant ($P < 0.01$) positive genetic changes. Birth weight increased by 0.03 kg/year, nine-month weight by 0.25 kg/year and off-shear live weight by 0.34 kg/year. Growth rate to weaning significantly ($P < 0.01$) showed positive genetic change of 1.37 kg/year. Fleece weights also showed significant increases of 0.01 kg/year for greasy, clean and skirted fleece weights. Fibre diameter declined significantly by 0.02 microns/year.

The regression coefficients for the genetic changes per generation in correlated traits when selection was relaxed for the Upward, Downward and Divergent selection in terms of actual deviation are given in Table 5.9. Similar to the annual genetic changes mentioned above, all live weight traits significantly ($P < 0.01$) increased for Upward selection. Birth weight decreased by 0.05 kg/generation while nine-month and off-shear live weight increased being heavier by 0.35 and 0.47 kg/generation. Wool traits, on the other hand, showed significant ($P < 0.01$) negative genetic changes for greasy, skirted and clean fleece weights but with fibre diameter showing a significant decrease of 0.03 microns/generation. For the downward selection, except for birth-coat score, yield and fibre diameter, all lamb and hogget traits showed significant decreases during the period when selection was suspended. Lambs were lighter per generation by 0.04, 0.43 and 0.57 kg/generation at birth, nine, months old and prior to shearing, It also grew to weaning lesser by 2.87 kilograms/generation. Lamb survival also declined by 1%. A decline by 0.05, 0.4, and 0.04 kg/generation of greasy, clean and skirted fleece were observed.

Table 5.8 Annual genetic responses in correlated traits for Upward, Downward and Divergent responses. Standard errors are from usual regression analysis.

Traits	Upward	Downward	Divergent
<i>Lamb traits</i>			
Birthcoat score	-0.016 ± 0.002 ^{***}	-0.007 ± 0.004 ^{ns}	-0.009 ± 0.005 ^{ns}
Birth weight	0.015 ± 0.002 ^{***}	-0.013 ± 0.002 ^{***}	0.028 ± 0.003 ^{***}
Lamb survival	0.000 ± 0.000 ^{ns}	-0.003 ± 0.001 [*]	0.003 ± 0.001 ^{**}
Growth rate	0.454 ± 0.179 [*]	-0.915 ± 0.145 ^{***}	1.369 ± 0.105 ^{***}
Nine-month weight	0.115 ± 0.016 ^{***}	-0.138 ± 0.013 ^{***}	0.253 ± 0.020 ^{***}
<i>Hogget traits</i>			
Greasy fleece	-0.003 ± 0.001 [*]	-0.016 ± 0.007 ^{***}	0.013 ± 0.002 ^{***}
Clean fleece	-0.003 ± 0.001 [*]	-0.014 ± 0.001 ^{***}	0.011 ± 0.001 ^{***}
Skirted fleece	-0.004 ± 0.001 ^{**}	-0.013 ± 0.002 ^{***}	0.009 ± 0.002 ^{***}
Yield	0.016 ± 0.013 ^{ns}	0.009 ± 0.029 ^{ns}	0.007 ± 0.034 ^{ns}
Fibre diameter	-0.032 ± 0.004 ^{**}	-0.009 ± 0.005 ^{ns}	-0.023 ± 0.005 ^{**}
Off-shear live weight	0.155 ± 0.023 ^{**}	-0.184 ± 0.014 ^{**}	0.336 ± 0.029 ^{***}

ns = non-significant * - P<0.05 ** P<0.01 *** 0.001

For the Divergent selection, all lamb and hogget traits except for yield, showed significant (P<0.01) changes on per generation basis. Birth weight significantly increased by 0.09 kg/generation, 0.80 kg/generation increase for nine-month weight, 1.057 kg/generation for off-shear live weight and a growth rate to weaning of 4.311 kg/generation. Greasy, clean, and skirted fleece weights significantly increased by 0.04, 0.03 and 0.02 kg/generation, respectively while fibre diameter was significantly finer by 0.07 microns per generation. Lamb survival increased by 1% per generation.

Table 5.9. Genetic responses per generation of correlated traits for Upward, Downward and Divergent responses. Standard errors are from usual regression analysis.

