GENETIC ANALYSES OF SOUTH AFRICAN TERMINAL SIRE SHEEP BREEDS

by

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Thesis presented in partial fulfilment of the requirements for the degree of Master of Science in Agriculture (Animal Sciences)

at

Stellenbosch University

Faculty of AgriSciences

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Date: *March 2009*

DECLARATION

By submitting this thesis electronically, I declare that the entirety of the work contained is my own, original work, and that I have not previously in its entirety or in part submitted it for obtaining any qualification.

Date…………………………………………

Abstract

Genetic analyses of South African terminal sire sheep breeds

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Fluctuations and a general decline in the ratio between wool and meat prices resulted in marked changes in the South African sheep industry. Commercial producers now exploit other mechanisms such as terminal crossbreeding of Merino-type with meat type breeds or dual-purpose breeds to attain short-term benefits resulting from price fluctuations between wool and mutton without compromising the wool-producing capacities of ewe flocks. Most components of lamb production have low heritability. However, heterosis can be achieved by mating wool-type breeds with specialist meat breed rams. Genetic improvement of livestock depends on defining breeding objectives, estimation of genetic parameters and accurately identifying the right animals to be used for future breeding. Genetic parameters for traits of economic importance in terminal sire sheep breeds that could be used on Merino-type ewes in commercial operations in South Africa had not been published for the national flock apart from a preliminary study having been conducted by Olivier *et al*. (2004). Selection objectives were poorly defined due to lack of parameter estimates for variance and covariance components. Against this background, this study obtained pedigree information and live weight data from the National Small Stock Improvement Scheme for the Dormer, Ile de France and Merino Landsheep and estimated non-genetic factors and genetic parameters influencing early growth traits. Genetic and phenotypic trends for early growth traits were constructed for the three breeds to monitor genetic progress.

Non-genetic factors influencing early growth traits in the Dormer, Ile de France and Merino Landsheep were estimated using data obtained from the National Small Stock Improvement Scheme of South Africa. The original data sets for the Dormer, Ile de France and Merino Landsheep consisted of the following number of records respectively: 52 202, 35 553 and 7 772. However, pre-weaning weights were available for the Ile de France and Merino Landsheep breeds only and post-weaning weights were available only for the Dormer breed. The data sets were complicated to such an extent that smaller data sets had to be generated to analyse for fixed effects. The traits that were analysed were birth weight, pre-weaning weight, weaning weight and post-weaning weight. The fixed effects, identified as having a significant effect ($P < 0.01$) on early growth traits were sex of lamb, birth type, age of dam, contemporary groups, age at which the trait was recorded and month of birth and year of birth in the Merino Landsheep breed. Although some significant interactions were found, they were subsequently ignored owing to their very small effects. In all three breeds, male lambs were significantly ($P < 0.001$) heavier than female lambs and single-borne lambs were significantly heavier at birth than multiple borne lambs. The age of dam had a significant curvilinear regression on all early growth traits in all three terminal sire sheep breeds. It was concluded from the study that the influence of non-genetic factors on early growth traits should be adjusted for or eliminated statistically in genetic evaluations to get accurate genetic parameter estimations.

(Co)variance estimates for birth weight, weaning weight and post-weaning weight were obtained for the Dormer breed using restricted maximum likelihood procedures (REML). Direct heritabilities (h^2) in single-trait analyses were 0.21 ± 0.03, 0.23 ± 0.02 and 0.29 ± 0.05 for birth weight, weaning weight and post-weaning weight, respectively. Direct heritabilities of 0.28 ± 0.04, 0.55 ± 0.06 and 0.32 ± 0.02 for birth weight, weaning weight and post-weaning weight respectively were obtained using three-trait analysis. Direct maternal genetic effects (m^2) were excluded from the analyses because of the failure to partition maternal effects into maternal genetic and maternal permanent environmental effects (m^2 and c^2). This culminated as a consequence of poor data and population structures emanating from the loss of genetic links across flocks due to the random entrance and exit of flocks from the recording scheme. Maternal permanent environment was estimated at 0.15 ± 0.02, 0.13 ± 0.02 and 0.20 ± 0.03 for birth weight, weaning weight and post-weaning weight respectively using single-trait analysis. The correlation between direct effects and maternal effects (r_{am}) was excluded from the analyses due the structure of the data. Genetic, phenotypic and environmental correlations between early growth traits were low to moderate. The medium to high heritability estimates for early growth traits obtained in the study led to the conclusion that Dormer sheep can successfully be used in terminal crossbreeding programs to improve meat production characteristics.

Direct heritability estimates were 0.31 ± 0.14, 0.09 ± 0.02 and 0.14 ± 0.003 for birth weight, pre-weaning weight and weaning weight respectively using single-trait analysis for the Ile de France breed. Maternal effects were significant for all the traits studied despite the failure to properly partition them into their components due to the loss of genetic linkages across generations emanating from poor data structure. Genetic, phenotypic and environmental correlations were estimated using three-trait analysis and were found to be low to moderate for early growth traits. Direct genetic and maternal permanent environmental ratios were also computed and they did not differ much from the results obtained using single-trait analyses. The reasonable genetic parameter estimates obtained in the study led to the conclusion that the Ile de France can be selected to use as sires in crossbreeding programs.

Genetic parameters were estimated for early growth traits in the Merino Landsheep breed. REML estimates of birth weight, pre-weaning weight and weaning weight were obtained using animal models in single-trait analyses. The direct heritability estimate for birth weight was 0.23 ± 0.13 using an animal model with additive direct genetic effects and dam permanent environmental effects as the only random factors. The dam permanent environmental effect for birth weight amounted to 0.10 ± 0.07. Direct heritability for pre-weaning weight was 0.36 ± 0.05 and the dam permanent environmental effect 0.56 ± 0.03. Weaning weight was estimated using an animal model that contained direct additive effects and dam permanent environmental effects. The direct heritability estimate for weaning weight was 0.17 ± 0.03. Maternal genetic effects were estimated to be 0.02 ± 0.01.

Genetic and phenotypic trends were constructed for early growth traits in the Dormer, Ile de France and Merino Landsheep breeds. The traits that were considered were birth weight, pre-weaning weight, weaning weight and post-weaning weight. However, pre-weaning weights were available for the Ile de France and Merino Landsheep breeds only and post-weaning weights were available only for the Dormer breed. The Dormer exhibited significant improvement in the phenotypic and genetic aspects of early growth traits during the 17 years of evaluation (1990-2007). The average predicted direct breeding values of birth weight decreased by 0.055 % during the evaluation period. The predicted direct breeding value for weaning weight increased by 0.12 % during the 17 year period. Post-weaning weight improved by 0.32 % per annum. The Ile de France registered an increase in the predicted breeding value of birth weight which amounted to 0.025 % per annum. Averaged direct breeding values for pre-weaning weight increased at an annual rate of 0.23 %. and that of weaning weight increased by 1.21 %. In the Merino Landsheep the predicted direct breeding value for birth weights decreased by 0.04 % per annum and pre-weaning and weaning weights increased by 0.36 % and 0.10 % respectively. The trends were obviously biased due to inconsistencies in data structure and very few records available for analysis in this breed.

In conclusion, it was evident that the additive genetic variation was available for all the early growth traits in all the three breeds. Although adequate genetic variation for substantial genetic progress was available, only modest rates of progress were attained for all the traits in all three breeds. The only possible exception was weaning weight in the Ile de France breed, which improved at > 1 % per annum. At least all changes were in the desired direction. Breeders should be encouraged to record data consistently, as one of the major shortcomings in the data for all breeds were a lack of continuity in the submission of data to the NSIS. More informative analyses ought to be feasible if this requisite could be met.

Opsomming

Genetiese analise van die verskillende Suid-Afrikaanse terminale kruisvaarrasse

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Die wisselende en algemene afname in die prysverhouding van wol tot vleis het merkbare veranderinge in die Suid-Afrikaanse skaapbedryf teweeggebring. Kommersïele produsente maak nou gebruik van ander metodes soos terminale kruisteling van Merino-tipe ooie met vleis tipe vaars of dubbel-doel rasse om korttermynvoordele uit die wisselende wol en vleis pryse te behaal, sonder om die wol-produksie potensiaal van die ooi-kudde te benadeel. Die meeste van die lamproduksie eienskappe het ‘n lae oorerflikheid. Nietemin, kan heterose wel behaal word deur die kruisteling van wol-tipe rasse met spesialis vleisramme. Genetiese verbetering van vee is afhanklik van die beskrywing van die teeltdoelwitte, die akkurate beraming van genetiese parameters en die noukeurige identifikasie van die geskikste diere vir toekomstige teling. Genetiese parameters vir ekonomies belangrike eienskappe van terminale ramrasse wat gebruik kan word op Merino-tipe ooie in die kommersiële skaapbedryf in Suid-Afrika is nog nie gepubliseer vir die nasionale kudde nie, behalwe vir ‘n voorlopige studie wat gedoen is deur Olivier *et al.* (2004). Seleksiedoelwitte is nie duidelik beskryf nie a.g.v ‘n tekort aan akkurate parameterberamings vir (ko)variansie komponente. Hierdie studie het dus stamboominligting en lewende gewig data verkry vanaf die Nasionele Kleinveeverbeteringsskema vir die Dormer-, Ile de France- en die Merino landskaaprasse en nie-genetiese faktore sowel genetiese parameters vir vroeë lamgewigte beraam. Genetiese en fenotipiese tendense vir vroeë lamgewigte is vervolgens opgestel vir drie rasse om genetiese vordering te evalueer.

Die oorspronklike datastelle vir die Dormer, Ile de France en die Merino Landskaap het uit die volgende aantal rekords bestaan, onderskeidelik: 52 202, 35 553 en 7 772. Voor-speen gewigte was net beskikbaar vir die Ile de France- en die Merino Landskaaprasse, en na-speen gewigte was net beskikbaar vir die Dormerras. Die beperkings in die datastelle het genoodsaak dat dat kleiner datastelle ontwikkel moes word om die vaste effekte te analiseer. Die eienskappe wat ge-analiseer was, was geboortegewig, voor-speengewig, speengewig en na-speengewig. Die vaste effekte wat vroeë lamgewigte betekenisvol ($P < 0.01$) beïnvloed het, was geslag van die lam, geboortestatus, ouderdom van die ooi, kontemporêre groep, die ouderdom waarop die eienskap aangeteken is en (in sommige gevalle) die maand en jaar van geboorte. Alhoewel daar sommige betekenisvolle interaksies was, is dit nie in die finale modelle ingesluit nie, omdat dit min tot die verklaarde variasie bygedra het.

In al die rasse het ramlammers swaarder ($P < 0.001$) geweeg as ooilammers. Enkelinge was ook swaarder ($P<0.001$) as meerlinge. Die ouderdom van die moer van die lam het ‘n beduidende kromlynige invloed op alle vroeë lamgewigte by al drie terminale ramrasse gehad. Die gevolgtrekking van hierdie studie is dat die invloed van nie-genetiese faktore op vroeë lamgewigte in ag geneem moet word, of dat dit moet statisies elimineer word in die genetiese evaluasie om akkurate genetiese beramings te verkry.

(Ko)variansie beramings vir geboortegewig, speengewig en na-speengewig is deur gebruik te maak van die “restricted maximum likelihood procedures” (REML) vir die Dormerras verkry. Die direkte oorerflikheid (h^2) wat verkry was deur die mees geskikste diere model in ‘n enkel-eienskap analise te gebruik was onderskeidelik 0.21 ±0.02, 0.23 ±0.02 en 0.29± 0.05 vir geboortegewig, speengewig en na-speengewig. Direkte ooreenstemende oorerflikheid wat uit die drie-eienskap analise was 0.28±0.04, 0.55±0.06 en 0.32±0.02 onderskeidelik vir geboortegewig, speengewig en na-speengewig. Direkte maternale genetiese effekte (m^2) is uitgesluit vanaf die analise weens die onvermoë om die maternale effekte te verdeel in maternale genetiese effekte en maternale permanente omgewings effekte (m^2 en c^2). Dit was a.g.v onvolledige data en populasiestrukture wat gelei het tot die gebrek in genetiese bande oor kuddes, wat ontstaan het weens kuddes wat slegs tydelik data tot die skema bygedra het. Maternale permanente omgewingeffekte is geskat op onderskeidelik 0.15±0.02, 0.13±0.02 en 0.20±0.03 vir geboortegewig, speengewig en na-speengewig met die gebruik van die enkel-eienskap analise. Die korrelasie tussen direkte effekte en maternale effekte (r_{am}) is uitgesluit a.g.v die gebrekkige struktuur van die data. Genetiese-, fenotipiese- en omgewingskorrelasies tussen die vroeë lamgewigte was laag tot matig. Die matige tot hoë oorerflikheidberamings vir vroeë lamgewigte uit hierdie studie het gelei tot die gevolgtrekking dat Dormer skape suksesvol gebruik kan word in terminale kruisteel programme om vleisproduksie te verbeter.

Direkte oorerflikheid skattings was 0.31±0.14, 0.09±0.02 en 0.14±0.003 vir die geboorte gewig, voor-speen gewig en speen gewig onderskeidelik met die gebruik van ‘n enkel-faktor analise vir dir Ile de France skaap ras. Maternale effekte was beduidend vir al die eienskappe wat bestudeer was , ten spyte van die onvermoë om dit behoorlik te verdeel in hul komponente weens die verlies van genetiese bande dwarsoor die generasies wat uitvloei vanaf ‘n swak data struktuur. Genetiese, fenotipiese en omgewings korrelasies was geskat deur gebruik te maak van ‘n drie-faktor analise en was gevind om laag tot matig te wees vir die vroeë groei eienskappe. Direkte genetiese en maternale permanente omgewings ratios was bereken en dit het nie veel verskil van die resultate verkry deur die enkel-faktor analise. Die aanvaarbare genetiese parameter skattings verkry in hierdie studie het gelei tot die gevolgtrekking dat die Ile de France geselekteer kan word as teelramme in kruisteel programme.

Genetiese parameters was geskat vir vroeë groei eienskappe in die Merino Landskaa ras. REML skattings van geboorte gewig, voor-speen gewig en speen gewig was verkry deur diere modelle in enkel-faktor analises. Die direkte oorerflikheid skatting vir geboorte gewig was 0.23±0.13 met die gebruik van die diere model met additiewe direkte genetiese effekte en ooi permanente omgewings faktore as die enigste ewekansige faktore. Die ooi permanente omewings effek vir geboorte gewig was 0.10±0.07.

Direkte oorerflikheid vir voor-speen gewig was 0.36±0.05 en die ooi permanente omgewings effek 0.56±0.03. Speen gewig was geskat deur die gebruik van ‘n diere model wat die direkte additiewe effekte en die ooi permanente omgewings effekte bevat het. Die direkte oorerflikheids skatting vir speen gewig was 0.17±0.03. Maternale genetiese effekte was geskat as 0.02±0.01.

Genetiese en fenotipiese tendense is verkry vir vroeë lamgewigte in die Dormer-, Ile de France- en Merino Landskaaprasse. Die eienskappe wat oorweeg is, was geboortegewig, voor-speengewig, speengewig en na-speengewig. Voor-speengewigte was net beskikbaar was vir die Ile de France- en die Merino Landskaap rasse en die na-speense gewigte net vir die Dormerras. Die Dormer het beduidende verbetering vertoon in die fenotipiese en genetiese aspekte vir vroeë lamgewigte gedurende die 17 jaar van evaluasie (1990-2007). Die gemiddelde voorspelde direkte teeltwaarde van speen gewig het met 0.12% per jaar gestyg gedurende die 17-jaar periode. Na-speen gewig het met 0.32% per jaar verbeter. By die Ile de France het ‘n toename in die voorspelde teelwaarde van geboortegewig (0.025% per jaar) voorgekom. Gemiddelde direkte teelwaardes vir voor-speengewig het toegeneem teen ‘n jaarlikse tempo van 0.23% en speengewig het met 1.21% per jaar toegeneem. In die Merino Landskaapras het die voorspelde direkte teelwaarde vir geboortegewig met 0.04% per jaar gedaal, terwyl voor-speen- en speengewigte met 0.36% en 0.10% onderskeidelik toegeneem het. Die tendense was ooglopend gekompromiteer weens probleme met die data struktuur, en a.g.v van die relatief min rekords wat beskikbaar was vir die analise in die ras.

Dit was duidelik dat die additiewe genetiese variasie beskikbaar was vir al die vroeë groei eienskappe in al die drie rasse. Alhoewel voldoende genetiese variasie vir wesentlike genetiese vordering beskikbaar was, is daar slegs matige vordering verkry vir al die eienskappe in al drie rasse. Die enigste moontlike uitsondering was speengewig in die Ile de France ras, wat met 1.21 % per jaar gestyg het. Alle veranderinge was minstens in die gewensde rigting. Telers word versoek om data deurlopend en akkuraat aan te teken , aangesien een van die groot tekortkominge met die data van al die rasse ‘n tekort aan deurlopendheid in die indiening van die data aan die NISS was. ‘n Meer verteenwoordigende analise sal uitvoerbaar wees, as daar aan al die bogenoemde aanbeveling voldoen kan word.

DEDICATION

This work is dedicated to my orthopaedic surgeon **Dr Maxwell Fungai Gova** whose hands and expertise the Lord used to bring me back to life and made it possible for me to walk and also use my hands again.

ACKNOWLEDGEMENTS

First and foremost I thank our Lord and saviour, **Jesus Christ**, who has enabled me to accomplish this study.

My most sincere gratitude to:

Professor S.W.P. Cloete: for facilitating this study, being the study leader, his fatherly support, his motivation and guidance throughout the study and above all being my main mentor.

Professor K. Dzama: for facilitating my enrolment for postgraduate studies, being a co-study leader, providing motivation, guidance and encouragement during the course of my studies.

Dr. J.J. Olivier: for being a co-study leader, the kind permission to use the data, his constructive comments and teaching me to think.

The Western Cape Animal Production Research Trust: for funding my studies and catering for all my needs.

The Technology and Human Resources for Industry Program (THRIP) of South Africa: for their financial contributions.

The National Small Stock Improvement Scheme: for kind permission to use the data.

The Western Cape Department of Agriculture: for usage of their facilities.

All Colleagues in the Institute of Animal Production: for loving me, caring for me and creating an atmosphere conducive to study.

My late father: Onesimo Joseph Zishiri: for granting me the opportunity to learn, always motivating and believing in me, for all the love and support until he went to be with the Lord whilst I was in the middle of this study and for always visiting me everyday during several months of hospitalization especially during the periods before long surgeries.

My mother: Chiedza Barbara Zishiri: for loving me and always being there for me.

My sister Lettie: for loving me and dressing my wounds everyday during my recovery period.

My sister Irene: for the financial support in order to commence these studies and also for the love.

My sister Afra: for loving me, feeding me when I could not use my hands and sourcing the foreign currency which enabled me to commence these studies.

My brother Edwin: for encouragement and support in numerous ways.

My brother Vincent: for being a friend for life.

My sister Fiona: for teaching me to be careful.

Chiedza (Jr): for love and motivation.

Virginiah Nyika: for being nice and supportive.

Mr and Mrs Chokuda: for their unwavering support and love ever since I relocated to South Africa.

All the staff in Avenues Clinic: for taking care of me for several months until I recovered.

The Anesthetist: Dr Masara: for monitoring me during all surgeries.

Theatre Nurse: Sister Vuma: for doing a good job and always making me smile.

To all my Christian friends for their prayers and supplications.

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Chapter 1

GENERAL INTRODUCTION

Approximately 80% of agricultural land in South Africa is mainly suitable for extensive livestock production (National Department of Agriculture, 2003). Sheep and goat farming occupies about 590 000 square kilometers which represents almost 53% of all agricultural land in the country. Small stock production takes place in the vast Karoo areas of the Northern and Western Cape Provinces and the mixed veld types of the Eastern Cape and the Southern Free State and has an overall gross turnover of approximately R 3.5 billion nationwide (Campher *et al*., 1998). Commercial sheep farms are also found in other areas such as the Kalahari, the winter rainfall areas, and the grasslands of Mpumalanga, eastern Free State and KwaZulu-Natal, where other farming enterprises such as cattle farming are also practiced.