Traits	Upward	Downward	Divergent
<i>Lamb traits</i>			
Birthcoat score	-0.050 ± 0.008 ^{***}	-0.021 ± 0.013 ^{ns}	-0.030 ± 0.016 ^{ns}
Birth weight	0.046 ± 0.006 ^{***}	-0.039 ± 0.007 ^{***}	0.087 ± 0.008 ^{***}
Lamb survival	0.001 ± 0.002 ^{ns}	-0.009 ± 0.003 [*]	0.010 ± 0.002 ^{**}
Growth rate	1.385 ± 0.547 [*]	-2.861 ± 0.458 ^{***}	4.311 ± 0.327 ^{***}
Nine-month weight	0.352 ± 0.049 ^{***}	-0.432 ± 0.042 ^{***}	0.796 ± 0.061 ^{***}
<i>Hogget traits</i>			
Greasy fleece	-0.010 ± 0.003 [*]	-0.050 ± 0.007 ^{***}	0.040 ± 0.007 ^{***}
Clean fleece	-0.008 ± 0.003 [*]	-0.043 ± 0.004 ^{***}	0.034 ± 0.004 ^{***}
Skirted fleece	-0.011 ± 0.002 ^{**}	-0.040 ± 0.005 ^{***}	0.029 ± 0.005 ^{***}
Yield	0.048 ± 0.039 ^{ns}	0.028 ± 0.090 ^{ns}	0.020 ± 0.106 ^{ns}
Fibre diameter	-0.099 ± 0.011 ^{***}	-0.029 ± 0.014 ^{ns}	-0.072 ± 0.016 ^{***}
Off-shear live weight	0.474 ± 0.072 ^{***}	-0.566 ± 0.043 ^{***}	1.057 ± 0.090 ^{***}

ns = non-significant * P<0.05 ** P<0.01 *** 0.001

5.4.5.2 Realised genetic correlation

Estimates for realised genetic correlations for divergent response are presented in Table 5.10. The heritabilities and genetic correlations presented are based from the control line analysis in Chapter 3.

Realised genetic correlations for growth traits were positive for Divergent selection on weaning weight. The realised genetic correlations between weaning weight and live weights at different ages were very high. Birth weight registered a high correlation to weaning weight with 0.95, 0.70 for growth rate, 0.66 for nine-month and 0.76 for off-shear live weight. Realised genetic correlations of fleece weights to weaning weight were low and positive; 0.25 for greasy fleece, 0.30 for clean fleece and 0.22 for skirted fleece weight. Yield has a very low positive correlation to weaning weight at 0.02. Birth-coat score and fibre diameter were both negatively correlated with a negligible correlations of -

.07 and -0.17, respectively. On the other hand, lamb survival showed low but positive correlation to weaning weight.

Table 5.10 Realised genetic correlation (\hat{r}_A) and approximate standard error between weaning weight and various lamb and hogget traits calculated from divergence of the Weight Plus and Weight Minus lines at different periods.

Traits	h_x^2	r_A	\hat{r}_A
<i>Lamb traits</i>			
Birthcoat score	0.538 ± 0.078	0.005 ± 0.05	-0.074 ± 0.074
Birth weight	0.230 ± 0.064	0.78 ± 0.03	0.954 ± 0.048
Lamb survival	0.121 ± 0.054		0.208 ± 0.069
Growth rate	0.439 ± 0.102	0.83 ± 0.01	0.697 ± 0.094
Nine-month weight	0.593 ± 0.086	0.82 ± 0.04	0.665 ± 0.073
<i>Hogget traits</i>			
Greasy fleece	0.503 ± 0.085	0.49 ± 0.05	0.252 ± 0.057
Clean fleece	0.492 ± 0.097	0.57 ± 0.06	0.304 ± 0.086
Skirted fleece	0.632 ± 0.094	0.59 ± 0.065	0.218 ± 0.076
Yield	0.604 ± 0.100	0.007 ± 0.06	0.017 ± 0.066
Fibre diameter	0.626 ± 0.080	0.17 ± 0.05	-0.168 ± 0.075
Off-shear live weight	0.596 ± 0.067	0.78 ± 0.03	0.756 ± 0.044

h_x^2 - heritability r_A - genetic correlation \hat{r}_A - realised genetic correlation

The realised genetic correlation calculated for upward and downward responses to selection are shown in Table 5.11. For the upward response, growth traits were all positively correlated to weaning weight ranging from the moderate correlation for growth rate (0.46) and nine-month weight (0.59) to a high correlation for off-shear live weight (0.67). The upward realised genetic correlation between weaning weight and birth weight was very high and above the theoretical limit for a genetic correlation of +1.0. Wool traits, on the other hand, all showed negative correlations with greasy and clean fleece weights and yield negligibly correlated and fibre diameter with a negative moderate correlation.

Birth-coat score also showed a negative and low correlation to weaning weight. Realised genetic correlation for Upward selection for lamb survival was very low but positive.

Table 5.11 Realised genetic correlations (\hat{r}_A) and standard errors between weaning weight and various lamb and hogget traits calculated from Upward and Downward selections.

Traits	Upward	Downward
<i>Lamb traits</i>		
Birthcoat score	-0.247 ± 0.072	0.120 ± 0.075
Birth weight	1.074 ± 0.042	0.936 ± 0.045
Lamb survival	0.055 ± 0.053	0.379 ± 0.057
Growth rate	0.462 ± 0.098	0.980 ± 0.095
Nine-month weight	0.588 ± 0.076	0.755 ± 0.070
<i>Hogget traits</i>		
Greasy fleece	-0.127 ± 0.056	0.680 ± 0.049
Clean fleece	-0.145 ± 0.083	0.795 ± 0.085
Skirted fleece	-0.157 ± 0.073	0.637 ± 0.067
Yield	0.066 ± 0.053	-0.040 ± 0.054
Fibre diameter	-0.466 ± 0.067	0.145 ± 0.062
Off-shear live weight	0.672 ± 0.047	0.852 ± 0.052

For the downward response, all lamb and hogget traits were positively correlated to weaning weight except for yield. The realised genetic correlations for live weights and growth rate to weaning were all very high ranging from 0.76 to 0.98. Greasy, clean and skirted fleece weights showed high correlations with greasy fleece weight registering a very high correlation of 0.80. Fibre diameter and birth-coat score were lowly correlated while yield had a negative and very low correlation (-0.04). On the other hand, lamb survival showed a low but positive correlation of 0.38.

5.5 Discussion

The realised heritability estimate of 0.17 ± 0.01 obtained from the Divergence of Weight Plus and Weight Minus lines is in close agreement with the estimates of Davis (1987) in the later periods and for the whole period of the experiment. Davis (1987) reported heritability estimates of 0.151 ± 0.022 for the second period of the experiment (1962-1972), 0.19 ± 0.22 for the third period (1973-83) or 0.17 ± 0.02 (the aberrant years of 1974 and 1975 are ignored) and 0.16 ± 0.018 and 0.16 ± 0.017 (ignoring years 1974 and 1975) for the whole period of the selection experiment (1951-1983). However, these estimates were much lower than the estimates of Pattie (1965), McGuirk and Davis (1987) (0.25 ± 0.10 , 0.22 ± 0.027 and 0.29 ± 0.04) obtained during the first period of the experiment (1951-61).

The realised heritability estimates in the present study are also lower than the ASREML estimate of 0.37 ± 0.01 presented in Chapter 3. Davis (1987) also reported that the realised heritability estimates for the Divergence, Upward and Downward selections in the later period and the whole period of the experiment were lower compared to the half-sib estimates for the base population. McGuirk *et al.* (1987) explained that the realised heritabilities for the divergent selection were often slightly smaller than expected for those traits in which maternal effects were relatively important. Bulmer (1980) attributed the difference in estimates to the decline in the genetic variation via negative linkage disequilibrium as a result of selection. This phenomenon referred to as 'Bulmer effect' or *gamete phase disequilibrium* results in the reduction of total phenotypic variance and more importantly additive genetic variance since selected animals are going to be parents of the next generation. The reduction in additive genetic variance remains over generations.

Sorensen and Kennedy (1984a) explained that the decline in genetic variation is not being accounted for in the regression of response on cumulative selection differentials. To achieve a much closer agreement between the two estimates, Atkins and Thompson (1986a) recommends making allowance for it, although the discrepancy between observed and predicted responses depends on the heritability and intensity of selection, and age structure of the population (James 1990). When such a reduction in variance occurs, most of the effect on response is in the early generations of selection, such that the observed

response in these years is greater than expected. The subsequent responses, though, tend to be relatively constant.

Falconer (1993) reported that realised heritability does not provide for an estimate of the heritability of the base population for several reasons. First, the responses of characters with high heritabilities are expected to be somewhat reduced after the first generation of selection, so that the realised heritability after the first generation will underestimate the heritability of the base population. Second, systematic changes due to environmental trends, random drift, or inbreeding depression will be included in the response unless they are removed by comparison with a control line.