Sheep are mainly kept for wool and meat production, and therefore the industry is represented by organizations from both the meat and wool industry. The sheep industry also has various breeder associations among others, the Dormer Sheep Breeders' Society, Dorper Sheep Breeders' Society, Ile de France Breeders' Society, Merino Landsheep Society, SA Mutton Merino Breeders' Society, Suffolk Sheep Breeders' Society and the Vandor Breeders' Society. The total number of sheep was estimated to be 29 million in 2003 (National Department of Agriculture, 2003).The most popular sheep breeds in South Africa are the Merino, Dohne Merino, SA Mutton Merino (SAMM) and the Dorper (Campher *et al*., 1998). Sheep breeding enterprises have to be dynamic in the rapidly changing macro-economic environment where there are always fluctuations in the meat: wool price ratio (Van Wyk *et al*., 2003). In order to effect changes to selection criteria to meet the ever-changing needs, accurate genetic parameter estimation for traits of economic importance is of cardinal vitality. Improved statistical methodology such as Restricted Maximum Likelihood (REML), advances in computer technology, hardware and software give animal breeders the capacity to re-evaluate genetic parameters to better define selection strategies for the modern market (Van Wyk *et al.*, 2003). The development of sophisticated computer software (Meyer, 1993; Groeneveld & Garcia-Cortes, 1998; Gilmour, 1999) has enabled estimation of additional variance components and/ or the partitioning of animal variance into direct and maternal effects, animal and dam permanent environmental effects, litter effects as well as the correlation between direct and maternal effects. Partitioning of the (co)variances enables the estimation of the contribution of each individual effect to the overall performance of the animal.

Genetic improvement of livestock depends on defining breeding objectives, estimation of genetic parameters and accurately identifying the right animals to be used for breeding. The South African government established the National Small Stock Improvement Scheme (NSIS) in 1964. The NSIS is currently managed by a division within the Agricultural Research Council (ARC). The NSIS serves as a basis for accurate recording of economically important traits in various sheep and goat breeds. Performance data combined with pedigree information are used to accurately identify animals of superior value free of the usual bias associated with visual appraisal (ARC, 2006). In South Africa, the genetic evaluation program for slaughter lamb production is not well structured. The NSIS captures data for a number of breeds, including terminal sire breeds with potential usage in commercial slaughter lamb production (Olivier *et al*., 2004). Analyses are conducted within breeds, comprising specialist wool breeds, dual-purpose breeds and specialist meat breeds. Since the inception of the NSIS, estimation of breeding values was based on individual measurements within contemporary groups. These comparisons still form part of all the schemes and serve as early indicators for more precise estimations. Breeders receive within flock and contemporary group performance indices for the different traits. Genetic evaluation of sheep in South Africa started in 1986 with the analyses of the experimental Merino flock at Klerefontein, near Carnarvon (ARC, 2006). This was followed by single flock evaluation as part of post-graduate studies and the evaluation of progeny groups of rams for the industry.

The aim of the NSIS is to genetically improve economic production traits in a “holistic” manner while breed standards are maintained (Olivier, 1993). This means that the perceptions of breeders have to be changed to focus on traits of monetary value to their clients. In spite of all these developments, genetic parameters for traits of economic importance in terminal sire breeds in South Africa have not been published for the national flock. Selection objectives are not directed to production, as indicated by a lack of direction in the genetic trends of all terminal sire sheep breeds (Olivier *et al.*, 2004). This indicates sub-optimal genetic progress in economically important traits, while selection decisions are based on factors not contributing to the overall breeding objectives such as visual assessment of stock.

Genetic change resulting from within-flock selection is comparatively slow, while it also takes time to filter through the structures of a breed (Cloete & Durand, 2000). Until recently, lamb (meat) has been a by-product of the wool industry. At present, 65-88 % of the total South African income from wooled sheep is derived from meat, contributions are even higher in the case of meat and dual-purpose sheep (Hoon *et al*., 2000). Commercial producers now exploit other mechanisms such as terminal crossbreeding of Merino-type ewes with meat type breeds or dual-purpose breeds in order to attain short term benefits resulting from price fluctuations between wool and meat without compromising the wool-producing capacities of ewe flocks. Against this background, the current study obtained pedigree information and live weight production data from the NSIS for the Ile de France, Dormer and Merino Landsheep breeds. These breeds are considered as the most important terminal sire sheep breeds used in South Africa. The primary goal of animal breeding is to genetically improve production and/or reproduction traits in animal populations, mainly through selection (Snyman & Olivier, 2002). To achieve this objective, knowledge of genetic parameter estimates is required to construct breeding plans.

1.1 Justification

Merino breeders in South Africa have traditionally selected animals for breeding predominantly on wool traits. With frequent fluctuations in the wool market, many Merino breeders are interested in producing a high quality Merino fleece on a large bodied Merino ewe, which can also be used for prime-lamb production. To achieve this requires knowledge of the heritabilities and genetic correlations for these traits. Despite preliminary studies on direct and maternal responses of early growth traits to selection by Olivier *et al*. (2004), genetic parameters for traits of economic importance in terminal sire sheep breeds that could be used on Merino-type ewes in commercial operations in South Africa have not been published for the national flock. Selection objectives are poorly defined due to lack of parameter estimates for variance and covariance components such as heritabilities and correlations among traits of economic importance. Genetic trends in all terminal sire breeds lack direction because of the absence of comprehensive and published genetic trends for traits of economic importance in the national terminal sire sheep flocks. This indicates sub-optimal genetic progress, while selection decisions are obviously based on factors not contributing to the overall economic breeding objectives.

1.2 Study objectives

The purpose of this study was to use recorded performance data of the Dormer, Ile de France and Merino Landsheep breeds from the NSIS database and estimate the following:

1. Non-genetic factors influencing birth weight, pre-weaning weight, weaning weight and post-weaning weight in the Dormer, Ile de France and Merino Landsheep breeds .

2. The genetic parameters i.e. direct heritabilities, additive maternal effects, dam permanent environmental effects, genetic and phenotypic correlations between birth weight, pre-weaning weight, weaning weight and post-weaning weight for the Dormer, Ile de France and Merino Landsheep breeds.

3. To obtain breeding values for birth weight, pre-weaning weight (where applicable), weaning weight and post-weaning weights using different models and derive genetic and phenotypic trends over the years in order to assess genetic progress over time per breed.

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Chapter 2

LITERATURE REVIEW

This literature review explores the concept of crossbreeding in commercial sheep production systems and the use of breed diversity to improve meat production systems. Historical backgrounds are provided for the Dormer, Ile de France and Merino Landsheep breeds. Evaluation of studies on the estimation of non-genetic factors and genetic parameters for growth traits (which are a precursor of meat production traits) are highlighted. Finally the significance of genotype by environmental interactions in across-flock genetic evaluation systems is visited briefly.

2.1 Crossbreeding in sheep production systems

Crossbreeding is a traditional practice that is used as a rapid, frugal and cost-effective tool to improve efficiency of meat production by mating ewes and rams of two or more pure breeds (Leymaster, 2002). The practical objective is to improve efficiency relative to the pure breed that performs best in a given production environment and marketing situation. The consequences of crossbreeding depend on the gene frequency differences among the breeds with the resulting increase of the heterozygotes in the cross and the degree of dominance (Willham, 1970). Rams of specialized sire breeds are mated to purebred, first cross, rotational, or composite ewes to produce terminally sired market lambs that express 100% of lamb heterosis (Nitter, 1978). Terminal crossbreeding takes advantage of breed diversity, heterosis, sexual dimorphism and complementarity.

Specialized sire breeds focus on growth and carcass traits. The genetic merit of terminally-sired lambs is thus different from other replacement and market lambs produced within a system. Terminal crossbreeding is more complex to manage than general-purpose crossbreeding systems because an additional flock (ewes mated to the specialized sired breed) is present. However, terminal crossbreeding systems have powerful genetic advantages such as the greater use of lamb heterosis, complementarily and sexual dimorphism (Leymaster, 2002).

Crossbreeding to exploit heterosis has been practiced for a long time with livestock (Restage *et al.,* 1982). However, much of the effort directed at commercial crossbreeding of sheep has been haphazard. A specific three-breed crossing system utilizing crossbred dams and meat-type sire breeds should result in nearly maximum performance (Dickerson, 1969). Information on combining ability, as well as maternal and individual heterosis is needed to make the proper choice of breeds employed in a crossbreeding system. If crossbreeding is the mating plan chosen, one needs to have a good assessment of the available breeds to know which breeds excel for specific traits. The information is then planned into the mating program so that each breed is used in the specific niche in the total breeding programme where it will make the greatest contribution (Fitch, 1990). Against this background, this study evaluated important terminal sire sheep breeds in South Africa.

2.1.1 Heterosis

Heterosis is defined as the average performance of crossbred sheep relative to the average performance of purebred breeds that produced the cross (Nitter, 1978). Effects of heterosis have the potential to enhance the productivity of crossbred sheep. When breeds are crossed, new combinations of gene forms are created in the crossbred sheep. Therefore, crossbred sheep have increased heterozygosity relative to those breeds that produced the cross. The increase in heterozygosity is the basis for heterosis or hybrid vigour. Lamb or direct heterosis represents the performance of crossbred lambs raised by the purebred ewes relative to purebred lambs raised by purebred ewes of both the parental breeds (Nitter, 1978). Effects of ewe or maternal heterosis represent the performance of crossbred ewes producing crossbred lambs relative to purebred ewes producing crossbred lambs. Crossbred rams may also benefit from increased heterozygosity relative to purebred rams, but less is known about the magnitude of direct and maternal heterosis for ram traits. Ram heterosis influences traits such as libido, conception rate, hardiness and longevity (Leymaster, 2002). A common application of lamb production is the mating of a large fast growing meat sire to a small ewe breed with a high reproductive rate (a fair quantity of good quality wool is seen as an additional advantage). Generally the levels of heterosis are low for growth traits (3-10%), while lamb survival (10%) and reproduction traits (10-40%) are expected to benefit more (Fogarty, 2006).

2.1.2 Complementarity

Complementarity is the improved production efficiency that results from crossbreeding systems that let strengths of the sire breed offset weaknesses of the dam breed and strengths of the dam breed counter weaknesses of the sire breed (Nitter, 1978). Complementarity greatly improves the efficiency of meat production by mating ewes of specialised dam breeds to rams of specialised sire breeds. Breed diversity allows producers to benefit from complementarity. In summary, favourable effects of lamb and ewe heterosis greatly increase overall productivity of crossbred sheep beyond the average of pure breeds.

An example of the efficiency of different crossbreeding systems (relative to pure breeding) for total litter weight weaned is provided in Table 2.1a. Estimates of direct and maternal heterosis provided by the same sources are provided as example on Table 2.1b. The present study seeks to provide more information on the exploitation of direct heterosis though terminal crossbreeding. However, some information on maternal heterosis is required to draw attention to the utilization of the maternal crossbred ewe in a system designed to exploit both direct and maternal heterosis when such ewes are mated to specialist terminal sires. This crossbred dam line is underexploited in the local sheep industry at present (Cloete *et al*., 2006).

Table 2.1a. Relative production of different crossbreeding systems for weight of lamb weaned[a] (Nitter, 1978)

Genetic type	General Purpose	Terminal
Purebred	100	122
First cross	117	150
Rotation		
Two- breed	134	146
Three- breed	143	153
Composite		
Two- breed	125	141
Three- breed	131	145
Four breed	138	150

[a] Production relative to total kg weaned from a purebred flock.

Table 2.1b. Estimates of direct and maternal heterosis effects expressed as a % of the mid parental value[a] (Nitter, 1978)

Trait	Direct	Maternal
Birth weight	3.2	5.1
Weaning weight	5.0	6.3
Pre-weaning daily gain	5.3	-
Post weaning daily gain	6.6	-
Yearling weight	5.2	5.0
Conception rate	2.6	8.7
Lambing rate	2.8	3.2
Pre-weaning survival	9.8	2.7
Lambs born per ewe exposed	5.3	11.5
Lambs weaned per ewe exposed	15.2	14.7
Litter weaning weight per ewe exposed	17.8	18.0

2.2 Use of breed diversity to Improve efficiency of meat production

One of the most valuable resources in the sheep industry is breed diversity (Leymaster, 2002). Increased productivity through crossbreeding can mainly be achieved through breed diversity. Sheep breeders in many countries have imported breeds and genetic material in an attempt to obtain a quantum leap in productivity, to produce a better quality or a new product or to provide sheep with a major adaptive advantage (Fogarty, 2006).

These imported breeds may be used as “purebreds” or infused into the local population using crossbreeding. However, there needs to be caution in introducing new breeds as, while they may excel in a desirable trait, they are often inferior in other characteristics that contribute to overall merit for the sheep enterprise (Fogarty, 2006).

The sheep industry has to produce uniform, nutritious, lean lamb that satisfies the eating preferences of consumers to compete effectively with the beef, pork, poultry and fish industries. There is useful genetic variation among breeds for many traits that affect the efficiency of meat production. The value of breed diversity is that producers can identify and use a breed or breeds that perform at a level consistent with marketing goals and with production resources such as feed availability, labour facilities and managerial skills (Leymaster, 2002). Sheep breeds are classified in many ways. Key traits used for classification purposes include adaptability, longevity, seasonality, age at puberty, lambing rate, mothering ability, lamb survival, leanness, quantitative and qualitative wool traits, as well as mature weight. General-purpose breeds tend to have acceptable, average levels of performance for most key traits, with extreme performance limited to very few, if any, traits. Specialized dam breeds and specialized sire breeds have clear strengths and weaknesses in key traits. Such breeds fit into dam or sire roles largely on performance for adaptability, reproduction, and growth. Specialized dam and sire breeds are best suited to complement each other. Specialized dam breeds are used predominantly in terminal crossbreeding systems as the ewe flock to produce market lambs. Examples of dam breeds include Polypay, Rambouillet and Targhee. Under South African conditions, Merino-type ewes have been evaluated in this role by Cloete (2007). Rams of specialized sire breeds are mated to purebred or crossbred ewes of specialized dam breeds to produce market lambs in terminal crossbreeding systems. Specialized sire breeds should, therefore, excel for fertility and longevity of rams as well as growth and survival of crossbred lambs. They should also produce lambs that have desirable carcasses, conformation and meat quality characteristics that are desirable for specific production-marketing situations.

Sheep breeders are increasingly interested in making profits from both meat and wool. To achieve this aim, superior management and the optimum combination of genetics is required (Fogarty, 2006). In Merino flocks, the major production traits for wool and meat include fleece weight, fibre diameter, staple strength, live weight and reproduction. Other traits including product quality, such as wool staple length, carcass and meat quality (fat and muscle depth), disease resistance (worm resistance and foot rot), while feed intake or feed requirements may also contribute to profit (Fogarty, 2006). Accurate estimates of genetic correlations especially between some of these trait groups have not previously been available (Safari *et al*., 2005) and a major research effort is being undertaken to address these gaps in knowledge (Fogarty, 2006). These estimates facilitate improved accuracy of genetic evaluation and the development of more complex breeding objectives that better reflect future industry needs for genetic improvement (Fogarty, 2006).

2.3 Historic background of South African terminal sire sheep breeds

2.3.1 The Dormer

The Dormer originated from a cross between Dorset Horn rams and German Merino ewes (presently known as the South African Mutton Merino). It was developed at Elsenburg since 1940s over a period exceeding 10 years The name Dormer is therefore an abbreviation of Dorset-Merino (Dormer Breeders' Society, 2005). The main aim in developing the Dormer was to create a meat breed that would be adapted to the prevailing conditions in the winter rainfall region, and from which the right type of ram could be obtained for crossbreeding purposes with Merino-type ewes, which then formed the bulk of the ewe flock. The efficiency of the Dormer has improved markedly, especially over the past decade mainly due to performance testing being compulsory for all breeders (Dormer Breeders' Society, 2005).

The breeding and selection of the Dormer is focused on a smooth-bodied, hornless sheep. The ideal fat lamb carcass must be full and broad across the shoulders, back and loins, and must have a well-developed eye muscle and well-filled hindquarters, while good fat coverage and an even distribution of fat is essential. The average birth weight of lambs is approximately 4 kg. This claim was verified by Van Wyk *et al*. (1993a & 2003) and also by the results of this study (3.83 kg ± 1.00) presented in Chapter 2. The birth weight of lambs was reduced by more or less than 1 kg through selection, which is a great advantage for the easier birth of lambs as confirmed by the genetic and phenotypic trends computed in this study (Chapter 5) and also by Van Wyk *et al*. (1993e). At an age of 4 months, purebred Dormer lambs reach an average weight of 36 kg, while mature ewes have an average weight of 77 kg and mature rams have a weight of 100 kg. With meat as the most important source of income, and wool of secondary importance, a large surplus of lambs must be obtained to make the production of fat lambs profitable. The mean growth gain of Dormer lambs is 0.26 kg per day, measured over a period of 100 days. The maximum growth gain found in a lamb was 0.49 kg per day. While selection for rapid growth gain is taking place, indirect selection for milk production also takes place due to the positive correlation between the two traits. Such rapid growth can only be obtained when ewes produce sufficient milk of a good quality, and this in turn depends upon good and protein-rich nutritional conditions during the lambing season. On average, Dormer ewes produce 3.5 kg and rams 4 kg of wool over a period of 12 months. Coarse, white wool with a fibre diameter of ~27 micron and a length of > 10 cm is obtained at 12 months. Kemp may occur on the face, legs, and bare parts of the body. It is worth mentioning that most of the standards from the breed society are anecdotal and much scientific work still has to be done in order to verify these claims. At this juncture, it is crucial to stipulate that several key indicator traits have not been measured explicitly and reported in scientific literature.

2.3.2 The Merino Landsheep

The first Merino Landsheep animals were imported into South Africa from Germany in 1956 (The Merino Landsheep Society of South Africa, 1998). The breed adapted exceptionally well to the climatic and pastoral conditions in South Africa, being prepared to search for food and graze the available vegetation. The Merino Landsheep has adapted to the poorest natural mid-mountain grazing regions and to the best agricultural areas where cultivated pastures abound, in the semi-arid Karoo or in the high rainfall areas. Although numbers are small, Merino Landsheep are also found in Mpumalanga, Gauteng, North West and Free State Provinces. They are also found, although to a lesser extent, in the Northern and Eastern Cape Provinces. The Merino Landsheep is a medium to large sheep with an oval to long polled head with a typical fringe, wide and slightly dropping ears. The chest is wide and slightly protruding. The back is long and broad. It has an oval rib section with long deep flanks. The hindquarter is long and wide in the pelvic region, with well-developed inner and outer thighs. Skin folds or wrinkles are unacceptable (The Merino Landsheep Society of South Africa, 1998). With its exceptional length and depth and long strong legs, the Merino Landsheep produces a heavy carcass at an early age.

It is a sheep with a large but firm frame, good walking ability, and good grazing capacity, well adapted under both extensive and intensive conditions with a high fertility rate, good reproduction, high milk production and good wool. It produces medium strong white wool with Merino characteristics and a length of 75mm at 12 months. Wool production averages 6-7kg of fat wool per ram and 4-5kg per ewe, with a clean yield of 50-75%. The Merino Landsheep is known to be able to produce three lamb crops every two years. It produces small lambs for easy births, making it ideal for crossbreeding programs (The Merino Landsheep Society of South Africa, 1998). Crossing of Merino Landsheep rams to Dorper ewes was proven to increase birth weight by 7 % and weaning weight by 5% relative to purebred Dorper lambs (Cloete *et al*., 2005). Terminal crossbreeding of Dorper ewes with Merino Landsheep rams was also proven not to deleteriously affect lamb growth and survival or ewe reproduction. Claims from the breed society can be reported anecdotally in the interim but more scientific investigations still have to be conducted in order to verify these claims as this breed has been subjected to fewer scientific studies than the Dormer.