The realised heritability of 0.18 for the Divergent selection derived from the regression of estimated breeding values on cumulative selection differential did not significantly differ with the 0.17 estimate derived from the regression of cumulative response on cumulative selection differential. The estimates for the Upwards (0.17 vs 0.13) and Downward selections (0.17 vs 0.23) were statistically different for the two methods used in determining realised heritability. However, all estimated heritabilities were smaller than the base population heritability estimates. Crook (1992) reported that realised heritabilities for skin fold derived from regression mean expected breeding value on cumulative selection differential were smaller than the estimates derived for the regression of cumulative response on cumulative selection differential. Similarly, all heritabilities were smaller than the base population estimate of heritability. The mixed model methodology has been a popular tool to evaluate response to selection and to estimate genetic parameters in selection experiments. The BLUP EBV's in particular has been advocated an efficient method for the analysis of selection experiment. BLUP EBV's are found to be unbiased that they are unaffected by systematic environmental effects. The important genetic properties of BLUP and the animal model are due to the use of the Numerator Relationship Matrix (*i.e.* the matrix with additive genetic relationships between animals) which is needed to account for the additive genetic covariances between records of related animals, computing inbreeding coefficients for members of population and is therefore essential for appropriate evaluation of data on complex pedigrees (van der Werf 1999).

The genetic trends of 0.56 ± 0.043 for Divergent selection reported in the present study is much lower than the findings of Davis (1987); 2.36 ± 0.203 for the first period, 0.77 ± 0.03 and 0.84 ± 0.088 for the last period and 0.84 ± 0.078 and 0.90 ± 0.78 for the whole

period of the experiment. The finding is similar in the Downward and Upward selections. Davis (1987) reported that there was a dramatic response for the initial period and was generally lower and more consistent for other periods. Since the present study involved data from the later part of the experiment, the lower genetic trends result is to be expected. The suspension of selection is another possible factor that could have contributed to lower results.

The genetic trends obtained from the mean estimated breeding values showed varying results when compared to the findings of Davis (1987). For the direct and maternal effects, the results were lower than those obtained in the first period of the study but higher in the later period and for the whole period of the experiment. For the total of direct and maternal effects, the results were very much lower than the results in the various periods of the experiment. However, it should be noted that in the present experiment, sex, year, birth/rearing type and age of dam were fitted as fixed effects while the previous experiment fitted only year as fixed effect.

The lower genetic trends observed in the present study could be attributed to the suspension of selection. Roberts (1956a) reported that in small line selection in mice, relaxed selection results in the regression of the line moving towards the base population. The lack of response in live weight excluded the likelihood that the plateau was caused by natural selection opposing artificial selection. Eklund and Bradford (1977) also reported that relaxed selection resulted in no response, eliminating the likelihood of any major contribution of natural selection or overdominance to the plateau. The lower genetic trend also confirms the observation that response to selection tends to be greater in the initial phase of selection and lower, although consistent in the later phases (James 1990).

Another reason for the decreasing response over time is that the selection lines were approaching selection limits. Davis (1987) observed that the response was decreasing over time as shown by the decrease of genetic trends over time in direct and maternal components of weaning weight and their total, and to the reduced realised heritabilities after the first ten years of selection. These he attributed to selection lines approaching selection limits. Eisen (1980) reported that the classical selection response may be viewed as an initial linear change with generations of selection or cumulative selection differential followed by a gradual decrease of response until a selection limit is attained. The limit to selection is met when all the alleles affecting the trait have been fixed in the population or if the genetic variance have been exhausted. The limit may also be reached before the

genetic variance is exhausted and despite the reason that some loci are not fixed, selection may still fail to change the mean value of the population any further which happens when selection favours individuals that are heterozygous at some loci and if natural selection will oppose the direction of the artificial selection (Roberts 1966a).

The correlated genetic response observed annually or per generation from the various lamb and hogget traits examined only shows that suspension of selection for weaning weight would result in some degree of genetic response. For the responses derived from Divergence selection, most of the traits showed significant positive genetic responses in spite of the relaxation of selection. Similar to direct genetic response, the results were lower than the correlated responses before selection was suspended. The realised genetic correlation of the various traits were also observed to be in good agreement with the REML correlations calculated in Chapter 3 for the Random line and other published estimates.