2.3.3 The Ile de France

The Ile de France breed is found in more than 30 countries around the world, including South Africa. The breed is known for its excellent performance under semi-intensive, intensive and extensive conditions (Ile de France Sheep Breeders' Society of South Africa, 1998). The breed is renowned for its excellent growth rate, high fertility and good mothering ability. Its ability to breed out-of-season enables lambing to take place in autumn and for the lambing interval to be reduced to 7-8 months, allowing 3 lambings in 2 years. Anecdotal reports claim that as terminal sire, the Ile de France ram conveys its exceptional conformation, muscle development and fast growth rate to its progeny with a dominating effect. A study by Cloete *et al*. (2006) partially verified the meat characteristics and traits but still much convincing work has to be done in order to verify these claims (Tables 2.5a and 2.5d). It produces white strong wool (23-27 micron) with a fleece free of pigmentation. The Ile de France has outstanding carcass characteristics. It is well known that it is free from excessive fat, has outstanding muscle development, and therefore, a larger percentage of the higher priced cuts (Ile de France Sheep Breeders' Society of South Africa, 1998).

2.4 A review of studies on genetic analyses of growth traits in sheep

The primary objective of a breeding program for livestock species is to maximize the rate of genetic progress for economically important traits. The heritability of and genetic relationships between traits are needed for planning an efficient breeding system and development of effective genetic evaluation. REML procedures based on a derivative-free algorithm are normally used for the estimation of variance and covariance components under an animal model in which the additive genetic effect of the individual is fitted as a random effect (Torshizi *et al.,* 1996). The difference in profitability of different sheep breeds remains one of the most controversial issues among sheep producers (Snyman & Herselman, 2005). In South Africa and the world over, farmers continuously change from one breed to the other mainly due to short-term financial reasons and current trends as well as fluctuations in wool and meat prices. Profitability in sheep production for meat depends to a great extent on lamb weight, therefore selection objectives mostly include this trait as a component (Tosh & Kemp, 1994). Early lamb growth not only result in the production of good quality carcasses, but also results in a shorter production cycle and the ability to maintain a larger ewe flock (Olivier, 1999). Genetic parameters are needed to estimate breeding values and to compare responses from different selection programs.

2.4.1 Variance components and heritability estimates of early growth traits in the Elsenburg Dormer sheep stud

Early growth traits are essential factors influencing the profitability of any sheep meat production enterprise (Anon, 1970). Variance components and heritability estimates for early growth traits in the Elsenburg Dormer sheep stud have been conducted numerous times by Van der Merwe (1976), Van Wyk *et al.* (1993a; 1993b; 1993c; 1993d; 1993e; 2003) and Fair (2002). However, similar estimates have not been conducted on any other Dormer flock in South Africa. It was against this background that this study extracted data from the NSIS and carried out genetic parameter estimations for the national flock. Additive genetic variance and heritability estimates for birth weight (BW), weaning weight (WW), average daily gain (ADG) and Kleiber ratio (KL) were obtained initially by using Restricted Maximum Likelihood (REML) procedures and fitting three different models. Model selection regarding the random part was done according to log likelihoods. Heritability estimates were biased upwards when an animal model, ignoring maternal effects was fitted (Table 2.4a). A sire model yielded more realistic results for the direct additive genetic variance. Estimates for the maternal genetic variance and corresponding heritabilities were higher than estimates for direct additive variance and heritability when simultaneously fitted in an animal model. The heritability estimates were as follows: BW = 0.12, 0.42, 0.16, 0.43; WW = 0.12, 0.34, 0.13, 0.20; ADG = 0.13, 0.31, 0.13, 0.18; KL = 0.13, 0.26, 0.14, 0.14 for a sire model, an animal model, an animal model direct effects and an animal model maternal effects respectively (Van Wyk *et al.,* 1993b).

Table 2.4a. Estimates of variance components and heritabilities from single-trait DFREML analysis (Animal Model) (Van Wyk *et al.,* 1993b)

	Traits			
Parameters	**BW**	**WW**	**ADG**	**KL**
σ^2_a	0.2264	8.3339	693.7701	0.4889
σ^2_e	0.3104	16.1447	1527.0807	1.3820
σ^2_p	0.5368	24.4786	2220.8508	1.8709
h^2	0.4217	0.3405	0.3124	0.2613
±SE	0.0218	0.0295	0.0299	0.0304

From the study it was concluded that maternal effects had an appreciable influence on all traits studied and that if selection was done on direct effects alone, breeding values based on estimates of the variance components under a sire model were preferable to those from an animal model accounting for direct effects only.

2.4.2 Correlations between early growth traits in the Elsenburg Dormer sheep stud

Although the first step in genetic improvement of production efficiency in a population is to identify suitable selection criteria, other knowledge is also essential. Apart from heritabilities and variation of each trait, knowledge of how selection for one trait will influence others is needed (Van Wyk *et al.*, 1993d). This is important since unfavourable correlated responses could render improvement in a specific trait undesirable as far as total economic merit is concerned. Also if genetic improvement in a trait does not increase the efficiency of production, this improvement is of no economic consequence. The phenotypic, genetic and environmental correlations between live weights and average daily gain were found to be positive and medium to high (Table 2.4b). At this juncture it is worth mentioning that genetic correlations are strongly influenced by gene frequencies and because selection changes these frequencies, genetic correlations can change after a few generations of selection (Bohren *et al.,* 1969).

Table 2.4b. Phenotypic (r_p), genetic (r_g) and environmental (r_e) correlations between traits (Van Wyk *et al.*, 1993d)

Traits	r_p	r_g (±) SE	r_e
BW X WW	0.356	0.163(0.140)	0.381
ADG	0.220	0.010(0.144)	0.249
KL	-0.060	-0.279(0.138)	0.030
WW X ADG	0.990	0.988(0.003)	0.990
KL	0.894	0.888(0.030)	0.895
ADG X KL	0.942	0.943(0.016)	0.942

From reports of long-term selection experiments in sheep, it is evident that, although direct selection for WW was successful, unwanted correlated increases in BW and mature body weights were observed (Table 2.4c) (Van Wyk *et al.,* 1993d).

Table 2.4c. Percentage change in one trait with an increase in 10% in another trait (Van Wyk *et al.,* 1993d)

Increase of 10% in

% Change in	**BW**	**WW**	**ADG**	**KL**
Birth Weight (BW)	-	1.91	0.10	-7.49
Weaning Weight (WW)	1.39	-	8.70	20.38
Average daily gain (ADG)	1.58	11.23	-	24.6
Kleiber Ratio (KL)	-1.04	3.87	3.62	-
CV (%)	20.12	19.01	20.78	7.53
h^2	0.121	0.120	0.126	0.132

2.4.3 Updated genetic parameters for the Elsenburg Dormer sheep stud

Van Wyk *et al.* (2003) reported revised models and genetic parameter estimates for production and reproductive traits in the Elsenburg Dormer sheep stud. Estimates were made using records of 11 743 lambs born between 1943 and 2002. An animal model with direct and maternal additive, dam maternal permanent and dam temporary environmental (litter) effects was fitted for traits of the lamb i.e. birth weight, weaning weight and lamb survival. The fixed effects were sex, birth status, year and age of dam. Weaning weights were pre-adjusted to a 100 day equivalent. For reproductive traits, i.e. traits of the ewe, number and weight of lambs born and weaned, repeatability models were fitted. The random part consisted of direct additive and ewe and sire permanent environmental effects. Direct and maternal heritability estimates were 0.13 and 0.23 for birth weight and 0.07 and 0.09 for weaning weight (Table 2.4d). Corresponding proportions of total phenotypic variance due to the maternal permanent and temporary environment were 0.09 and 0.28 and 0.06 and 0.22 respectively. The genetic correlation between animal effects was –0.23 for birth weight. Maternal temporary environment had a major effect on all pre-weaning triats. The direct heritability estimate for lamb survival (employing an Animal Model with the logit link function) was low at 0.02 while the temporary maternal environmental variance as a proportion of phenotypic variance was 0.10 (Van Wyk *et al.*, 2003). Estimates of h^2 for number of lambs born and weight of lambs born and weaned were generally low, ranging from 0.03 for number of lambs born to 0.11 for total lamb weight at birth. The permanent environmental effects of the ewe accounted for 6-7% of the total phenotypic variation. Genetic correlations of total weight of lamb weaned with other reproductive traits were generally high i.e. 0.64 to 0.92. It was also concluded from the study that implementing the correct model regarding random effects for the estimation of genetic parameters was essential.

The study also deduced that selection on direct breeding values for increased weaning weight will not detrimentally affect reproduction (Van Wyk *et al.*, 2003). Although live weights at joining or at hogget age are generally positively related to total weight of lamb weaned in Merinos (Cloete *et al.*, 2002; 2003b), it has not yet been studied in dual-purpose or meat sheep. In a study by Van der Merwe (1976) on the Elsenburg Dormer stud, reproduction was not phenotypically related to live weight. So far the genetic correlation between weaning weight and reproduction has only been studied in the Merino (Olivier *et al*., 2001).

Table 2.4d. Variance components and ratios (±s.e.) for production traits and survival as reported by Van Wyk *et al.* (2003)

	Weight		**Survival**	
	Birth Weight	**Weaning Weight**	**BW Included**	**Survival**
Variance Components				
Total phenotypic	0.553	22.22	3.729	3.741
Residual	0.174	12.47	1	1
Direct Additive	0.074	1.58	0.063	0.062
Maternal additive	0.123	1.81	-	-
Covariance	-0.022	-	-	-
Permanent environment	0.047	1.470	-	-
Temporary environment	0.155	4.89	0.376	0.389
Variance Ratios				
Direct additive (h^2)	0.133 (0.025)	0.071 (0.018)	0.017 (0.015)	0.017 (0.014)
Maternal additive (m^2)	0.227(0.029)	0.081 (0.018)	-	-
Permanent environment (c^2_{pe})	0.085 (0.016)	0.066 (0.014)	-	-
Temporary environment (c^2_{te})	0.281 (0.013)	0.220 (0.018)	0.101 (0.015)	0.104 (0.019)
Genetic correlation (r_{am})	-0.233 (0.098)	-		-

2.4.4 Non-genetic effects influencing performance in the Elsenburg Dormer sheep stud

Non-genetic factors also influence early growth traits in sheep. In a study conducted by Van Wyk *et al*. (1993a) with the records from the Elsenburg Dormer sheep stud, fixed effects identified as having a significant effect on birth weight, weaning weight, average daily gain and Kleiber ratio, were year-season, age of dam, sex, birth status and level of inbreeding. Fixed effects have to be controlled experimentally or eliminated statistically using adjustment factors. The study also proved that birth weight, weaning weight and early growth of a lamb is greatly influenced by the age of the dam. The average weaning weight of lambs increased with the age of the dam up to four years and decreased afterwards. The heaviest lambs (at birth) were born to seven-year-old dams and the lightest from two-, eight- and nine-year-old dams. Single lambs were also heavier at birth and weaning and had a higher pre-weaning growth rate and Kleiber ratio than twins or triplets. Male lambs were consistently heavier, grew faster and had a higher Kleiber ratio than female lambs. An increase in the level of inbreeding had an adverse effect on all traits studied. As expected, non-inbred lambs out-performed their inbred partners except for birth weight where a non-significant difference was observed between 0% and <5% inbreeding (Van Wyk *et al.,* 1993c). Since the effect of non-genetic factors on early growth traits was elucidated on one stud, one of the objectives of this study is to estimate these effects on the national flock.

2.4.5 Genetic parameters for Australian Maternal and Dual Purpose Meat Sheep

2.4.5.1 Liveweight, Fat Depth and Wool Production in Coopworth Sheep

The Coopworth breed was developed in New Zealand in the 1950s from a cross between Border Leicester and Romney sheep with the objective of improving reproductive ability, wool production and growth rate (Brash *et al.*, 1994). The Coopworth is widely used in New Zealand but has also gained popularity in Australia only in more recent years. New Zealand Coopworth ewes and rams have been imported and Border Leicester X Merino (BLM) ewes have been used in grading-up programs (Brash *et al.*, 1994). For Australian lamb production, the Coopworth is used in straight breeding flocks, single-tier crossbreeding with terminal sire breeds mated to Coopworth ewes and two-tier crossbreeding using Coopworth X Merino ewes. Genetic improvement in the Coopworth aims to increase productivity and profitability of lamb production by improved performance of Coopworth ewes when joined to Coopworth or terminal sire breed rams, as well as the production of first cross Coopworth X Merino ewes. Estimates of heritability, genetic and phenotypic correlations (±s.e.) for liveweights, greasy fleece weight, fibre diameter and ultrasonic fat depth are shown in Table 2.4 e.

Table 2.4e. Estimates of heritability, genetic and phenotypic correlations (±s.e.) for liveweights, greasy fleece weight, fibre diameter and ultrasonic fat depth in Coopworth sheep (Brash *et al*., 1994)
Heritabilities on diagonal, genetic correlations below and phenotypic correlations above the diagonal

Trait	Weaning Weght	Yearling weight	GFW	Fibre Diameter	Fat depth
Weaning weight	**0.45±0.07**	0.61±0.01	0.24±0.02	0.09±0.03	0.21±0.02
Yearling weight	0.84±0.05	**0.38±0.07**	0.40±0.02	0.04±0.03	0.41±0.02
GFW	0.40±0.11	0.15±0.13	**0.28±0.05**	0.31±0.03	0.14±0.03
Fibre Diameter	0.06±0.26	-0.20±0.24	0.42±0.25	**0.18±0.08**	-0.00±0.03
Fat depth	0.53±0.22	0.64±0.20	0.15±0.34	0.55±0.28	**0.13±0.04**

In general the results depicted in Table 2.4e indicate that significant genetic variation exists in the major production traits for Coopworth sheep, and that major gains in liveweight, fleece weight, fibre diameter and fat depth can be made by selection (Brash *et al.*, 1994). Coopworth sheep can therefore play an essential role if they are used as terminal sires in crossbreeding programmes with the main objective of prime lamb production because the direct heritabilities of weaning weight and yearling weight are quite high, whilst that of fat depth is low. However, the wool traits are not really of consequence in a terminal crossbreeding programme.

2.4.5.2 Live weight traits in Corriedale Sheep

The Corriedale is the second most numerous breed of sheep in Australia. It was developed in Australia and New Zealand in the 1870s and 1880s by interbreeding the half-bred Lincoln-Merino cross (Brash *et al.*, 1994). It is a dual-purpose breed used for apparel wool and prime lamb production. The Corriedale is used in several types of breeding enterprises, including straightbred flocks, straightbred ewes mated to terminal sire breeds and occasionally as first cross prime lamb dams such as Border Leicester X Corriedale and Corriedale X Merino. The self-replacing dual-purpose breeds, of which the Corriedale is the most important and contributes about 10 % to the genes in the Australian slaughter lamb industry, and 12 % to the genes in the dams of slaughter lambs (Fogarty *et al.* 1992). Estimates of parameters obtained for Corriedale sheep are depicted in Table 2.4 f. The estimated heritability for weaning weight was 0.34±0.07 while that for yearling weight was 0.13±0.04. The genetic correlation between the two traits was 0.83±0.10 which was higher than the phenotypic correlation (0.49±0.01) (Brash *et al.*, 1994). The results obtained indicated that Corriedale sheep have got a lot of potential to achieve high output in prime lamb production if they are used as dam lines in crossbreeding programmes.

Table 2.4f. Estimates of heritability, genetic and phenotypic correlations (±s.e.) for liveweights traits Corriedale sheep (Brash *et al.*, 1994)

Heritabilities on diagonal, genetic correlations below and phenotypic correlations above the diagonal

Trait	Weaning weight	Yearling weight
Weaning weight	**0.34±0.07**	0.49±0.01
Yearling weight	0.83±0.10	**0.13±0.04**

2.4.5.3 Live weight at 14 months and Wool Production in Border Leicester and Related Types

The Border Leicester is widely used in Australia as a maternal sire breed joined to Merino ewes for the production of crossbred ewes. First cross Border Leicester X Merino ewes are the predominant dams used for slaughter lamb production (Brash *et al.*, 1994). The Border Leicester is a longwool breed that contributes about 16 % of the genes of Australian slaughter lamb and 23 % of the genes of the dams of slaughter lambs (Fogarty *et al.,* 1992). It has a large body size, heavy fleece of high fibre diameter and high ovulation rate (Brash *et al*., 1994). The Glen Vale is a related breed developed by NSW Agriculture and stabilized at approximately 82 % Border Leicester and 18 % Merino (Barwick *et al*., 1989). From an Australian national perspective the genetic improvement in the Border Leicester aims to improve the performance of first cross Border Leicester X Merino ewes and increase productivity and profitability in the lamb industry (Brash *et al.*, 1994). Genetic parameters were estimated for 14 month liveweight and greasy fleece weight from 1312 ewe and ram records representing 75 sires of the Border Leicester and Glen Vale breeds using REML procedures. The parameters obtained are presented in Table 2.4g.

Table 2.4g. Estimates of heritability, genetic and phenotypic correlations for liveweight and greasy fleece weight for Border Leicester and Glen Vale hogget ewes and rams (Brash *et al*., 1994)
Heritabilities on diagonal, genetic correlations below and phenotypic correlations above the diagonal

Trait	**Liveweight (at 14 months)**	**Greasy fleece weight**
Live weight	**0.24±0.07**	0.54±0.02
Greasy fleece weight	-0.21±0.30	**0.17±0.05**

The results indicate that significant gains in fleece weight and liveweight are expected from selection. The heritability for hogget weight was in the moderate range. Wool production and liveweight are important components in the breeding objectives of Border Leicester studs as they are a major source of income for the owners of commercial first cross ewe flocks. The unfavourable genetic correlation between liveweight and wool production means that both traits need to be measured and combined in an efficient selection index to overcome the antagonistic relationship (Brash *et al.*, 1994).

2.4.6 Genetic parameter estimates of early growth traits in the Tygerhoek Merino Flock

Genetic parameters were estimated for birth weight, (BWT), weaning weight (WWT) and pre-weaning average daily gain (ADG) using records from 8 310 lambs born from 2 538 ewes and sired by 681 rams of the Tygerhoek Merino flock from 1970 to 1998 (Duguma *et al*., 2002). The study was reviewed basing on the fact that the second-cross Merino ewes may potentially be crossbred with terminal sires to achieve prime lamb production. Estimates of (co)variance components, direct (h^2) and maternal (m^2) heritability, as well as values for maternal permanent environmental effects (c^2) are shown in Table 2.4h.

Table 2.4h. Estimates of (co)variance components and genetic parameters for growth traits in Merino sheep (Duguma *et al*., 2002)

Traits	σ^2_a	σ_m^2	σ_c^2	σ_{am}	σ_e^2	σ_p^2	h^2	m^2	r_{am}
BW	0.08	0.15	-	-0.03	0.23	0.43	0.19	0.38	-0.23
WWT	3.73	1.64	-	0.04	9.34	14.75	0.25	0.11	0.02
ADG	355.05	136.05	-	-11.85	882.19	1361.44	0.26	0.10	-0.05

The estimates for direct heritability (h^2) were substantially higher when maternal effects, either genetic or environmental were ignored from the model. The maternal heritability (m^2) for BWT was 0.38 when maternal genetic effects were fitted in the model but decreased to 0.25 when the maternal permanent environmental effect (c^2) was fitted. Moderate negative direct-maternal genetic correlations (r_{am}) were observed for birth weight, while close to zero estimates were obtained for WWT and ADG (Duguma *et al*., 2002).

In this study, fitting the maternal genetic effects as the only random effect in addition to the direct genetic effect resulted in improved log likelihood ratios compared to the models that ignored the maternal genetic effects. In young mammals the milk production of the dam and the maternal care she provides largely contribute to their growth (Bradford, 1972; Lewis & Beatson, 1999). The dam's genes for these traits affect the environment experienced by the offspring through milk production and mothering ability (Bourdon, 2000). Maternal effects may be expected to be more important in sheep than in cattle because of the variation in litter size in sheep and the competition between the lambs for their mother's milk supply. It incorporates both the similarities between twins and similarities between lambs born to the same ewe in different years (Snyman *et al*., 1995). The authors also deduced that failure to account for maternal permanent environment effects (c^2) and maternal breeding values would result in higher maternal genetic variances (σ_m^2), probably resulting in an overestimation of m^2. It was evident that the values for h^2 and m^2 were greatly influenced by the model used in the analysis. The estimate of the total maternal effect ($m^2 + c^2 + 1/4h^2 + \sqrt{h^2}\sqrt{m^2}\ r_{am}$) is more important than the direct effect (Notter, 1998). Genetic correlations between growth traits were positive and varied from low to high as depicted in Table 2.4i. A small direct genetic correlation was estimated between BWT and WWT. That particular observation indicated that selecting for heavier WWT in this flock may possibly not result in substantial increases in BWT, though the standard error of the estimate is expected to be relatively large owing to the relatively small data set (Duguma *et al*., 2002). Another observation in this flock was a significant reduction in survival rate of lambs as they became heavier (> 5.0kg) at birth.