The result of the present study is in close agreement with the very high realised genetic correlations reported by Davis (1987) for birth weight (0.81), growth rate (0.75) and liveweight (0.64) and the realised genetic correlation for live weight reported by Pattie (1965) of 0.72. The realised genetic correlation between weaning weight and fleece weights were low (0.25 ± 0.057 for greasy fleece, 0.30 ± 0.86 for clean and 0.218 ± 0.076 for skirted fleece weight) and were lower than the REML estimate in Chapter 3. Davis (1987) explained that while there is a considerable divergence in mature body size between the selection lines, there is little change in wool production traits. These result for clean fleece weight is in agreement with the low realised genetic correlations of Pattie (1965a) but higher than the negligible results reported by Pattie (1965b) and Davis (1987). This higher correlation for greasy fleece weight could be attributed to the decreasing divergence in body size between selection lines after the suspension of selection.

5.6 Conclusion

The suspension of selection for weaning weight among the three lines of Merino sheep resulted in a changed response in comparison to responses prior to the suspension of selection. The direct genetic responses, calculated annually or on a per generation basis, were significantly lower compared to those of previously published estimates. Correlated

responses of other lamb and hogget traits showed similar trends. Although, the realised heritability and realised correlated response were in agreement with the findings in the later part of the selection experiment of previously published estimates, the result were significantly lower than the findings at the first stage of the selection experiment.

The decline in genetic responses could be attributed to the effect of the suspension of selection that may have caused the regression of the selection lines towards the base population. A more possible explanation is that the decreasing response could also be due to the selection lines approaching selection limits, which results in a gradual decrease of response due to the exhaustion of genetic variance or the fixation of the alleles affecting the trait.

Chapter 6

General discussion and implications for the small ruminant industry in the Philippines

6.1 General discussion

Sheep are a very important source of meat and wool and consequently sheep producers have practiced selection for the improvement of both growth rates and wool weights for many decades. Specifically, they aim to produce fast growing animals with high quality saleable tender meat and also to increase clean fleece weight and other wool components. These wool components which can influence clean price includes fibre diameter, staple length and strength, colour and style.

The present study involved three lines of Australian Merino sheep previously selected for high and low weaning weights. The genotypes were evaluated for the traits of economic importance for sheep production. The evaluation of lambs and hoggets was based on growth traits and wool weights based on the response, direct and correlated, when selection for high and low weaning weight was suspended after thirty years of selection. The genotypes were also evaluated for their growth and wool performance at two locations, and phenotypic and genetic parameters were determined with emphasis on the importance and influence of maternal effects.

Maternal effects are of great importance for growth traits. Bradford (1972) suggested that maternal influence is reported to be more pronounced in sheep than in cattle

or swine. This is attributed to the greater relative variation in litter size in sheep and the larger proportion of the sale weight that is dependent on the dam's mothering ability and milk production. The result of the study showed that for body weights, birth weight has a moderate estimate of maternal heritability, but the value decreased as the animal aged. Maternal effects on wool traits were very minimal. Similarly, the permanent maternal environmental effect decreases with age for body weights, and has small effects on wool traits. Direct additive and maternal correlation for body weights was found to be low and positive and was low and negative for wool traits.

The result is in total agreement with previously published estimates, which confirms the importance of maternal effects. Meyer (1994) suggested that selection schemes aimed at improving growth need to account for both direct and maternal genetic effects in order to achieve optimum genetic progress. Mortimer (1996 – personal communication) further added that ignoring genetic and environmental effects in the prediction of selection responses when these effects actually influence a trait could result in substantial prediction errors. In the present study, only one model was used with six co-variances fitted; residual variance, direct additive variance, maternal additive variance, direct-maternal additive co-variance, permanent environmental variance and temporary environmental variance. The single model, fitted due to limited time, served its purpose in determining the influence of maternal effects. However, a more improved and concrete prediction of maternal effects could be realised if more models were fitted. Meyer (1992) fitted a sequence of six models to estimate variance components and assessed their significance. The models allowed for both maternal effects as a direct-maternal genetic covariance. The increase in log likelihood as each effect was added to the model was used to assess the importance of that effect in the model for a trait in a test of significance. To establish which model best fitted the data; the models were fitted sequentially.

The genotype effect is dependent on the environment or the production system. Genotype x environment interaction explores the potential for maximum performance of a genotype in a particular environment. In this study, locations provided different environments with a number of genotype x location interactions being significant for lamb traits. This shows the differential response of the three lines of Merino to the environment in two locations. However, since no change in ranking was observed, one could conclude

that variations between locations were not so great to result to rank changes. Significant location x year interactions also indicated the presence of large yearly fluctuations in environmental factors in the two locations.

The significant differences of performance for growth rates and wool traits of the three lines after the suspension of selection have a great implication to selection experiments. It indicated that even after two or more generations after the suspension of selection, with replacement rams and ewes randomly chosen from each line, its effect did not greatly alter the performance of the lines, with the Weight Plus line still performing better than the Random and Weight Minus lines for most traits. Effects, which could have change responses in the lines, appear not to have been operating greatly during the limited period of the study.

When compared to responses when selection was being implemented, the suspension of selection for weaning weight among the lines resulted to a significantly reduced response. The realised heritability of 0.17 ± 0.01 obtained from the divergence of the Weight Plus and Weight Minus lines is in close agreement with estimates of Davis (1987) in the later periods of the experiment, but lower during the first period of the experiment when selection for weaning weight was being implemented. Correlated responses of other lamb and hogget traits showed similar results. The decline in genetic response could be attributed to the effect of the suspension, which have caused a regression of the selection lines towards the base population.

6.2 Implication for the small ruminant industry in the Philippines

The Philippines is an archipelago of over 7,100 islands and islets of which only 12% are permanently inhabited. The total area of this beautiful country is 299,000 square kilometres with a population of 70 million inhabitants. The Philippines is divided into three geographical areas, Luzon, Visayas, and Mindanao. Luzon is the major northern island, where Manila, the capital city is located. The Visayas, in the central part is a cluster of islands, and Mindanao; the second largest island is in the southern part of the archipelago. The climate is tropical: hot and humid. The average year-round temperature at sea level is 32 degrees Celsius. There are two distinct seasons: rainy season is from June through November and the dry season is from March through May with dry, unpleasantly hot weather.

The agriculture sector is a major contributor to the Philippine economy. Of the total land area, 30% is devoted to agriculture and 42% of the human population is employed in agriculture. The sector contributes a 20% share in the export earnings. Moreover, the country has a large agricultural base that grows at an average of 3.2% annually.

The livestock industry within the agricultural sector contributes about 28% to income. There has been a pattern of sustained growth in the development of livestock products brought about by the 2.3% per annum increase in human population. The livestock industry is characterised by developing pig and poultry industry and a poorly developed ruminant sector. The Philippines livestock industry has basically remained a backyard enterprise. Despite the entry of multinational firms into the country, employing high-technology practices, backyard raising of animals continued to be the backbone of the industry with more than 90% of the major livestock species in the backyard of the farmers. In 1998, the population of the ruminant animals were as follows: 3.02 million carabao, 2.32 million cattle (including 11,000 dairy cattle), 3.083 million goat and 26,500 sheep.

The small ruminant sector of the Philippines animal industries is an emerging industry. It has become a conspicuous enterprise in some regions especially in Mindanao, the second largest island in the southern part of the country. Goat has established itself as

a good source of meat and milk. For the past five years, the goat inventory has increased from 2.6 to 3.1 millions during the first half of 1998. On the other hand, imported lamb and mutton are complementing the value of local sheep production. Sheep raising offers good prospect and opportunities particularly for small-and medium-scale farmers who have very limited farmland areas. However, raising of sheep needs to be further promoted among small hold farmers, as its population is very low. In 1987, a total of 7,308 head of sheep was reported and in 1998, the number of head has increased to 26,500.

There are four production systems employed in the small ruminant farming. These include the following;

1. Tethering - This is traditional and the most common method among backyard raisers. Farmers tie their animals with a rope about five meters long in areas where vegetation abound with the animals staying in the particular grazing area the whole day. They are transferred once or twice to other areas where more native forage crops are available. Animals are usually tethered by women and children.
2. Extensive production - Herds of sheep and goat under the extensive management system are allowed to graze freely in communal areas, empty paddy fields, or vegetable areas after harvest.
3. Semi-intensive or partial grazing – Animals are allowed to graze in communal grazing areas or under plantations for at least four hours. Then the animals are herded back to the stall or barn and given forage or crop residues.
4. Intensive production system - This system is characterized by the complete confinement of animals in elevated stall and feeding of cultivated forage crops. Commercial farms, research and development institutions, and government stock farms adopt this system of production.