Table 2.4 i. Estimated direct genetic, maternal genetic, maternal permanent environmental and residual correlations (above diagonal) and the corresponding covariance (below diagonal) between birth weight (BWT), weaning weight (WWT) and average daily gain (ADG) in Merino sheep (Duguma *et al*., 2002)

Trait	**BWT**	**WWT**	**ADG**
Direct genetic effects			
BWT	-	0.16	0.04
WWT	0.16	-	0.99
ADG	0.42	85.49	-
Maternal genetic effects			
BWT	-	0.93	0.60
WWT	0.20	-	0.85
ADG	0.57	1.21	-
Maternal permanent environmental effect			
BWT	-	0.89	0.82
WWT	0.08	-	0.99
ADG	0.60	2.92	-
Residual effects			
BWT	-	0.16	0.02
WWT	0.30	-	0.99
ADG	0.41	126.83	-

2.4.5 Genetic parameter estimates for pre-weaning weight traits in Dorper sheep

The Dorper is a composite meat breed, developed in the early 1950s in South Africa from a cross between the Dorset Horn and the Black Headed Persian sheep breeds. The aim was to develop a composite breed capable of producing a high quality carcass, without localized fat in the tail and rump areas, for utilising the arid areas of South Africa (Cloete *et al*., 2000). Presently the Dorper, the second most popular breed in South Africa, has been exported to a number of countries including Israel, USA and Australia. Genetic parameters were estimated for birth-, 42 day-, and 100 day (weaning) weight in the Dorper flock of the Glen Agricultural Institute in South Africa. Complete and accurate records were available for over 20 years (Neser *et al*., 2001). A total number of 4 217 records, comprising the progeny of 89 sires were analysed. Genetic parameter estimates for body weights at birth, 42-days and 100-days are shown in Table 2.4j.

Table 2.4j. Genetic parameter estimates for body weights at birth, 42-day and 100-day in the Dorper breed (Neser *et al*., 2001)

(Co)variance component	Birth Weight	42-Day Weight	100-Day Weight
h^2	0.11±0.04	0.28±0.04	0.20±0.07
m^2	0.10±0.04	0.10±0.03	0.10±0.07
c^2	0.12±0.03	0.11±0.03	0.08±0.04
h^2_T	0.21	0.17	0.13
σ^2_a	0.06	1.55	3.83
σ_m^2	0.05	0.56	1.83
σ_c^2	0.06	0.61	1.62
σ_{am}	0.02	-0.59	-1.53
σ_e^2	0.34	3.48	13.58
σ_p^2	0.53	5.61	19.32
r_{am}	0.35	-0.63	-0.58

The direct and maternal heritability estimates obtained in the study were all within the range of those obtained in literature (Van Wyk *et al*., 1993; Tosh & Kemp, 1994; Fogarty, 1995; Snyman *et al*., 1995; Mousa *et al*., 1999; Okut *et al*., 1999). They were however, mostly at the lower end of the scale. Permanent maternal environmental effects for birth weight can be attributed to the uterine environment provided by the dam as well as the effect of multiple births, which are quite common in this breed (Neser *et al*., 2001). The c^2 estimate for permanent maternal environment in this study was higher in absolute terms than both the direct and maternal heritability estimates (0.12 versus 0.11 and 0.10). The permanent maternal environment effect on 42-day weight is mainly determined by the milk production of the dam. In this study the c^2 estimate was again slightly higher than m^2 despite the high standard error that could render the difference insignificant. This could be an indication of the large influence the environment has on milk production (Neser *et al*., 2001).

Table 2.4k. Estimated direct (above diagonal) and maternal (below diagonal) genetic correlations among body weights at birth, 42days and 100 days (weaning) (standard error in brackets) (Neser *et al*., 2001)

	Birth Weight	42- Day Weight	100- Day Weight
Birth Weight	-	0.51 (0.12)	0.27 (0.24)
42- Day Weight	0.42 (0.22)	-	0.59 (0.10)
100- Day Weight	0.54 (0.27)	0.71 (0.16)	-

The genetic correlation between animal effects for 42-day-weight in this study was high and negative (-0.63) while published estimates varied between -0.39 and -0.90 (Tosh & Kemp, 1994; Notter, 1998; Mousa *et al*., 1999; Neser *et al*., 2000). This high negative correlation is an indication of how difficult it is to simultaneously improve both these traits in a selection program. Anecdotal reports from Tosh and Kemp (1994) suggest that the antagonism between the effects of an individual's genes for growth and those of its dam for maternal contribution might be due to natural selection for an intermediate optimum.

Table 2.4l. Permanent environmental (above diagonal) and phenotypic (below diagonal) correlation estimates among body weights at birth, 42- day and 100- day (weaning)[a] (Neser *et al*., 2001)

	Birth Weight	42- Day Weight	100- Day Weight
Birth Weight	-	0.68 (0.06)	0.52 (0.13)
42- Day Weight	0.48	-	0.89 (0.10)
100- Day Weight	0.38	0.68	-

[a] Standard error in parenthesis.

Results from the study tended to favour single trait selection because more consistent estimates were obtained. However correlated responses, in the case of multiple trait selection would depend on genetic correlations. Fogarty (1995) reported a weighted average genetic correlation estimate between birth weight and weaning weight of 0.39. This value is higher than 0.12 estimated by Maria *et al*. (1993) but lower than an estimate of 0.45 derived by Mousa *et al*. (1999). The results from the former study indicated that it is possible to improve weaning weight without significant increases in birth weight. Both birth and weaning weight had a moderate direct genetic correlation with 42-day weight (0.51 and 0.59) in the study of Neser *et al*. (2001) (Table 2.4k). The maternal genetic correlation between weaning weight and 42-day weight was higher (0.71) and moderate between birth and 42-day weight (0.42), as well as between birth weight and weaning weight (0.54). This indicated that selection for weaning weight would lead to concomitant increases in weight at the other ages. The dam permanent maternal environmental correlation estimates between the different weights varied from moderate to high (Table 2.4l). This could have been due to a carry-over effect, particularly between body weight at 42 days and weaning as well as the multiple births that occur in the breed. Phenotypic correlations represent the combined effect of genotypic and environmental influences (Neser *et al*., 2001).

2.4.6 Direct and maternal (co)variance components and heritability estimates for body weights at different ages and fleece traits in Afrino sheep

The Afrino is a dual-purpose (meat and wool production) sheep breed developed for arid regions. It was the first South African sheep breed in which the separation of ram and ewe selection objectives was investigated and applied (Snyman *et al*., 1995). Rams are selected on growth and fleece traits and ewes on ewe productivity (total weight of lamb produced) which incorporates fertility and mothering ability. Selection is thus based on traits that are largely maternally influenced. The Afrino was developed as a white-woolled terminal sire breed for crossing with Merino ewes in a terminal crossbreeding system. Genetic parameters were estimated for birth weight, monthly body weight from weaning at 4 months to 12 months of age, 18 month body weight, 16 month clean fleece weight (CFW) and 16 month mean fibre diameter (MFD) using REML procedures. Results are depicted in Table 2.5m.

Table 2.4m Estimates of genetic parameters for BW, WW, W5 to W12, W18, CFW and MFD in Afrino sheep (Snyman *et al*., 1995)

Trait	Direct heritability (h_a^2)	Maternal heritability (h_m^2)	Dam permanent environment (c^2)	Total heritability (h_T^2)
BW	0.22	0.09	0.12	0.27
WW	0.33	0.17		0.41
W5	0.38	0.17		0.46
W6	0.47	0.14		0.53
W7	0.50	0.11		0.55
W8	0.59	0.10		0.63
W9	0.59	0.08		0.63
W10	0.60	0.06		0.63
W11	0.55	0.07		0.58
W12	0.58	0.05		0.61
W18	0.56	0.06		0.60
CFW	0.62			0.62
MFD	0.73			0.73

Direct heritability estimates obtained for body weights (Table 2.4m) were within the scope reported by various authors for several sheep breeds worldwide (Snyman *et al*., 1995). It was evident from the study that the direct heritability (h_a^2) estimate of body weight increased up to 8 months of age, then seemed to stabilize. Maternal heritability estimates (h_m^2) for body weight, on the other hand, increased from birth (0.09) to 5 months (0.17), whereafter it decreased gradually (Snyman *et al*., 1995). The results confirmed that growth traits can successfully be improved through selection in Afrino sheep and that the breed has got so much potential when used as terminal sire in crossbreeding programs with the objective of improving meat production.

2.4.7 Summary of genetic parameters for birth and weaning weights reported in literature for various breeds

To get an overview of genetic parameter estimates in the current study, literature was explored and the results are reported in Table 2.4n and Table 2.4o. The reported literature values were used as benchmarks in comparison for any consistencies and deviations with those obtained in the current study.

Table 2.4n. Summary of reported direct (h^2), maternal (m^2), permanent environmental (c^2) estimates and correlations between direct and maternal genetic effects (r_{am}) for birth weight

Breed	**h^2**	**m^2**	**c^2**	**r_{am}**	**References**
Chios	0.13-0.38	0.13-0.33	0.16-0.28	0.00 to –0.44	Ligda *et al*. (2000)
Various breeds	0.19-0.34	0.30-0.65		-0.18 to –0.74	Burfening & Kress (1993)
Horro	0.18-0.32	0.10-0.26		-0.64	Abegaz & Duguma (2000)
Elsenburg Dormer	0.16-0.42	0.43		-0.35	Van Wyk *et al*. (1993b)
Romanov	0.04	0.22	0.10	-0.99	Maria *et al* (1993)
Hampshire	0.39	0.22	0.37	-0.56	Tosh & Kemp (1994)
Polled Dorset	0.12	0.31	0.27	-0.35	Tosh & Kemp (1994)
Romanov	0.07	0.13	0.32	-0.13	Tosh & Kemp (1994
Swedish Finewool	0.07	0.30		0.11	Nasholm & Danell (1996)
Afrino	0.22	0.09	0.12		Snyman *et al*. (1995)
Baluchi	0.14	0.12		0.18	Yazdi *et al.* (1997)
Australian Merino	0.30	0.29		-0.43	Torshizi *et al.* (1996)
Dohne Merino	0.04	0.10	0.17		Cloete *et al*. (1998)
Moroccan Timahdit	0.18	0.59		-1.00	Fadili *et al*. (2000)
Dorper sheep	0.11	0.10	0.12	0.35	Neser *et al*. (2001)
Merino	0.18	0.15	0.08		Cloete *et al*. (2001)

The summary of literature in Table 2.4n clearly indicates that maternal effects contibute significantly to the observed phenotypic variation for birth weight. Estimates of h^2 can be biased if maternal effects (either genetic or environmental) are ignored when using an animal model. The table partially confirms the importance of implementing the correct model pertaining to random effects for the estimation of genetic parameters. Exclusion of important components in such genetic analyses obviously has the effect of inflating the remaining parameter estimates.

The interpretation of genetic parameter estimates for traits that are influenced by maternal effects in an animal model context is dependent on both the population structure and the model used in the analysis (Safari *et al.*, 2004). Genetic evaluation of growth traits needs to adopt a model that includes direct and maternal genetic, as well as maternal environmental effects. It is essential to partition maternal environmental effects into across year dam effects (permanent environmental effects) and litter effects (the within year common environmental effect unique to the litter) in breeds where multiple births are relatively common (Safari *et al.,* 2004).

Table 2.4o. Summary of reported direct (h^2), maternal (m^2), permanent environmental (c^2) estimates and correlations between direct and maternal genetic effects (r_{am}) for weaning weight

Breed	**h^2**	**m^2**	**c^2**	**r_{am}**	**References**
Chios	0.15-0.29	0.05-0.16	0.08-0.12	-0.22to-0.26	Ligda *et al*. (2000)
Various breeds	0.09-0.22	0.07-0.48		-0.41 to –0.88	Burfening & Kress (1993)
Elsenburg Dormer	0.13-0.34	0.20		-0.16	Van Wyk *et al*. (1993b)
Horro	0.10-0.26	0.10-0.26		-0.42	Abegaz & Duguma (2000)
Romanov	0.34	0.25	0.00	-0.97	Maria *et al* (1993)
Hampshire	0.39	0.19	0.20	-0.74	Tosh & Kemp (1994)
Polled Dorset	0.25	0.08	0.19	-0.31	Tosh & Kemp (1994)
Romanov	0.14	0.02	0.12	0.43	Tosh & Kemp (1994
Swedish Finewool	0.12	0.13		0.47	Nasholm & Danell (1996)
Afrino	0.33	0.17			Snyman *et al*. (1995)
Baluchi	0.19	0.03		0.51	Yazdi *et al.* (1997)
Australian Merino	0.28	0.41		-0.59	Torshizi *et al.* (1996)
S.A.Mutton Merino	0.19	0.09	0.10	-0.55	Neser *et al.* (2000)
Moroccan Timahdit	0.50	0.24		-0.94	Fadili *et al*. (2000)
Dorper sheep	0.20	0.10	0.08	-0.58	Neser *et al*. (2001)
Merino	0.30	0.08	0.07		Cloete *et al*. (2001)

Tables 2.4n and 2.4o clearly exhibit a trend of an increasing direct variance ratio but a decreasing maternal variance ratio from birth to weaning. The increased h^2 of lamb weight at weaning is most likely caused by an increased expression of genes with direct effects on body development (Yazdi *et al.*, 1997). The tabulated results from the various studies indicate that maternal effects in mammals diminish with age. Early growth traits in sheep are commonly characterized by negative r_{am} estimates. Environmental covariances between the dam and her offspring that are not accounted for may bias the direct and maternal genetic correlations downwards (Meyer, 1992; Swalve, 1993).

2.5 Terminal Crossbreeding of Sheep in South Africa

In the past 10 years South Africa has experienced fluctuations in the ratio between wool and meat prices. This has resulted in breeders changing their breeding goals to incorporate meat production as a complementary enterprise to their wool enterprises (Oliver & Cloete, 1998). Genetic change resulting from within-flock selection is comparatively slow, while it takes time to filter through the structures of the breed (Cloete & Durand, 2000). Therefore, commercial producers often seek alternative methods of improving their meat yield without compromising wool production. Crossbreeding of Merino-type ewes with dual-purpose or mutton rams are often utilized as a method to achieve this goal.

In a study by Cloete *et al.* (2005), ewe production and lamb performance were investigated after terminal crossbreeding of Dorper ewes to Ile de France (IdF), Merino Landsheep (ML) and SA Mutton Merino sires. The average birth weight of IdF cross and Merino Landsheep (ML) cross were increased by 12% and 7% respectively expressed as a percentage of purebred Dorper Lambs (Table2.5a). At weaning, ram lambs and singles were heavier ($P < 0.01$) than ewes and multiples. Hence it was essential to adjust for the effect of sex when the mixed model equations were constructed for estimating random effects and predicting breeding values. Progeny sired by IdF rams were 10% heavier ($P < 0.01$) than purebred Dorper lambs at weaning. Progeny sired by ML were 5% heavier ($P < 0.05$) than purebred Dorpers at this stage. The breed of the service sire did not influence number of lambs born or weaned (Table 2.5c) and percentage of lambs weaned (i.e. lamb survival) (Table 2.5a). The breed of sire did however affect the number of ewes lambed per ewe mated especially in the ML breed (Table 2.5b).

Table 2.5a. Least square means (±S.E) for lamb birth weight, weaning weight at an average weaning age and survival prior to weaning as affected by terminal sire breed (Cloete *et al.,* 2005)

Sire breed	Birth weight (kg)	Weaning weight (kg)	Lamb mortality
Ile de France	4.6±0.1	34.5±0.5	0.18
Merino Landsheep	4.4±0.1	32.9±0.7	0.22
SA Mutton Merino	4.2±0.1	31.1±0.6	0.22
Dorper	4.1±0.1	31.3±0.5	0.24

Lambs sired by IdF and ML were 3.1 and 2.6% respectively heavier than purebred Dorpers at slaughter, although it was attempted to slaughter all lambs at a constant weight. The variation between sires within sire breeds was low in the analysis of lamb traits in this study. It was crucial to take note of the fact that significant variation in some production traits was attributed to breeds, rather than to variation between sires within breeds.

Table 2.5b. Lambing rate of ewes in the terminal crossbreeding study, as affected by the breed of the service sire (Cloete *et al*., 2005)

Breed of sire	Number of ewes mated	Ewes lambed per ewe mated
Ile de France	111	0.72
Merino Landsheep	110	0.50
SA Mutton Merino	101	0.68
Dorper	170	0.75
X^2		21.1*

*Critical X^2 for 3 d.f = 7.82.

Table 2.5c. Least square means (±S.E.) for ewe reproduction as affected by sire breed (Cloete *et al.,* 2005)

Sire breed	Ewe joining weight (kg)	Number of lambs born	Number of lambs weaned	Weight of lamb weaned (kg)
Ile de France	63.5±0.8	1.50±0.06	1.22±0.07	45.9±2.3
Merino Landsheep	64.0±0.9	1.42±0.07	1.11±0.08	40.4±2.7
SA Mutton Merino	63.7±0.8	1.59±0.06	1.29±0.07	43.0±2.3
Dorper	62.9±0.8	1.49±0.06	1.12±0.05	38.4±1.8

It was evident from the study that crossbred progeny outperformed purebred Dorper lambs in cases where genotypic differences were observed. Differences in fat depth (Table 2.4d) were in favour of the crossbred genotypes i.e. a reduced fat depth in nearly all crossbred genotypes. The study also concluded that terminal crossbreeding of Dorper ewes with leaner specialist meat breeds may become a viable option for commercial Dorper producers.

The meat quality of Merino and Merino crossbred lambs was considered in a related study (Cloete *et al*., 2006). Ram breeds that were used were the Dormer, Ile de France, Merino Landsheep, Suffolk and Dorper. Merino sires were also used as a control. Data included 274 slaughter and carcass records of lambs. It was intended to slaughter all lambs at a live weight of 45kg but some were slaughtered at 42 kg, as they did not reach the intended slaughter weight on good time. Purebred Merino lambs were slaughtered at 340±7 days of age, which was between 40-50 days later than the crossbred lambs (Table 2.5d). The crossbred lambs were also between 9-11% heavier at slaughter than purebred Merinos. The fat cover of the purebred Merino and ML cross lambs was lower than that of the other crossbred lambs. Cooking loss of muscle from Merino lambs was higher than that of crossbred lambs, but no differences were found for drip loss between the different breed combinations (Cloete *et al.,* 2006).

Table 2.5d. Least square means (±se) depicting carcass traits and fat depths of Merino and Merino crossbred lambs (with slaughter mass as co-variant) (Cloete *et al.*, 2006)

Sire Breed

Trait	**Merino**	**Dormer**	**IdF**	**ML**	**Suffolk**	**Dorper**
Slaughter age (days)	340±7	289±5	278±7	282±7	300±7	296±6
Slaughter weight (kg)	38.7±0.8	43.0±0.6	43.5±0.8	43.5±0.8	42.7±0.8	43.2±0.6
Back fat depth (13th rib) (mm)	1.73±0.20	2.76±0.14	2.15±0.19	1.78±0.18	2.14±0.18	2.67±0.14
Back fat depth (3rd&4th lumber) mm	2.13±0.21	3.29±0.15	3.01±2.05	1.88±0.20	2.64±0.19	340±0.16

The study showed that crossbred lambs attained slaughter weight at an earlier age than purebred Merino lambs. No conclusive advantages as pertaining to physical meat quality in favour of any of the terminal sire breeds on Merino ewes were noted (Table 2.5.e). Breed combinations did not significantly affect initial pH measurements (45min after slaughter). However final pH values (measured 48 hours after slaughter) of Merino, IdF cross and ML cross lambs were higher than those of Dormer and Dorper sired lambs. Cooking loss of muscle from Merino lambs was higher than that of the crossbred lambs, but no differences were found for drip loss between the different breed combinations (Cloete *et al.*, 2006). There were no significant differences between *M. longissimus dorsi* shearing values between the crossbred combinations (Cloete *et al.*, 2006).