In 1977, the Department of Agriculture of the Philippines established the National Genetic Improvement Program for Livestock. An essential ingredient of the modern program is a modern genetic evaluation system, which can be applied to all ruminant species. Specific for the sheep and goat sector, a Small Ruminant Genetic Improvement Program was also established. The program hopes to improve productivity and efficiency of the appropriate breeds of small ruminants through an organised breeding program.

Specifically, it aims to develop and establish breed performance standards in the Philippines. Over 2,000 purebred sheep and goats were imported from the U.S. for the project. These include the breeds Rambouillet, Merino, St. Croix, Border Leicester and Katahdin. The animals are now raised in 17 nucleus farms located in various regions of the country. All progeny will be performance recorded and data submitted for analysis. Apart from improving the pure lines under Philippine conditions, various crossbreds will be evaluated and suitable crossbreds increased in numbers in multiplier farms before being released to village farms.

The implications of the present study can be linked to the ruminant industry of the Philippines, in particular to the small ruminant sector. The genotype differences and genotype x environment interactions will provide a guide to the development of a viable, sustainable and efficient small ruminant production. With the present program of importation of breeds of sheep from the United States and other countries, it is expected that genotype x environment interaction will occur due to considerable variation in climate. The imported animals may be the best and perform optimally in their original environment, but under Philippine climatic conditions may not perform as well as expected. Therefore, there is a need to evaluate their adaptability and performance under a variety of climatic conditions.

Environmental variations could involve systems of management and feed quantity and quality, where genotype and environment interactions are more likely to exist. Evaluations of the new imported breeds are being made in government operated livestock farms where the animals are expected to perform better due to good management practices and higher feed quality and availability. Therefore, the results obtained on government livestock farms cannot be directly implemented on other farms due to poorer management practices and problems in feed supply and quality. This considerable environmental variations would further be magnified when these animals are dispersed to the backyard farmers, which comprise 90% of the industry. Significant and real genotype x environment interactions may be observed and result in the changes in rankings of the genotypes. Therefore, there is a need to evaluate the genotypes x environment interactions for growth rate, carcass characteristics, reproductive performance, feed efficiency and overall productivity before these are dispersed to the backyard raisers. There will also be

a need to improve the feed resources because of higher feed requirement of imported purebreds and crossbreeds.

The Philippine government has a well-established plan for genetic improvement of ruminant species. However, this has remained a plan and not much has been done in practice. In the Philippines, estimates of genetic and phenotypic parameters for indigenous breeds, crossbreeds and even purebreds are lacking, if not totally absent. This is true even in government run-livestock farms which has been existing for long period of years. No government farms are measuring the estimated breeding values (EBV's), fixed effects and genetic and environmental trends and are breeding animals mainly on their phenotypic traits. These estimates, which have been calculated in the present study, are essential for the genetic improvement of the ruminant livestock production in order to increase the productivity and profitability.

In the Philippine situation, the majority (over 90%) of ruminant species (beef cattle, dairy cattle, goats and sheep) are raised by smallholders or backyard raisers. Genetic improvement by selection within these farms seems impossible due of the limited number of stock on each farm. To sustain the long-term livelihood of small holders, it is essential for the government and other development agencies to initiate research into estimation of genetic parameters for traits of production and reproduction using data from institutional farms. Of more importance is the establishment of nucleus and multiplier farms where a continuous genetic evaluation program is implemented and allow this genetic improvement to flow down to the backyard or small holder herds and flocks. Systematic record keeping, techniques to gather, traits of adaptation and disease and parasites resistance should be instituted and are very essential for future genetic parameter estimation and the prediction of superior genotypes.

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LIST OF APPENDECIS

Appendix 1. Observed weaning weights, and standard errors of Weight Plus, Random and Weight Minus lines

Year	Weight Plus		Random		Weight Minus	
	Mean	s.e.	Mean	s.e.	Mean	s.e.
1983	23.77	0.71	19.21	0.42	16.65	0.90
1984	22.92	0.54	18.13	0.44	15.26	0.84
1985	25.68	0.46	20.85	0.29	16.09	0.81
1986	23.86	0.56	19.74	0.27	15.89	0.62
1987	24.00	0.39	18.89	0.29	16.09	0.53
1988	18.16	0.38	14.24	0.29	13.09	1.10
1989	24.93	0.62	19.63	0.29	16.54	0.84
1990	21.42	0.49	21.36	0.30	15.52	0.50
1991	21.95	0.61	21.11	0.40	14.47	0.69
1992	23.16	0.58	19.70	0.36	17.57	0.59