Table 2.5e. Least square means (±s.e.) depicting meat quality traits of Merino and Merino crossbreds (Cloete *et al.,* 2006)

Trait	**Merino**	**Dormer**	**IdF**	**ML**	**Suffolk**	**Dorper**
pH45	6.47±0.07	6.49±0.05	6.47±0.05	6.41±0.07	6.59±0.07	6.47±0.05
pH48	5.61±0.02^{a}	5.54±0.01^{b}	5.58±0.02^{a}	5.59±0.02^{a}	5.56±0.02^{ab}	5.56±0.01^{b}
Cooking loss%	30.5±0.7^{a}	27.2±0.7^{b}	27.9±0.7^{b}	29.9±0.7^{ab}	27.9±0.7^{b}	28.2±0.7^{b}
Drip loss %	0.95±0.08	0.98±0.07	1.00±0.07	1.08±0.07	1.02±0.07	1.13±0.08
Colour L*	35.2±0.4	34.9±0.3	35.8±0.4	36.0±0.3	35.4±0.3	34.8±0.4
a*	15.1±0.5^{a}	12.8±04^{c}	12.9±0.4^{c}	13.7±0.4^{b}	13.8±0.4^{b}	14.2±0.5^{b}
b*	8.33±0.33^{ab}	8.31±0.3^{ab}	8.29±0.31^{ab}	8.49±0.30^{ab}	7.94±0.29^{b}	9.33±0.33^{a}
Shearing value (N)	80.7±4.9	69.3±4.5	69.3±4.5	83.8±4.5	85.2±4.4	74.4±5.0

At this juncture it is worth mentioning that the use of ML rams in terminal crossbreeding will also result in other positive attributes apart from the usual heterosis being achieved. ML sheep are known to be fairly resistant to gastro-intestinal parasites as suggested by evidence gathered through crossbreeding ML rams to other breeds under natural challenge conditions (Hielscher *et al.,* 2006). A crossbreeding program was conducted to evaluate the resistance status to *Haemonchus contortus* in reciprocal crossbred (F_1) lambs and their Merino Landsheep (ML) and Rhoen sheep (Rh) parents. A total of 406 lambs were included in the study. Faecal egg counts (FEC) and hematocrit values (Hc) of all the lambs were collected 4 and 6 weeks after an artificial infection with *H. contortus.* Worm counts of all lambs were obtained after slaughtering at 21 weeks of age. The purebred ML group had better weights and carcass performances than the purebred Rh group. The heterosis analysis of body weight and carcass parameters showed a tendency to favour the Rh x ML breed combination. The Rh group had higher values for FEC and lower Hc values compared to the Merino Landsheep. Nematode counts were not significantly different between the pure breeds. In comparison, the worm counts of Rh x ML crosses were significantly different from those in the ML x Rh crosses. A heterosis analysis showed that FEC, Hc and worm count in the F_1 group favoured the RH x ML crossbreeding group. The results also suggest that crossbreeding Rh to ML sheep may be a suitable method of producing lambs with an improved resistance to *H. contortus* infestation without any negative effects on production traits (Hielscher *et al.*, 2006).

2.6 Research on terminal sire sheep in the United States of America

Numerous studies have evaluated various sheep breeds as potential terminal sires breeds in the United States (Sidwell & Miller, 1971a,b; Dickerson *et al*., 1974; Nitter, 1975a,b; Leymaster & Smith, 1981). Commercial lamb production in the United States has benefited over the years through the use of the genetic diversity among breeds of sheep in structured crossbreeding systems (Leymaster, 2002). Comprehensive evaluation of breeds provides necessary information on the use of breeds in crossbreeding systems that exploit effects of heterosis and complementarity to meet specific production and marketing objectives (Freking & Leymaster, 2004). Records of 9 055 lambs from a composite population originating from crossing Columbia rams to Hampshire x Suffolk ewes at the U.S. Meat Animal Research Centre was used to estimate genetic parameters for growth traits. Growth traits were analysed based on the fact that lamb weight and daily gain are important components of lamb market production. One way to increase meat output or achieve rapid growth and heavy market weight is by using terminal sire breeds. Traits that were analysed were weights at birth (BWT), weaning (7 wk, WWT), 19 week (W19), and 31 week (W31) and post-weaning ADG from 9 to 18 or 19 weeks of age. The genetic parameters from single trait analysis are presented in table 2.6a. The estimates obtained from the analysis were all in accordance with available literature. The study concluded that the heritabilities obtained were large enough to warrant an improvement in growth traits if selection is implemented (Mousa *et al*., 1999). Selection for greater weaning weight would need to consider maternal genetic and maternal permanent environmental effects as well as the negative genetic correlation between direct and maternal effects (Mousa *et al*., 1999).

Table 2.6a. Estimates of genetic parameters from single trait analyses of weight (kg) at birth (BWT), weaning (7 wk, WWT), 19 week (W19), and 31 week (W31) and post-weaning ADG (Mousa *et al*., 1999)

Trait	h^2	m^2	r_{am}	c^2	σ_p^2
BWT	0.09	0.17	0.01	0.09	1.02
WWT	0.09	0.09	-0.39	0.12	14.64
W19	0.26	0.01	1.00	0.02	42.27
W31	0.45	0.03	-0.12	0.00	51.68
ADG	0.21	0.01	-0.52	0.03	0.005

2.7 Genotype by environmental interactions

The idea that the same genotypes may perform differently in a variety of environments has given rise to the concept of a genotype by environmental interaction (Maniatis & Pollott, 2002). This concept is most commonly thought of in terms of the ranking of breeds in different countries, regions or production systems, but can also be used to describe how sires' or dams' progeny perform on different farms or in different years. Where the same genotypes are used in two different environments it is common to investigate the genotype by environmental interaction using the genetic correlation between breeding values in each environment (Falconer, 1952). When considering more than two environments a different approach is necessary. In this case genotype by environmental interaction is a useful guide (Dickerson, 1962). In the usual estimation and interpretation of genetic effects in mixed models it is assumed that the variation accounted for by the genotype X environmental interaction (G X E) is equal to zero. This is equivalent to state that ranking of genotypes is the same across environments. Studies of general G X E interaction in livestock have mostly involved sire X environmental factors such as contemporary groups, or more specifically, herds (flocks) or years, and permanent maternal effects of the dam (Maniatis & Pollott, 2002). It is essential to ensure a well-structured distribution of genotypes across environments for an accurate estimation of such interactions. Variation due to sire X environmental (S X E) effect may also be due to heterogeneous variances among environmental groups i.e. different within-group genetic variances within the overall population. Some investigations in which sire X year were fitted as significant effects were accompanied by significant reductions in the direct-maternal correlation compared to the models in which the interaction was ignored (Robinson, 1996; Lee & Pollack, 1997).

2.7.1 An investigation into the possible genotype by environmental interactions for weaning weight in South African Mutton Merino sheep

Weaning weight records available for the South African Mutton Merino were utilized to investigate the possibility of a genotype by environment interaction in the breed (Neser *et al.*, 1998). Two data sets were analysed. In the first, weaning weight records of 43 715 South African Mutton Merino lambs, the progeny of 970 sires in 87 flocks were used. These were all the records for the breed from all over South Africa as at that time. A high number of rams exchange hands each year on ram sales. The result is that genetic links exist between the flocks. The number of sires with progeny across flocks in the same year was, however, limited. It is obvious that for meaningful results, sires should be nested within flock-year-season concatenations. It was possible to extract four flocks in which this did not seem to be a problem as a second data set. This data set consisted of 10 344 weaning weight records, the progeny of 172 sires (Neser *et al.*, 1998).The results obtained are depicted in tables 2.7a and 2.7b. A direct heritability estimate of 0.308±0.022 was obtained for weaning weight when FYS X S were excluded. Inclusion of the FYS X S led to marked reduction in the direct heritability to 0.017±0.00 and a $c^2_{\text{FYS X S}}$ estimate of 0.111±0.00. Although flocks were genetically related by the use of rams from other flocks, very few of these rams were used in different flocks in the same year.

Table 2.7a. Heritability (±s.e.) and (co) variance component estimates obtained in the first two analyses using the complete dataset for weaning weight (Neser *et al.*, 1998)

(Co)variance components	Analysis 1 (FYS XS excluded)	Analysis 2 (FYS X S included)
Direct heritability	0.308 ±0.022	0.017±0.000
Maternal heritability	0.176±0.021	0.074±0.002
Covariance as proportion of total	-0.158±0.019	-0.007±0.000
Dam permanent environment	0.085±0.013	0.085±0.008
FYS X S as additional random factor	n.a.	0.111±0.000
Direct additive variance	7.456	0.418
Maternal additive variance	4.268	1.813
Covariance between animal effects	-3.189	0.166
Variance owing to permanent maternal	2.058	2.076
Variance owing to FYS X S	n.a.	2.7132.713
Error Variance	14.273	17.205
Phenotypic variance	24.237	24.390
Correlation between direct and maternal effects	-0.677	0.191

n.a. – Not applicable

Table 2.7b. Heritability (±s.e.) and (co) variance component estimates obtained in the first two analyses using the second dataset (Neser *et al.*, 1998)

(Co)variance components	Analysis 3 (FYS XS excluded)	Analysis 4 (FYS X S included)
Direct heritability	0.353±0.035	0.125±0.061
Maternal heritability	0.171±0.032	0.087±0.037
Covariance as proportion of total	-0.167±0.030	-0.038±0.037
Permanent maternal as additional random factor	0.072±0.018	0.071±0.024
FYS X S as additional random factor	n.a.	0.107±0.019
Direct additive variance	7.696	2.766
Maternal additive variance	3.735	1.920
Covariance between animal effects	-3.649	-0.846
Variance owing to permanent maternal	1.566	1.571
Variance owing to FYS X S	n.a.	2.365
Error Variance	12.460	14.358
Phenotypic variance	21.809	22.134
Correlation between direct and maternal effects	-0.681	-0.367

n.a. – Not applicable

Results from the second data set are therefore presented in table 2.7b. The inclusion of FYS X S led to a direct heritability estimate of 0.125±0.061 for weaning weight compared to an estimate of 0.353±0.035 when it was ignored. The $c^2_{\text{FYS X S}}$ in the former analysis amounted to 0.107±0.019. The results indicated that a genotype by environmental interaction existed in South African Mutton Merino lambs of the relevant flocks. It was, however impossible to quantify the effect of the interaction in a breed analysis because of the structure of the data. This was considered as a general problem in South African across flock analyses at that time partly due to the lack of the usage of artificial insermination across flocks (Neser *et al.*, 1998). It was deduced from the study that FYS X S interaction should be included as an additional random factor to obtain more accurate unbiased results. Analysis 2 was merely undertaken to illustrate how an inappropriate data structure can lead to unrealistic estimations of for instance, heritability, a key factor determining selection response (Neser *et al.*, 1998). Meyer (1987) reported that the exclusion of even a small genotype X environmental interaction effect can lead to an overestimation of predicted breeding values. It is obvious that a genotype by environment interaction in South African Mutton Merino breed exists but the structure of the data in the breed analysis at that time prevented the quantification of this effect.

2.8 Conclusion

The literature review highlighted the different investigations that have been conducted under mainly South African conditions with regards to terminal sire sheep breeds and their capacity in improving meat yield when used in crossbreeding. The importance of breed diversity as a potential solution to counteract the price fluctuations between wool and meat to achieve optimum productivity has been emphasized. The evaluation of genetic parameters for growth traits in mainly terminal sire sheep breeds have given background information and benchmarks for comparison with the current study. Within the South African scenario, very litte research has been conducted on the estimation of non-genetic and genetic parameters in terminal sire sheep breeds, hence the current study was conducted in order to rectify the situation. The full potential of crossbreeding Merino type ewes to terminal sire sheep breeds has been clearly demonstrated as a viable option for industry to fully capitalize on the economic gains associated with crossbreeding and breed diversity. In South Africa the genetic evaluation program for slaughter lamb production is not well structured for the exploitation of heterosis and sexual dimorphism involving specialist sire and dam breeds. The NSIS provides good infrastructure for the recording and evaluation of all major small stock breeds, hence remarkable genetic improvement and significant economic gains will be realized if across flock genetic evaluations are routinely conducted.

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Chapter 3

NON-GENETIC FACTORS INFLUENCING EARLY GROWTH TRAITS IN SOUTH AFRICAN TERMINAL SIRE SHEEP BREEDS

3.1 Abstract

Non-genetic factors influencing early growth traits in the Dormer, Ile de France and Merino Landsheep were estimated using data obtained from the National Small Stock Improvement Scheme of South Africa. The original data sets for the Dormer, Ile de France and Merino Landsheep consisted of the following number of records, respectively: 52 202, 35 553 and 7 772. The data sets were complicated to such an extent that smaller data sets had to be generated to analyse for fixed effects. The traits analysed were birth weight, pre-weaning weight, weaning weight and post-weaning weight. The fixed effects identified as having a significant effect ($P < 0.01$) on early growth traits were sex of lamb, birth type, age of dam, contemporary groups, flock, age at which trait was recorded and in some cases month of birth and year of birth. Although some significant interactions were found, they were subsequently ignored owing to their very small effects. In all three breeds, male lambs were significantly ($P < 0.001$) heavier than female lambs and single borne lambs were significantly ($P < 0.001$) heavier at birth than multiples. Age of dam was related to early growth traits of the lambs through a significant curvilinear regression in all three terminal sire sheep breeds. It was concluded from the study that the influence of non-genetic factors on early growth traits should be adjusted for or eliminated statistically in genetic evaluations in order to get accurate genetic parameter estimations. The effects of birth type and dam age in particular should also be considered in the selection of replacements. If this is not done, they will be discriminated against multiple lambs and the progeny of young and old ewes.

Keywords: Birth weight, pre-weaning weight, weaning weight, post-weaning weight, curvilinear, regression, significant.

3.2 Introduction

The level of production in sheep is a combination of the genes that the animal has inherited from both its parents as well as a mixture of seasonal, animal and husbandry factors peculiar to the prevailing environment (Lewis & Beatson, 1999). Genetic improvement through selection in a breeding program depends on the accuracy of identifying genetically superior animals. This requires that non-genetic factors (fixed effects) influencing the accuracy of predicted breeding values be either controlled experimentally or eliminated statistically (Van Wyk *et al.*, 1993a). Prior to the estimation of breeding values, a model must be specified to describe the biological processes that influence the specific measured trait (Van Wyk *et al.*, 1993a). Identification of superior animals and subsequent selection decisions should be based on genetic merit rather than on differences due to environmental effects (Safari *et al.*, 2007). Therefore, performance records of animals need to be adjusted for the non-genetic sources of variation either before or during the process of estimation of breeding values. Adjustment factors external to the data are preferred for pragmatic and operational reasons and are applied in many genetic evaluation systems throughout the world (Notter *et al.*, 2005). Development of effective genetic evaluation and improvement programs requires knowledge of the genetic parameters and environmental effects that need to be adjusted in economically important traits. These parameters need to be estimated from relevant populations as parameters and fixed effects may vary among breeds and different populations (Safari *et al.*, 2007).

One way of compensating for the unpredictable environment inherent to genetic analyses is to assign similarly raised animals to uniform groups referred to as contemporary groups. A contemporary group is a group of animals of similar breed composition, age and sex that are reared under the same managerial conditions and have had an equal opportunity to perform. Contemporary groups form the basis for all genetic evaluations, which depend on all animals in a contemporary group being subjected to similar conditions (Lofgren & Wood, 2001). The size of each contemporary group must be balanced with uniformity in each group, which is why single sire contemporary groups are normally avoided. The general rule that is followed in genetic evaluations is to include offspring of at least three sires in each contemporary group, with offspring from several litters per sire. Adjustment of performance records for known environmental effects aims at reducing the non-genetic or environmental components of the phenotypic variance (Raymond, 1982).

The effects of known non-genetic factors such as age of the animal, sex, birth status (type of birth) and age of the dam of the animal have been well documented. However, information on the magnitude of these effects is limited in national analyses on South African terminal sire sheep breeds. Against this background, the objectives of this study were to assess the significance of non-genetic factors and estimate their least square means for the Dormer, Ile de France and Merino Landsheep breeds. This information is necessary if prior adjustments for the accurate prediction of breeding values are to be made.

3.3 Materials and Methods

The original across-trait data sets for the Dormer, Ile de France and Merino Landsheep consisted of the following number of animal records respectively: 52 202, 35 553 and 7 772. Due to the complexity of the data sets across the flocks smaller data sets were created after thorough editing (Table 3.3 a-c). The original data sets were complex due some of the following reasons: (i) in many cases weights were recorded over varying periods of time depending on the breeder, some breeders lacked one or more of the four weights that could potentially be recorded, (ii) some groups of animals were not allocated to contemporary groups whilst some contemporary groups consisted of less than 10 animals, (iii) some contemporary groups had single sires, (iv) some dams had very few progeny (in some cases one or two progeny per dam over her lifetime), and (v) some sires and dams did not have recorded performance records.

3.3.1 Data Editing

Initially the data was exported to a spreadsheet in the format that could be analysed by the Statistical Analysis System (SAS, 2004). One-way frequency procedures were then implemented using the SAS programme with the aim of obtaining a general overview of the data. The implementation of one-way frequency determined the number of records each breeder contributed, the number of contemporary groups that the breeder had, the weights that were recorded by specific breeders over various age ranges, the number of progeny that each sire and dam had respectively, the number of animals in each contemporary group, the number of progeny in each birth type classification and also the number of progeny in each sex. Each contemporary group included after editing progeny of at least two sires. Progeny records of sires with fewer than 20 progeny in the data set and sires with progeny in only one flock were omitted. Since the occurrence of triplets was low, triplets and twins were pooled together as multiples. Dams which were eight years and above were pooled together. Dams which were one year old were deleted since they were very few in number. Their progeny also had very low birth weights, since there is normally competition for the partitioning of nutrients between the developing embryo and the requirements for growth in the maiden ewe. Contemporary groups which had less than 10 animals were discarded from the analyses. Also due to the complexity of the data sets the ranges of ages at which traits were recorded were determined statistically. The univariate procedure in SAS was then utilized to determine the ranges of the pre-weaning age, weaning age as well as the post-weaning age. After elucidating the means and standard deviations, 95 % confidence intervals were constructed. Only lambs with age records within the 95% confidence interval for the age associated with a specific weight were retained in the analyses. When treated in this way, weaning age ranged from 74 to 126 days and post-weaning age ranged from 127 to 399 days in the Dormer breed. Pre-weaning age accordingly ranged from 27 to 71 days and weaning age ranged from 73 to 129 days in the Ile de France breed, while pre-weaning age ranged from 29 to 77 days and weaning age ranged from 78 to 127 days in the Merino Landsheep breed.

Table 3.3a Description of the raw data used after editing for early growth traits in the Dormer breed (n = number of records, CV% = coefficient of variation and SD = standard deviation)

Trait	n	Mean	SD	CV%	Range
Birth weight (kg)	11 768	3.83	1.03	26.83	1.0 - 8.5
Weaning weight (kg)	44 776	33.06	7.50	22.69	8.0 – 60.0
Post-weaning weight (kg)	7 668	53.06	14.32	27.00	15.0 – 120.0

Table 3.3b Description of the raw data used after editing for early growth traits in the Ile de France breed (n = number of records, CV% = coefficient of variation and SD = standard deviation)

Trait	**n**	**Mean**	**SD**	**CV%**	**Range**
Birth weight (kg)	13 951	3.99	1.00	27.00	1.0 - 9.0
Pre-weaning weight (kg)	27 269	11.31	5.00	29.00	6.0 - 46.0
Weaning weight (kg)	5 903	28.47	7.74	27.29	10.0 - 58.0

Table 3.3c Description of the raw data used after editing for early growth traits in Merino Landsheep (n = number of records, CV% = coefficient of variation and SD = standard deviation)

Trait	**n**	**Mean**	**SD**	**CV%**	**Range**
Birth weight	673	3.91	0.87	21.89	2.3 – 8.2
Pre-weaning weight	1 502	20.56	5.92	28.82	6.0 – 39.0
Weaning weight	6 051	29.91	7.07	23.63	10.0 – 60.0

3.3.2 Estimation of fixed effects influencing early growth traits in South African terminal sire sheep

The General Linear Models (GLM) procedure in Statistical Analysis System (SAS, 2004) was utilized to test the significance of fixed effects on the fitted models. The operational models for analysis of each trait included only those effects that had an influence on the data ($P < 0.05$). After significance was determined for the various fixed effects, predictions of least-squares means were obtained by using the ASREML statistical package (Gilmour *et al*., 2002). The software allows the estimation of various random effects in animal breeding, while it is also capable to predict least square means for the selected fixed effects.

The following fixed effects models were adopted for the traits in each of the three breeds:

Dormer

Birth weight

$$\mathbf{Y_{ijkl} = \mu + S_i + B_j + F_k + C_l + D_m + e_{ijklm}}$$

Where:
Y_{ijkl} = birth weight of the ijkl'th lamb (kg)
μ = population mean
S_i = fixed effect of the i^{th} sex (i = 1, 2) (male/female)
B_j = fixed effect of the j^{th} birth type (j = 1, 2) (single/multiple)

F_k = fixed effect of the k^{th} flock (k = 1, 2, 3………18)

C_l = effect of the l^{th} contemporary group (l = 1, 2, 3…571)

D_m = fixed effect of the m^{th} dam age (m = 2, 3, 4,…..8)

e_{ijklm} = random error

Weaning weight

$$\mathbf{Y_{ijklm} = \mu + D_i + F_j + S_k + B_l + C_m + b_o(WA_{ijklm}) + e_{ijklm}}$$

Where:

Y_{ijklm} = weaning weight of the ijklm'th lamb (kg)

μ = population mean

D_i = fixed effect of the i^{th} dam age (i = 2, 3, 4…….8)

F_j = fixed effect of the j^{th} flock (j = 1, 2, 3……86)

S_k = fixed effect of the k^{th} sex (k= 1, 2) (male/female)

B_l = fixed effect of the l^{th} birth type (l = 1, 2) (single/multiple)

C_m = effect of the m^{th} contemporary group (m= 1, 2, 3…2038)

WA_{ijklm} = weaning age fitted as a linear covariate

b_o = regression coefficient of Y_{ijklm} on weaning age (WA_{ijklm})

e_{ijklm} = random error

Post-weaning weight

$$\mathbf{Y_{ijklm} = \mu + D_i + F_j + S_k + B_l + C_m + b_o(PWA_{ijklm}) + e_{ijklm}}$$

Where:

Y_{ijklm} = post-weaning weight of the ijklm'th lamb (kg)

μ = population mean

D_i = fixed effect of the i^{th} dam age (i = 2, 3, 4…….8)

F_j = fixed effect of the j^{th} flock (j = 1, 2, 3……48)

S_k = fixed effect of the k^{th} sex (k= 1, 2) (male/female)

B_l = fixed effect of the l^{th} birth type (l = 1, 2) (single/multiple)

C_m = effect of the m^{th} contemporary group (m= 1, 2, 3…383)

PWA_{ijklm} = post-weaning age fitted as a linear covariate

b_o = regression coefficient of Y_{ijklm} on post-weaning age (PWA_{ijklm})

e_{ijklm} = random error

Ile de France

Birth weight

$$\mathbf{Y_{ijklm} = \mu + S_i + B_j + F_k + C_l + D_m + e_{ijklm}}$$

Where:

Y_{ijklm} = birth weight of the ijklm'th lamb (kg)
μ = population mean
S_i = fixed effect of the i^{th} sex (i = 1, 2) (male/female)
B_j = fixed effect of the j^{th} birth type (k = 1, 2) (single/multiple)
F_k = fixed effect of the k^{th} flock (k = 1, 2, 3………68)
C_l = effect of the l^{th} contemporary group (l = 1, 2, 3…654)
D_m = fixed effect of the m^{th} dam age (m = 2, 3, 4,…..8)
e_{ijklm} = random error

Pre-weaning weight

$$\mathbf{Y_{ijklm} = \mu + D_i + F_j + S_k + B_l + C_m + b_o(PWA_{ijklm}) + e_{ijklm}}$$

Where:

Y_{ijklm} = pre-weaning weight of the ijklm'th lamb (kg)
μ = population mean
D_i = fixed effect of the i^{th} dam age (i = 2, 3, 4…….8)
F_j = fixed effect of the j^{th} flock (j = 1, 2, 3……144)
S_k = fixed effect of the k^{th} sex (k= 1, 2) (male/female)
B_l = fixed effect of the l^{th} birth type (l = 1, 2) (single/multiple)
C_m = effect of the m^{th} contemporary group (m= 1, 2, 3…988)
PWA_{ijklm} = Pre-weaning age fitted as a linear covariate
b_o = regression coefficient of Y_{ijklm} on pre-weaning age ($PWA_{\mathbf{ijklm}}$)
e_{ijklm} = random error

Weaning weight

$$\mathbf{Y_{ijklm} = \mu + D_i + F_j + S_k + B_l + C_m + b_o(WA_{ijklm}) + e_{ijklm}}$$

Where:

Y_{ijklm} = Weaning weight of the ijklm’th lamb (kg)
μ = population mean
D_i = fixed effect of the i^{th} dam age (i = 2, 3, 4…….8)
F_j = fixed effect of the j^{th} flock (j = 1, 2, 3……58)
S_k = fixed effect of the k^{th} sex (k= 1, 2) (male/female)
B_l = fixed effect of the l^{th} birth type (l = 1, 2) (single/multiple)
C_m = effect of the m^{th} contemporary group (m= 1, 2, 3…268)
WA_{ijklm} = Weaning age fitted as a linear covariate
b_o = regression coefficient of Y_{ijklm} on weaning age ($WA_{\mathbf{ijklm}}$)
e_{ijklm} = random error

Merino Landsheep

Birth weight

$$\mathbf{Y_{ijklmn} = \mu + S_i + B_j + M_k + C_l + F_m + D_n + e_{ijklmn}}$$

Where:
Y_{ijkmn} = birth weight of the ijklm’th lamb (kg)
μ = population mean
S_i = fixed effect of the i^{th} sex (i = 1, 2) (male/female)
B_j = fixed effect of the j^{th} birth type (j = 1, 2) (single/multiple)
M_k = fixed effect of the k^{th} month of birth (k = 1, 2, 3………12)
C_l = effect of the l^{th} year of birth (l= 1999, 2000…….2007)
F_m = effect of the m^{th} flock (m = 1, 2)
D_n = fixed effect of the n^{th} dam age (m = 2, 3, 4,…..8)
e_{ijklmn} = random error

Pre-weaning weight

$$\mathbf{Y_{ijklmn} = \mu + D_i + F_j + S_k + B_l + C_m + P_n + b_o(PWA_{ijklmn}) + e_{ijklmn}}$$

Where:

Y_{ijklmn} = pre-weaning weight of the ijklmn'th lamb (kg)

μ = population mean

D_i = fixed effect of the i^{th} dam age (i = 2, 3, 4…….8)

F_j = fixed effect of the j^{th} month of birth (j = 1, 2, 3……12)

S_k = fixed effect of the k^{th} sex (k= 1, 2) (male/female)

B_l = fixed effect of the l^{th} birth type (l = 1, 2) (single/multiple)

C_m = effect of the m^{th} year of birth (m= 1983, 1984…..2005)

P_n = effect of the n^{th} flock (n= 1, 2, ….6)

PWA_{ijklmn} = Pre-weaning age fitted as a linear covariate

b_o = regression coefficient of Y_{ijklmn} on pre-weaning age (PWA_{ijklmn})

e_{ijklmn} = random error

Weaning weight

$$\mathbf{Y_{ijklmn} = \mu + D_i + F_j + S_k + B_l + C_m + E_n + b_o(WA_{ijklmn}) + e_{ijklmn}}$$

Where:

Y_{ijklm} = Weaning weight ijklm'th (kg)

μ = population mean

D_i = fixed effect of the i^{th} dam age (i = 2, 3, 4…….8)

F_j = fixed effect of the j^{th} flock (j = 1, 2, 3……19)

S_k = fixed effect of the k^{th} sex (k= 1, 2) (male/female)

B_l = fixed effect of the l^{th} birth type (l = 1, 2) (single/multiple)

C_m = effect of the m^{th} year of birth (m= 1982, 1983…..2005)

E_n = effect of the n^{th} month of birth (n= 1, 2 ….12)

WA_{ijklmn} = Weaning age fitted as a linear covariate

b_o = regression coefficient of Y_{ijklmn} on weaning age (WA_{ijklmn})

e_{ijklmn} = random error

3.4 Results and Discussion

Analysis of variance indicated that the effects included were highly significant (P < 0.001) for all of the following variables analysed: contemporary group, sex of lamb (male or female), birth type (single or multiple), dam age (2-8 years), the ages at which weights were recorded and flock. No significant interactions were obtained between the variable combinations such as contemporary group by sex. Least square means and standard errors of fixed effects affecting early growth traits in the Dormer, Ile de France and Merino Landsheep are presented in Tables 3.4a, 3.4b and 3.4c, respectively.

Table 3.4a. Least square means (±s.e.) depicting the influence of fixed effects on early growth traits in Dormer sheep

Fixed Effect	**Birth Weight (kg)**	**Weaning Weight (kg)**	**Post-weaning weight (kg)**
Overall mean	3.83 ± 0.03	33.06 ± 0.21	53.06 ± 0.30
Contemporary group	***	***	***
Sex[a]	***	***	***
Ram	3.79 ± 0.04	32.56 ± 0.21	56.02 ± 0.10
Ewe	3.52 ± 0.04	30.06 ± 0.21	47.38 ± 0.10
Birth type[b]	***	***	***
Single	3.96 ± 0.04	33.01± 0.21	53.17 ± 0.10
Multiple	3.36 ± 0.04	29.61 ± 0.21	50.22 ± 0.10
Dam age	***	***	***
2 years	3.58 ± 0.05	31.12 ± 0.20	50.79 ± 0.56
3 years	3.66 ± 0.05	31.76 ± 0.20	52.33 ± 0.56
4 years	3.69 ± 0.05	31.73 ± 0.21	52.57 ± 0.60
5 years	3.72 ± 0.05	31.65 ± 0.21	52.90 ± 0.59
6 years	3.69 ± 0.05	31.40 ± 0.22	52.48 ± 0.65
7 years	3.65 ± 0.07	30.99 ± 0.27	52.28 ± 0.90
8 years	3.65 ± 0.09	30.53 ± 0.42	50.73 ± 1.57
Flock	***	***	***
Weaning age	na	0.30 ± 0.02***	na
Post-weaning age	na	na	0.35 ± 0.01***

***Significant P < 0.001

na- not applicable

[a] Adjusted to a dam age of 4 years

[b] Adjusted to a dam age of 4 years

Table 3.4b. Least square means (±s.e.) depicting the influence of fixed effects on early growth traits in Ile de France sheep

Fixed Effect	**Birth Weight (kg)**	**Pre-weaning weight (kg)**	**Weaning weight (kg)**
Overall mean	3.99 ± 0.02	11.31 ± 0.11	28.47 ± 0.31
Contemporary group	***	***	***
Sex[a]	***	***	***
Ram	3.91 ± 0.03	12.53 ± 0.10	27.85 ± 0.13
Ewe	3.68 ± 0.03	12.18 ± 0.10	26.44 ± 0.13
Birth type[b]	***	***	***
Single	4.11 ± 0.03	12.84 ± 0.10	29.47 ± 0.10
Multiple	3.48 ± 0.03	12.13 ± 0.10	24.82 ± 0.10
Dam age	***	**	***
2 years	3.69 ± 0.05	12.52 ± 0.20	26.63 ± 0.34
3 years	3.85 ± 0.05	12.65 ± 0.20	27.86 ± 0.34
4 years	3.89 ± 0.05	12.68 ± 0.21	27.89 ± 0.33
5 years	3.85 ± 0.05	12.72 ± 0.21	27.94 ± 0.35
6 years	3.87 ± 0.05	12.68 ± 0.22	27.59 ± 0.38
7 years	3.78 ± 0.05	12.66 ± 0.27	26.51 ± 0.43
8 years	3.76 ± 0.06	12.57 ± 0.42	26.12 ± 0.54
Flock	***	***	***
Pre-weaning age	na	0.18 ± 0.02***	na
Weaning age	na	na	0.31 ± 0.02***

***Significant P < 0.001; **Significant at P < 0.01

na- not applicable

[a] Adjusted to a dam age of 4 years

[b] Adjusted to a dam age 4 years

Table 3.4c. Least square means (±s.e.) depicting the influence of fixed effects on early growth traits in Merino Landsheep.

Fixed Effect	Birth Weight (kg)	Pre-weaning weight (kg)	Weaning weight (kg)
Overall mean	3.91 ± 0.20	20.56 ± 0.19	29.91 ± 0.63
Sex	***	***	***
Ram	4.37 ± 0.04	17.26 ± 0.64	32.38 ± 0.20
Ewe	4.22 ± 0.04	16.61 ± 0.63	30.57 ± 0.20
Birth type	***	***	***
Single	4.72 ± 0.04	17.98 ± 0.64	34.21 ± 0.20
Multiple	3.87 ± 0.04	15.89 ± 0.64	28.73 ± 0.20
Dam age	***	**	***
2 years	3.92 ± 0.13	16.56 ± 0.52	30.81 ± 0.45
3 years	4.31 ± 0.13	17.21 ± 0.51	32.05 ± 0.46
4 years	4.57 ± 0.13	17.71 ± 0.52	32.22 ± 0.46
5 years	4.56 ± 0.13	17.61 ± 0.53	32.17 ± 0.47
6 years	4.51 ± 0.14	17.44 ± 0.53	32.13 ± 0.49
7 years	4.42 ± 0.15	17.29 ± 0.59	31.25 ± 0.51
8 years	4.13 ± 0.06	16.98 ± 0.75	30.50 ± 0.54
Flock	**	***	***
Pre-weaning age	na	0.20 ± 0.02***	na
Weaning age	na	na	0.29 ± 0.02***
Year of birth	*	*	*
Month of birth	*	*	*

***Significant at P < 0.001; **Significant at P < 0.01; *Significant at P < 0.05

na- not applicable

Ram lambs were heavier than ewe lambs at birth and single-borne lambs were heavier than multiples (twins and triplets) at birth (P < 0.001) for all the three terminal sire sheep breeds (Tables 3.4a-3.4c). The effects of gender and birth type on performance were in correspondence with the available literature (Bathaei & Leroy, 1998; Cloete *et al*., 1998; Lawrie, 1998; Snyman & Olivier, 2002; Greef *et al*., 2003; Cloete *et al*., 2007; Safari *et al*., 2007). Sex influences early growth traits mainly because of the effect of androgens (Jenkins *et al*., 1988). Intact males generally have a greater growth rate than castrated males and females. High levels of testosterone in male sheep result in an improved growth rate, feed efficiency and carcass composition (Jenkins *et al*., 1988). Preliminary reports by DeHaan *et al.* (1986; 1987) provide additional support for the improvement of growth rate, feed efficiency and carcass composition of ewe lambs by pre-natal exposure to testosterone. Variation in birth weight can also be affected by other factors that were not accounted for in this study. Gestation length is known to affect birth weight (Fogarty *et al*., 2005). The sex of the lambs affects gestation length of sheep. In a study by Fogarty *et al*. (2005), gestation length for ewes that had all male lambs was 0.3 days longer than for ewes with all female lambs, whereas it was intermediate when both sexes were present in the litter. Sire breed and its interaction with year was also demonstrated to affect gestation length and thus in turn birth weights. Significant influences of contemporary groups were found for all traits in all the three breeds. These effects constitute climatic, resource and managerial differences between flocks, years and seasons. Such effects are not repeatable, and therefore of little importance in the evaluation of livestock. However, they need to be considered, as they will become part of the residual variance if unaccounted for, therefore leading to deflated parameter estimates.

3.4.1 The effect of dam age on birth weight in terminal sire sheep breeds

There were significant ($P < 0.001$) curvilinear effects (R^2 values displayed on Figures 3.4a-3.4c) of dam age on birth weights in all the three breeds studied which was consistent with other studies (Lewis *et al*., 1989; Yazdi *et al*., 1998; Cloete *et al*., 2002; Notter *et al*., 2005). Birth weight increased for the progeny of 2-year old dams and peaked at a dam age of about 5 years before beginning to decline with advancing age of the ewe in all three breeds studied (Figures 3.4a-3.4c). The possible reason for this observation is that there is a competition for nutrients between the growing ewe and the developing foetus in maiden ewes. The capacity of ewes to provide nourishment for the developing fetus increases once they have reached reproductive maturity. Unfortunately this attribute is compromised as ewes mature to ages greater than 7 years. It also suggests a reduction of this ability in both younger and older ewes. Since first-lambing ewes are not physically or biologically mature and still developing themselves, the nutrients they consume are partitioned not only into lactation, maintenance and gestation, but also towards their own growth (Rumph & Van Vleck, 2004). Likewise, as ewes become older, their ability to provide an adequate uterine environment for the unborn lamb may diminish. A similar trend has been observed in other livestock species such as cattle (Swiger, 1961; Elzo *et al*., 1987). The biggest differences between age groups of ewes suggests that when enough records are available for different age groups, age specific adjustment factors are preferable, as was also concluded by Notter (2000).