Appendix 2. Selection differential of the Weight Plus, Random and Weight Minus lines

Year	Divergent	Random	Weight Minus
83	22.83	-1.22	-16.89
84	22.42	-0.46	-17.35
85	22.87	-0.58	-16.54
86	22.11	0.12	-16.07
87	22.59	-0.16	-15.7
88	23.50	-0.59	-16.55
89	22.85	0.43	-16.56
90	23.62	-1.32	-16.45
91	22.75	1.55	-17.88
92	23.53	-1.66	-16.34

Appendix 3. Estimated breeding values of Weight Plus, Random and Weight Minus lines

Year	Weight Plus	Random	Weight Minus
51	-1.399	0.299	0.673
53	0.937	0.389	-0.481
54	1.094	0.480	-0.182
55	2.201	1.500	-1.085
56	2.125	1.569	-1.320
57	2.365	1.772	-1.911
58	2.207	1.047	0.017
59	4.424	1.196	-3.687
60	5.818	0.694	-1.155
61	5.372	0.350	-4.242
62	7.672	1.877	-2.650
63	5.606	0.372	-5.060
64	8.538	1.415	-3.867
65	6.067	0.918	-5.352
68	6.886	-0.572	-5.664
69	6.654	-0.021	-5.488
71	5.286	-0.210	-5.448
73	2.387	-0.336	-1.939
74	2.847	0.305	-2.173
75	4.546	-0.043	-2.519
76	3.802	0.428	-3.088
77	5.196	-0.234	-2.793
78	3.648	0.041	-2.628
79	5.065	0.564	-3.690
80	4.402	0.204	-3.066
81	5.056	0.421	-3.214
82	4.861	0.538	-3.047
83	5.113	0.082	-2.824
84	4.598	0.550	-2.788
85	4.676	0.384	-2.804
86	3.916	0.705	-2.488
87	5.263	0.601	-1.731
88	3.427	0.819	-2.746
89	6.822	-0.032	-0.953
90	4.682	1.216	-1.948

91	5.117	1.856	-1.786
92	5.183	0.076	-1.313

Appendix 4. Abstract of the paper presented to the 6th World Congress on Genetics Applied to Livestock Production held at the University of New England, Armidale, NSW, Australia last January 11-16, 1998

RESPONSES OF LINES OF MERINO SHEEP SELECTED ON WEANING WEIGHT AFTER THE SUSPENSION OF SELECTION

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Lines previously selected for high and low weaning weight were different in lamb and hogget production traits following the suspension of selection. The Weight Plus lambs were heavier at birth and at weaning, grew faster to weaning and had lower birthcoat scores than Random lambs. The Weight Minus lambs, on the other hand, were significantly inferior to the Random lambs. For hogget production traits, the Random line performed significantly better in greasy, clean and skirted fleece weights than the lines selected for high and low weaning weights. The Weight Plus hoggets, however, had the heaviest body weight and finest wool fibre. The realised correlated responses showed that selection for high weaning weight resulted in increases in lamb and hogget production traits except for birthcoat score and fibre diameter. Environmental factors such as sex, birth/birth-rearing types, year and age of dam were significant influences on lamb and hogget production traits.

Appendix 5. Abstract of the paper presented to the 13th Association for the Advancement of Animal Breeding and Genetics held at Hotel Atrium, Mandurah, Western Australia on July 4 – 7, 1999

GENOTYPE X ENVIRONMENT INTERACTIONS FOR LAMB TRAITS OF MERINO SHEEP

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Lines of Australian Merino sheep previously selected for high and low weaning weight and a randomly selected control line were compared for a five-year period in two locations in Trangie and Armidale. The Weight Plus lambs were heavier at birth and at weaning and grew faster to weaning than the Weight Minus and Random lambs. Random lambs were superior to the selection lines for birthcoat score and in all traits to the Weight Minus lambs. Lambs raised at Trangie were superior to the lambs raised in Armidale while year effects showed significant influence for all traits. Significant line x location interactions were evident for birth weight, growth rate and weaning weight but involved no rank changes. Location x year interactions were large and highly significant for birth weight, birthcoat score, growth rate and weaning weight while line x year interactions were significant only for birth weight and birthcoat score. The second order interactions of line x location x year were significant for birth and weaning weight and growth rate.