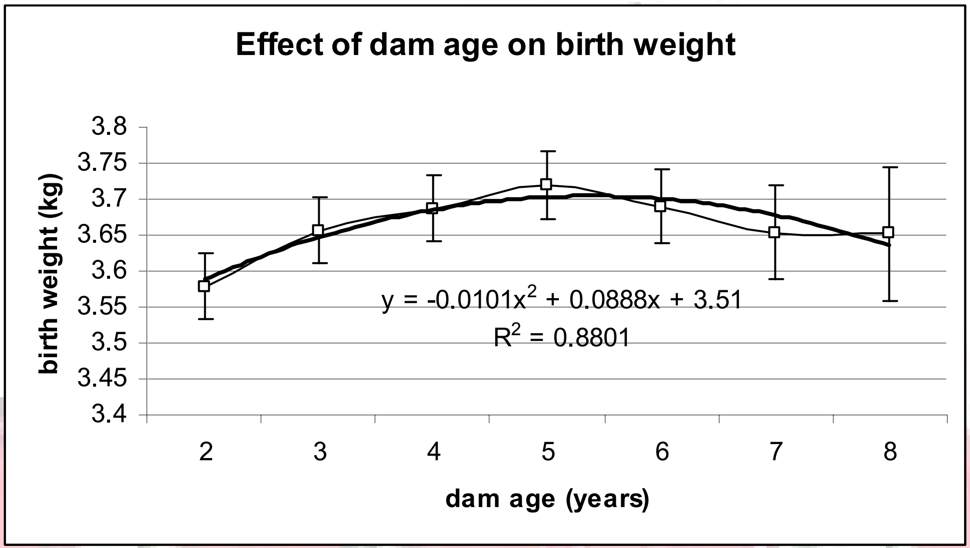

Figure 3.4a The regression of birth weight on dam age for the Dormer breed. Vertical bars around the observed means denote standard errors

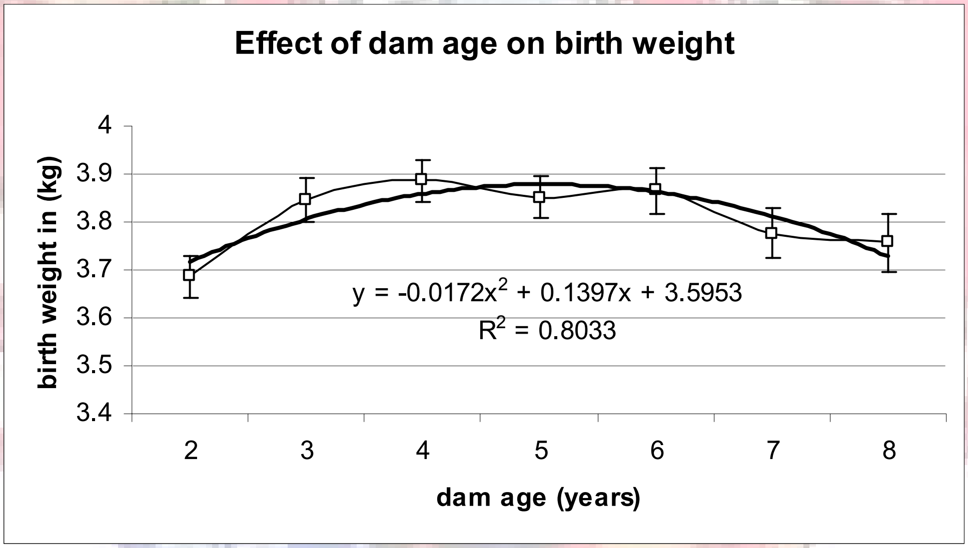

Figure 3.4b The regression of birth weight on dam age for the Ile de France breed. Vertical bars around the observed means denote standard errors

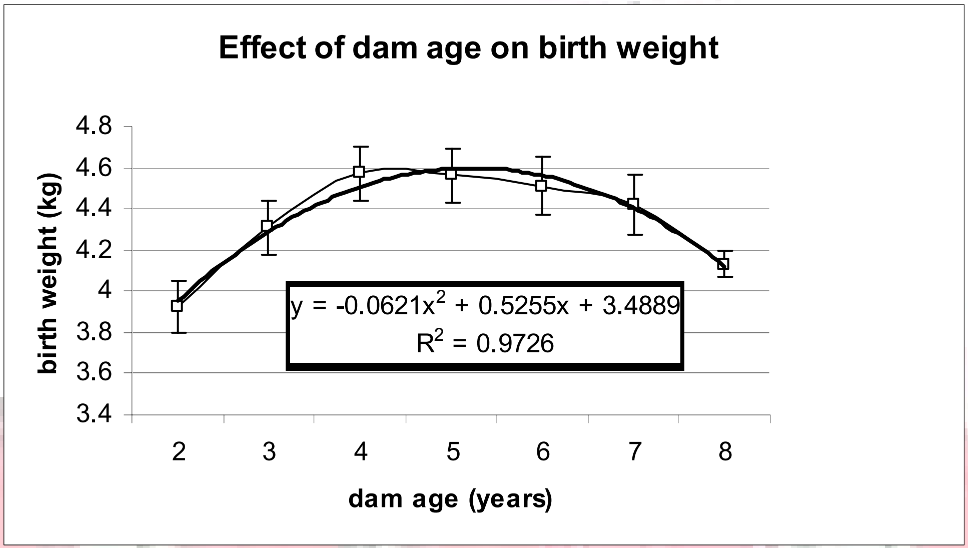

Figure 3.4c The regression of birth weight on dam age for the Merino Landsheep breed. Vertical bars around the observed means denote standard errors

3.4.2 The effect of dam age on pre-weaning weight in terminal sire sheep breeds

Dam age had a significant effect ($P < 0.01$) on pre-weaning weight in the Ile de France and Merino Landsheep breeds, where adequate records were available for the assessment of the effect of dam age on pre-weaning weight. There was a curvilinear regression (R^2 values displayed in Figures 3.4d-3.4e) of pre-weaning weight on dam age in the Ile de France and Merino Landsheep breeds. Pre-weaning weight increased for the progeny of 2-year old ewes and peaked at a dam age of about 5 years before beginning to decline with advancing age of the ewe. Since first-lambing ewes are not physically or biologically mature and still developing themselves, the nutrients they consume are partitioned not only into lactation, maintenance and gestation, but also towards their own growth (Rumph & Van Vleck, 2004). Production of sheep reflects the genes that an animal has inherited from both its parents as well as a mixture of seasonal and husbandry factors peculiar to the environment an animal finds itself in (Lewis & Beatson, 1999). In young mammals the milk production of the dam and the maternal care she provides largely contribute to their growth (Badford, 1972; Lewis & Beatson, 1999). The dam's genes for these traits affect the environment experienced by the offspring through milk production and the mothering ability (Bourdon, 2000). Maternal effects may be expected to be more important in sheep than in cattle because of the relative variation in litter size in sheep and the competition between the lambs for their mother's milk supply (Snyman *et al*., 1995).

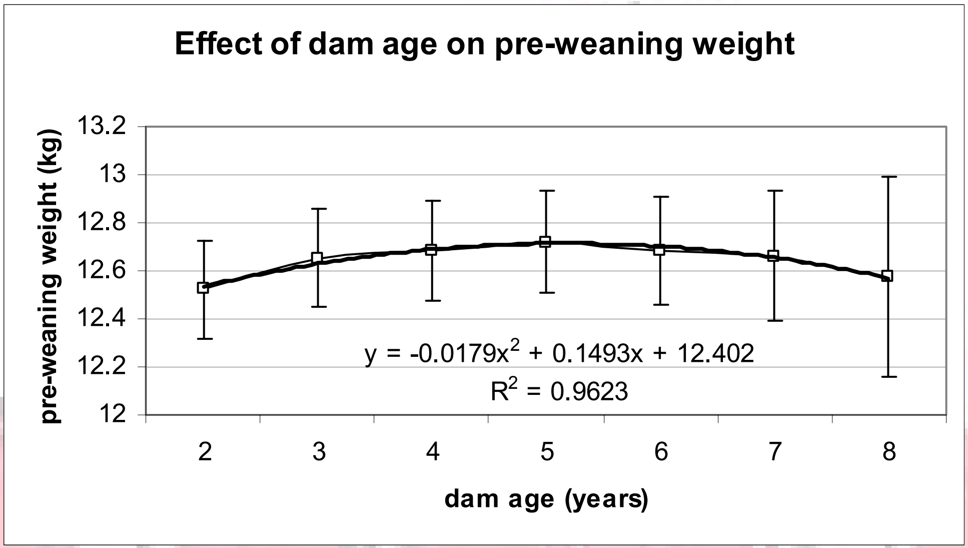

Figure 3.4d The regression of pre-weaning weight on dam age for the Ile de France breed. Vertical bars around the observed means denote standard errors

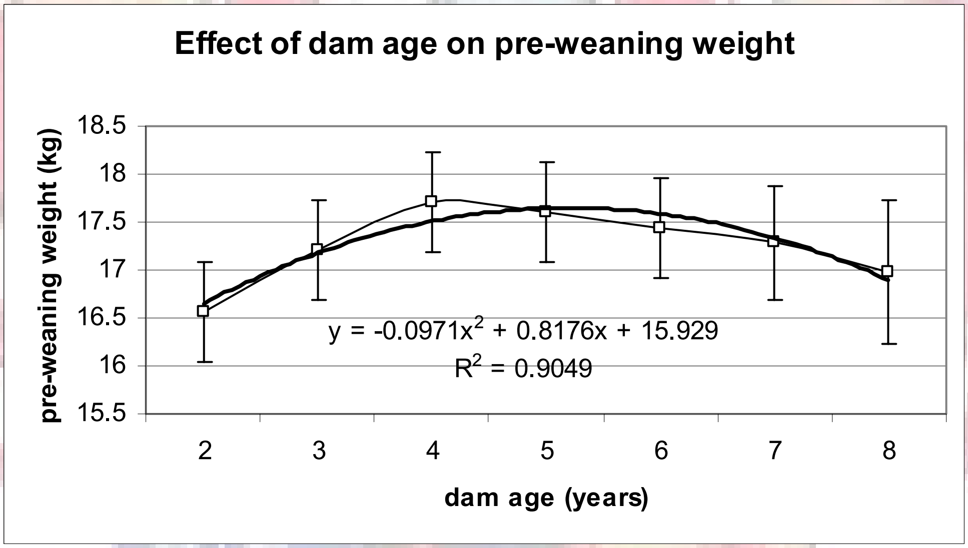

Figure 3.4e The regression of pre-weaning weight on dam age for the Merino Landsheep breed. Vertical bars around the observed means denote standard errors

3.4.3 The effect of dam age on weaning weight in terminal sire sheep breeds

There were significant ($P < 0.001$) curvilinear effects (R^2 values displayed in Figures 3.4f-h) of dam age on weaning weights in the three terminal sire sheep breeds studied. The average weaning weight of lambs increased from 31.12 kg at a dam age of 2 years and peaked at 31.76 kg at a dam age of 3 years ($P < 0.001$)

and declined thereafter as ewes got older in Dormer sheep. Weaning weight increased from 26.63 kg at a dam age of 2 years to a maximum of 27.94 kg at a dam age of 5 years in the Ile de France and gradually decreased thereafter. Two-year old ewes weaned lambs that weighed on average 30.80 kg in the Merino Landsheep. Weaning weight increased as the age of the dam increased up to a maximum of 32.23 kg at a dam age of 4 years in Merino Landsheep. The high weaning weights were maintained for up to approximately 6 years and thereafter gradually diminished. Generally, Dormer and Merino Landsheep were heavier at weaning than Ile de France sheep. The difference in weaning weight between the breeds could be attributed to the different ages at which the traits were taken (see section 3.3.1). The trend in weaning weight as affected by dam age were consistent with other findings from literature (Cloete & De Villiers, 1987; Lewis *et al*., 1989; Manyuchi *et al*., 1991; Shoeman & Buger, 1992; Van Wyk *et al*., 1993a Yazdi *et al*., 1998; Cloete *et al*., 2002; Notter *et al*., 2005). The biggest differences between age groups of ewes suggests that when sufficient records are available for different age groups, age specific adjustment factors are preferable, as was also concluded by Notter (2000). This outcome may further be explained by other factors apart from the lamb's own ability to grow. During the pre-weaning growth period (birth to weaning) the maternal influence provided by the dam is no longer the uterine environment but it is essentially mothering ability, which is mainly based on milk production and/ or maternal behaviour of the dam (Robison *et al*., 1978).

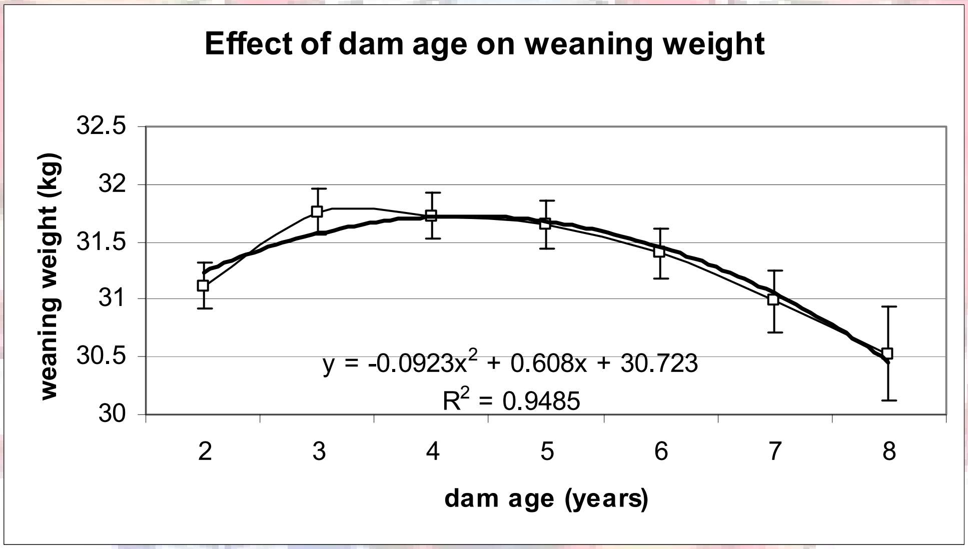

Figure 3.4f The regression of weaning weight on dam age for the Dormer breed. Vertical bars around the observed means denote standard errors

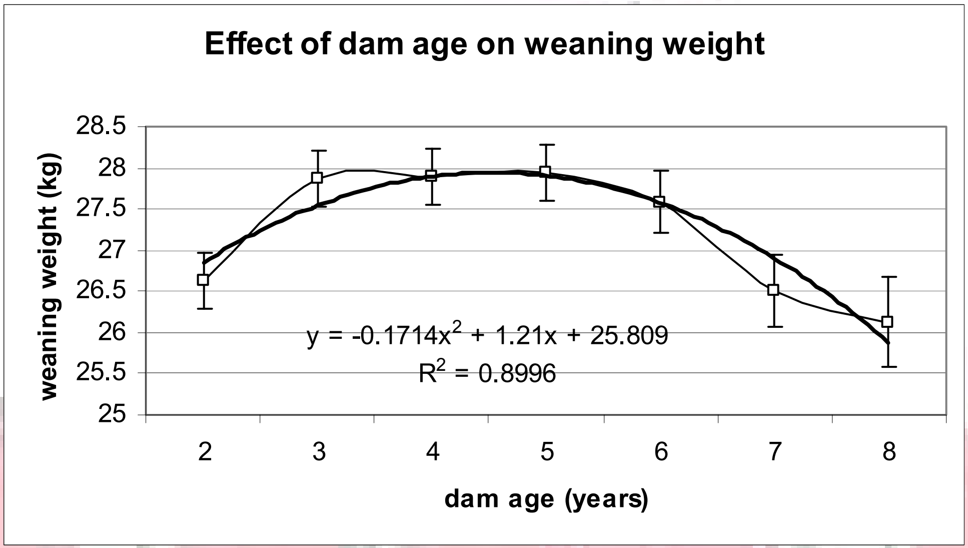

Figure 3.4g The regression of weaning weight on dam age for the Ile de France breed. Vertical bars around the observed means denote standard errors

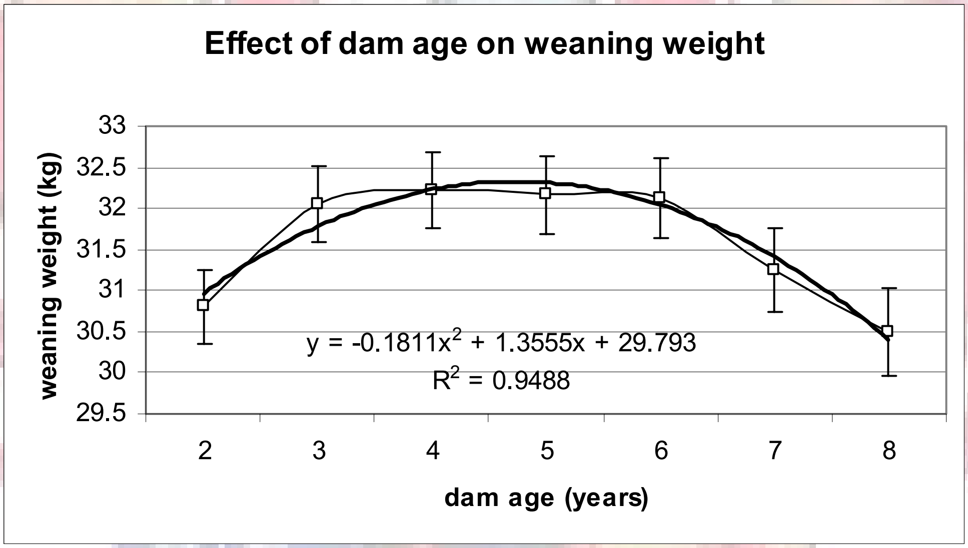

Figure 3.4h The regression of weaning weight on dam age for the Merino Landsheep breed. Vertical bars around the observed means denote standard errors

3.4.4 The effect of dam age on post-weaning weight in the Dormer breed

There was a significant ($P < 0.001$) curvilinear regression ($R^2 = 0.9429$) of post-weaning weight on dam age for the Dormer breed (Figure 3.4i). This effect can be attributed to carry-over effects from the pre-weaning stage. The post-weaning growth of lambs largely depends on their independent ability to grow. After weaning the lamb begins to express its individual genes for growth in the prevailing environment. However maternal effects have a carry-over effect at this stage. Post-weaning growth depends strongly on the birth and weaning weights of the lambs. Basing on this reasoning, weaning weight should be fitted as a covariate when analysing for post-weaning weight. Furthermore, if the pre-weaning environment provided by the dam was insufficient, post-weaning compensatory growth may be experienced (Tawonezvi, 1989). Conversely, if the maternal environment is too abundant, the lambs may gain less weight initially in the post-weaning period (Young *et al.*, 1978).

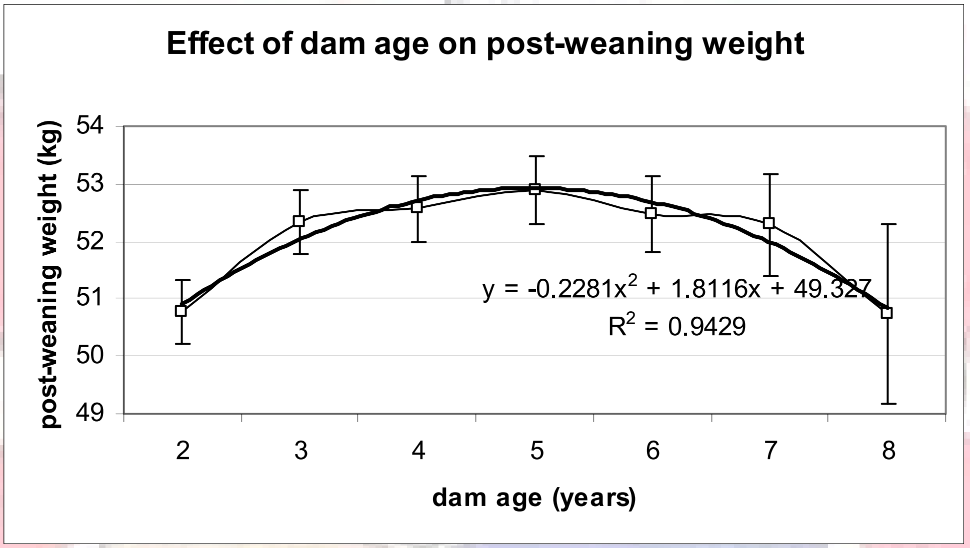

Figure 3.4i The regression of post-weaning weight on dam age for the Dormer breed. Vertical bars around the observed means denote standard errors

3.4 Conclusion

Early growth traits were affected by all the non-genetic factors studied in these investigations in all the terminal sire sheep breeds. Therefore, genetic evaluation and improvement programs need to include these factors in models used for the estimation of breeding values. The superiority of lambs born as singles over multiples is well documented in literature (Bichard & Cooper, 1966; Van der Merwe, 1976; Fourie & Heydenrych, 1982; Shrestha & Vesely, 1986; Mavrogenis & Constantinou, 1990). Failure to adjust for birth status will result in selection favouring lambs born as singles. As expected all the early growth traits were affected by age of dam. Older dams gave birth to heavier lambs than younger dams. This led to the conclusion that in order to obtain optimum growth rates and heavy lamb carcasses in terminal crossbreeding production systems, mature dams should be utilized. Diminishing returns in terms of live weights will definitely be obtained when dams older than 7 years are used in prime lamb production systems. Male lambs were consistently heavier than female lambs and attained higher weights than their female contemporaries leading to the conclusion that better live weights and more returns per capital employed can be achieved by using ram lambs than ewe lambs in slaughter lamb production systems. Contemporary groups should be well allocated in production systems to attain more accurate estimations. They should include progeny from at least three sires in each contemporary group, with offspring from several litters per sire and each dam contributing at least four progeny (Lofgren & Wood, 2001). The significant effect of age of dam on liveweight traits also led to the conclusion that when enough data are available for analysis, age specific adjustment factors should be developed. The regression of liveweight on age has been commonly used to adjust liveweight to a standard age (Brown & Reventer, 2002). This is achieved by using the within group relationship between age and weight. A number of methods for correcting liveweight for age have been investigated. These include pooled regression (within sire groups), average daily gain and least squares (Gregory *et al*., 1976; Gregory *et al*., 1977a). The method used to correct liveweight observations for age must also be capable of eliminating variation in weights caused by non-random use of sires during the mating period (Gregory *et al*., 1977b).

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Chapter 4

GENETIC FACTORS INFLUENCING EARLY GROWTH TRAITS IN SOUTH AFRICAN TERMINAL SIRE SHEEP BREEDS

4.1 Abstract

(Co)variance estimates for birth weight, pre-weaning weight, weaning weight and post-weaning weight were obtained using REML procedures for the Dormer, Ile de France and Merino Landsheep breeds. However, pre-weaning weights were available for the Ile de France and Merino Landsheep breeds only and post-weaning weights were available only for the Dormer breed. Direct heritabilities (h^2) using the most appropriate animal models in single-trait analyses were 0.21 ± 0.03, 0.23 ± 0.02 and 0.29 ± 0.05 for birth weight, weaning weight and post-weaning weight respectively for the Dormer breed. Direct heritability estimates were 0.31 ± 0.14, 0.09 ± 0.02 and 0.14 ± 0.003 for birth weight, pre-weaning weight and weaning weight respectively for the Ile de France breed also using single-trait analyses. Single-trait direct heritability estimates for birth weight, pre-weaning weight and weaning weight were 0.23 ± 0.13, 0.36 ± 0.05 and 0.17 ± 0.03 respectively for the Merino Landsheep breed. There was a difficulty in partitioning maternal effects into both m^2 and c^2 in almost all the analyses due to the poor population structures that culminated from the random entrance and exit of flocks from the scheme. The poor population structures resulted in the loss of genetic links across flocks and across generations within flocks. The poor data structures also resulted in the correlation between direct and maternal effects (r_{am}) being excluded from all the analyses because if they were conscripted into the models, uncharacteristic high and negative correlations were obtained. Genetic, phenotypic and environmental correlations were estimated using three-trait analysis and were found to be moderate to high for early growth traits for the Dormer and the Ile de France. The reasonable genetic parameter estimates obtained in the study led to the conclusion that the use of terminal sires in crossbreeding programs will probably result in an improvement in meat traits.

Keywords: Birth weight, pre-weaning weight, weaning weight, post-weaning weight, heritability, log likelihood, crossbreeding.

4.2 Introduction

Fluctuations and a general decline in the ratio between wool and meat prices resulted in marked changes in the South African Merino industry, also involving the breeding of Merino sheep for an improved meat production capability (Olivier & Cloete, 1998). When a species produces more than one commodity, such as meat and wool, as is the case with dual-purpose sheep, benefits from genetic response are expressed as increased profitability due to improvements in wool production, reproductive ability, and lamb weight (Bromley *et al*., 2000). Sheep breeders produce two major commodities for sale, namely: wool and meat. To ensure the best possible profit margins, superior management and the optimum combination of genetics is required (Fogarty, 2006). Research that has been undertaken to date shows that there are no major genetic antagonisms between wool and meat traits and that improvement can be achieved in both traits using an appropriate selection index (Fogarty, 2006).

Genetic change resulting from within-flock selection is comparatively slow, while it also takes time to filter through the structures of a breed (Cloete & Durand, 2000). Commercial producers now exploit other mechanisms such as terminal crossbreeding of Merino-type ewes with meat type breeds or dual-purpose breeds to attain short-term benefits resulting from price fluctuations between wool and meat without compromising the wool-producing capacity of their ewe flocks. Crossbreeding of Merino-type ewes with dual-purpose or meat rams are often seen as an option to achieve this objective (Cloete & Durand, 2000). Crossbreeding systems with specialized breeds is more profitable than a system based on a single dual-purpose breed (Van der Werf, 2006).

Other breeds have been developed in various countries for specialist meat or milk production (Fogarty, 2006). Sheep breeders in many countries have imported breeds and genetic material in an attempt to obtain a quantum leap in productivity, to produce a better quality or new product, or to provide sheep with a major adaptive advantage. The most appropriate production system for the environment and target markets for products need to be carefully defined in any sheep breeding enterprise (Fogarty, 2006). There is considerable genetic variation between breeds that can be exploited. Therefore breed substitution has to be approached with caution. A new breed may excel in a desirable trait but may be inferior in other characteristics that contribute to overall merit for the sheep enterprise.

Crossbreeding has long been practiced as an economical and frugal method of improving efficiency in sheep production. It utilizes differences in breeds and exploits hybrid vigour, which enhances the performance level of crossbred progeny above that of the mid-parental mean (Khusro *et al*., 2003). Structured crossbreeding systems exist in many countries, for example specialist meat sire breeds are mated to maternal breeds or crossbred dams in terminal crossbreeding programs. Markets for sheep products are varied and increasingly demanding for products to match particular specifications. This led to industry-wide changes in genetics and management to meet these market requirements (Fogarty, 2006).

One of the most important purposes of the terminal sire in the system is to improve the early growth of the crossbred progeny to ensure early slaughter and a reduced production cycle. According to Olivier (1999) the reduced production cycle allows the producer to maintain more ewes. However, it is crucial to note that female fertility as a trait is not that important in terminal crossbred sires. Heterosis can also be achieved by mating wool type breeds with specialist meat breed rams (Ch'ang & Atkins, 1982; Rae, 1982; Pitchford, 1993). Effects of heterosis greatly impact upon the productivity of crossbred sheep. When breeds are crossed, new combinations of gene forms are created. Therefore, crossbred sheep have increased heterozygosity relative to breeds that produced the crossbred. The increase in heterozygosity is the basis for heterosis or hybrid vigour. Other benefits arising from the use of terminal sires in crossbreeding are complementarity and sexual dimorphism. Complementarity is the improved production efficiency that results from crossbreeding systems that allow strengths of the sire breed to offset weaknesses of the dam breed and strengths of the dam breed to counter weaknesses of the sire breed (Nitter, 1978). Complementarity greatly improves the efficiency of meat production by mating ewes of specialised dam breeds to rams of specialised sire breeds. Sexual dimorphism is the systematic difference in the form between individuals of different sex in the same species. In sheep male lambs are usually heavier than female sheep of the same age and which have experienced the same birth type.

The primary goal of animal breeding is to genetically improve production and/or reproduction traits through selection (Snyman & Olivier, 2002). To achieve this objective, knowledge of genetic parameters is required for the construction of breeding plans. Against this background, the objectives of this study were to construct models and to select the most suitable random effects model for the estimation of (co)variance components for early growth traits in the Dormer, Ile de France and Merino Landsheep breeds and to estimate (co)variance components influencing birth weight, pre-weaning weight, weaning weight and post-weaning weight in the same breeds using restricted maximum likelihood (REML) procedures.

4.3 Materials and Methods

The original data sets for the Dormer, Ile de France and Merino Landsheep breeds consisted of the following number of records respectively: 52 202, 35 553 and 7 772. Due to the complexity of the data sets across the flocks smaller data sets were created after thorough editing (Table 3.3a-3.3c). The original data sets were complex due some of the following reasons: (i) in many cases weights were recorded over varying periods of time depending on the breeder, some breeders lacked one or more of the four weights that were recorded, (ii) some groups of animals were not allocated to contemporary groups whilst some had contemporary groups with less than 10 animals, (iii) some contemporary groups had single sires, (iv) some dams had very few progeny (in some cases one or two progeny per dam), and (v) some sires and dams did not have recorded performance records.

In view of the stated complications with the data structure, the correlation between direct effects and maternal effects (r_{am}) was excluded from all the final analyses. When fitted, uncharacteristically high negative direct-maternal correlations (r_{am}) were obtained. Although these correlations were within the range of estimates in the literature, more recent research indicated that such correlations may not always be a function of the underlying biological processes, and may rather be related to sampling issues (Robinson, 1995; Maniatis & Pollot, 2003; Heydarpour *et al*., 2008). There is conflicting evidence in literature on the magnitude and direction of r_{am} (Van Wyk *et al.,* 2003). This correlation is of major concern in animal breeding. According to Maniatis & Pollot (2002) such correlations could be negative for reasons other than the existence of a true antagonistic biological relationship between the direct and maternal genetic effects. It could be the result of the structure of the available data (Lewis & Beatson, 1999). In this regard, Robinson (1995) pointed out that the negative r_{am} in beef cattle results from other effects in the data rather than a true negative genetic relationship. Poor population structure can affect both the magnitude and standard error of estimates of r_{am}, and may explain some of the large negative estimates often obtained (Heydarpour *et al*., 2008). This may also hold true for sheep populations, as was thoroughly discussed by Notter & Hough (1997). Negative estimates of r_{am} are a common feature of most recent analyses of field data. In Romanov sheep it varied between -0.99 and 0.99 (Maria *et al*., 1993). Other high and negative correlations were also obtained for other growth traits in the recent past (Lewis & Beatson, 1999; Rao & Notter, 2000; Cloete *et al*., 2001; Maniatis & Pollot, 2002). It was conceded that the structure of the industry data used in this study was less than optimal, with a high proportion of dams without many repeated lamb records. After the data was edited for the Dormer breed the average number of progeny per dam was four. The Ile de France and Merino Landsheep breeds both had an average of five progeny per dam. The Ile de France breed had 851 pre-weaning records discarded because the dam in question had two or less progeny per dam. The Dormer breed had 2 611 weaning weight records discarded because of the same reason whilst the Merino Landsheep had 1 482 pre-weaning weight records discarded. In all the three breeds records of sires with less than 20 progeny within flocks or across flocks were discarded from the analyses. In both the Dormer and Ile de France breeds, records without contemporary groups were completely discarded. The Merino Landsheep breed had only 97 contemporary groups that were allocated haphazardly, hence the effect was excluded from the analyses and month and year effects were considered as an alternative. Basing on the previous arguments, the direct-maternal correlations were thus excluded from the final analyses in all breeds, as it was conceded that their size and magnitude could be related to sampling issues rather than a true biological relationship.

4.3.1 Estimation of (Co) variance components influencing early growth traits

The ASREML program (Gilmour *et al*., 2002) was used for the estimation of (co)variance components. The fixed effects that were found to be significant ($P < 0.05$; see Chapter 3) were incorporated into the operational models. Random terms were added to analytical models sequentially. Likelihood Ratio tests (LRT) were performed to assess the significance of the contribution of each random term to improvements in the model of analysis. The LRT is based on testing twice the increase in Log-likelihood resulting from adding a random term to the model of analysis as a Chi-square statistic. Alternatively, for two models with the same number of different random terms, and assuming identical fixed effect modelling, the model with the higher value for the Log-likelihood fits the data better. Random effects that were significant in the single-trait analyses were included in the three-trait analysis. Three-trait analyses were then performed to estimate correlations among traits.

The following single-trait animal models (in matrix notation) were fitted for each trait:

1. $Y = Xb + Z_1a + e$
2. $Y = Xb + Z_1a + Z_2c + e$ with $\mathrm{cov}(a,m) = 0$
3. $Y = Xb + Z_1a + Z_2m + Z_3c + e$ with $\mathrm{cov}(a,m) = 0$

Where:

Y = the vector of observations for growth traits
b = the vector of fixed effects
a = the vector of direct genetic effects
m = the vector of maternal genetic variances
c = the vector of maternal permanent environmental variances

e = the vector of residuals

X, Z_1, Z_2 and Z_3 are the corresponding incidence matrices relating the respective effects to y

It was assumed that:
$V(a) = A\sigma^2_a$; $V(m) = A\sigma^2_m$; $V(c) = A\sigma^2_c$ and $V(e) = I\sigma^2_e$

With I being an identity matrix; σ^2_a, σ^2_m, σ^2_c and σ^2_e direct genetic variance, maternal genetic variance, maternal permanent environmental variance and the environmental (residual) variance respectively.

Given the importance of genetic by environmental correlation in livestock field data, the effect of sire by contemporary group were included as a random term in the preliminary analysis on all breeds. The inclusion of this effect in all cases partitioned most of the genetic variation into the sire by contemporary group effect. As it had to be conceded that the genetic linkages across contemporary groups was less than optimum, it was decided to exclude sire by contemporary group from the final analysis. Similar results were reported by Neser *et al*. (2000) in a breed analysis on South African Mutton Merino sheep.

4.4 Results and Discussion

4.4.1 Model Selection

Log likelihood values were obtained for single-trait analyses on the respective traits. Inclusion of random factors such as direct additive effects, additive maternal effects and dam permanent environmental effects resulted in significant increments in log likelihood values. However, it was difficult to partition additive maternal effects (m^2) and dam permanent environmental effects (c^2) in most cases for all the three breeds because genetic links across the years were constantly being broken by flocks randomly entering and leaving the scheme. The results that were obtained during model construction are depicted in Tables 4.4a-4.4c.

Table 4.4a Log likelihood ratios for the respective random effects models fitted to early growth traits in the Dormer breed. The model of choice is depicted in bold figures*

Effects	Birth weight	Weaning weight	Post-weaning weight
Fixed effects only	-421.901	-2 057.700	-592.894
Fixed + h^2	-244.385	-1 603.990	-487.454
Fixed + h^2 + c^2	**-191.391**	**-1 496.600**	**-477.829**
Fixed + h^2 + m^2	-225.522	-1 568.870	-478.289
Fixed + h^2 + m^2 + c^2	-191.246	-1 496.600	-476.870

*** h^2 is the direct additive genetic effects, m^2 is the additive maternal genetic effects and c^2 is the dam permanent environment effects**

When the model for birth weight for the Dormer breed was constructed with the direct additive genetic effects as the only random factor the log likelihood increased significantly from -421.901 to -244.385 (Table 4.4a). That resulted in a direct heritability (h^2) estimate of 0.20 ± 0.02. Addition of the dam permanent environmental effect as the second random factor yielded the best model because there was a further increase in the log likelihood ratio to -191.39. The direct heritability (h^2) of birth weight of 0.21 ± 0.03 and a dam permanent environmental effect (c^2) of 0.15 ± 0.02 were estimated as depicted in Table 4.4a. However, the most intriguing attribute about the data structure was that it did not have sufficient power for partitioning m^2 and c^2. This was possibly due to the fact that there were too few granddam-dam-offspring relations. This emanated from flocks randomly moving in and out of the scheme thus, losing dam genetic ties across generations.

Likewise during model selection for weaning weight for the Dormer breed the most appropriate model included both the direct additive genetic effects as well as the dam permanent environment. Addition of direct additive genetic effects as the only random term resulted in a significant increase in the log likelihood ratio from -2 057.700 to -1 603.990. This yielded a direct heritability estimate of 0.16 ± 0.01. Addition dam permanent environment (c^2) further increased the log likelihood to -1 496.600 (Table 4.4a). As previously stated it was once again difficult to partition additive maternal genetic effects and dam permanent environmental effects due to the loss of genetic links across flocks. This feature also clearly indicates the role played by maternal effects in early growth traits in sheep. During model construction for post-weaning weight in the Dormer breed, addition of direct additive genetic effects and dam permanent environment as the only random terms resulted in a significant increase in the log likelihood ratio from -592.894 to -477.829 and yielded a direct heritability (h^2) estimate of 0.29 ± 0.05.

Table 4.4b Log likelihood ratios for the respective random effects models fitted to early growth traits in the Ile de France breed. The model of choice is depicted in bold figures*

Effects	Birth weight	Pre-weaning weight	Weaning weight
Fixed effects only	-5 386.57	-3 576.70	-2 725.99
Fixed + h^2	-4 396.67	-3 563.22	-2 687.57
Fixed + h^2 + c^2	-4 355.44	**-3 129.16**	**-2 662.84**
Fixed + h^2 + m^2	-4 356.54	-3 132.70	-2 670.65
Fixed + h^2 + m^2 + c^2	**-4 350.74**	-3 129.16	-2 662.84

*** h^2 is the direct additive genetic effects, m^2 is the additive maternal genetic effects and c^2 is the dam permanent environment effects**

The most appropriate model for birth weight in the Ile de France breed included fixed effects, direct additive effects (h^2), maternal additive effects (m^2), and dam permanent environmental effects (c^2) (Table 4.4b). The most suitable models for pre-weaning and weaning weights contained fixed effects, direct additive effects (h^2) and dam permanent environmental effects (c^2). Genetic links across generations between granddam-dam-offspring were also lost due to movement of flocks in and out of the scheme. This resulted in the failure to partition m^2 and c^2. Selection schemes for early growth and carcass traits that ignore maternal effects are likely to produce sub-optimal genetic responses (Gerstmayr, 1992). Genetic models including maternal effects and the covariance between direct and maternal genetic effects mostly fit data better than the simple additive model (Maniatis & Pollott, 2003). Exclusion of maternal effects results in biased direct heritability estimates (Nasholm & Danell, 1996; Zamani & Mohammadi, 2008). Results from earlier studies have shown that maternal effects account for much of the variation in early lamb weights (Hanrahan, 1976; Burferning & Kress, 1993; Maria *et al.*, 1993)

Table 4.4c Log likelihood ratios for the respective random effects models fitted to early growth traits in the Merino Landsheep breed. The model of choice is depicted in bold figures*

Effects	Birth weight	Pre-weaning weight	Weaning weight
Fixed effects only	0.52364	-2 998.43	-3 731.49
Fixed + h^2	4.56831	-2 875.70	-3 645.90
Fixed + h^2 + c^2	**5.25222**	-2 830.92	**-3 636.55**
Fixed + h^2 + m^2	5.25055	**-2 740.08**	-3 636.55
Fixed + h^2 + m^2 + c^2	5.25547	-2 740.08	-3 636.55

*** h^2 is the direct additive genetic effects, m^2 is the additive maternal genetic effects and c^2 is the dam permanent environment effects**

During model selection for birth weight in the Merino Landsheep breed the log likelihood ratio increased significantly from 0.52364 to 4.56831 when the additive genetic effects were added as the only random term (Table 4.4c). Extra addition of dam permanent environmental effects changed the log likelihood ratio slightly. This was probably because the Merino Landsheep data set only had 673 recorded birth weights from only 2 flocks out of a total of 7 772 records. During model selection for pre-weaning weight, the log likelihood ratio increased significantly from -2 875.70 to -2 740.08 when additive maternal genetic effect was added as an additional random factor to the additive direct genetic effects. Partitioning of m^2 and c^2 did not cause a change in the log likelihood hence the best model for pre-weaning weight contained fixed effects, h^2 and m^2. This particular feature demonstrates the significance of maternal effects in early growth traits in sheep. The model of choice for weaning weight also failed to partition maternal effects into its various components due complicated data structure which led to the loss genetic links across flocks. Although the data contained insufficient power for the partitioning of m^2 and c^2, in most analyses it is notable that a maternal variance component (of m^2 and c^2 or both) was significant in all analyses. This result underlines the importance of accounting for maternal variation in the analysis of early growth traits of sheep.

4.4.2 Single trait analyses in South African Terminal Sire Sheep Breeds

Results from the single-trait analyses are depicted in Tables 4.4d-4.4f

Table 4.4d Estimates of variance components and ratios from single-trait analysis of growth traits in the Dormer breed

Parameters	Birth weight	Weaning weight	Post-weaning weight
Direct additive (σ_a^2)	0.093152	9.46476	29.37520

Maternal permanent environment (σ_c^2)	0.0674118	5.12688	20.71193
Total phenotypic (σ_p^2)	0.439803	40.73474	102.5137
Residual (σ_e^2)	0.279239	26.14310	52.42660
Direct additive (h^2 ± SE)	0.21 (0.03)	0.23 (0.02)	0.29 (0.05)
Dam permanent environment (c^2 ± SE)	0.15 (0.02)	0.13 (0.02)	0.20 (0.03)

Table 4.4e Estimates of variance components and ratios from single-trait analysis of growth traits in the Ile de France breed

Parameters	**Birth weight**	**Pre- weaning weight**	**Weaning weight**
Direct additive (σ_a^2)	0.248102	1.31589	4.72776
Maternal additive (σ_m^2)	0.128604	-	-
Maternal permanent environment (σ_c^2)	0.0733859	3.66190	6.12685
Total phenotypic (σ_p^2)	0.791999	14.16369	32.91291
Residual (σ_e^2)	0.341907	9.18590	22.0583
Direct additive (h^2 ± SE)	0.31 (0.14)	0.09 (0.02)	0.14 (0.003)
Maternal additive (m^2 ± SE)	0.16 (0.05)	-	-
Dam permanent environment (c^2 ± SE)	0.09 (0.02)	0.26 (0.05)-	0.19 (0.02)

Table 4.4f Estimates of variance components and ratios from single- trait analysis of growth traits in the Merino Landsheep breed

Parameters	**Birth weight**	**Pre-weaning weight**	**Weaning weight**
Direct additive (σ_a^2)	0.0767159	8.39105	5.01458
Maternal additive (σ_m^2)	-	12.99080	-
Maternal permanent environment (σ_c^2)	0.0315270	-	0.445820
Total phenotypic (σ_p^2)	0.3271149	23.08341	30.3008
Residual (σ_e^2)	0.2188720	1.70156	24.8404
Direct additive (h^2 ± SE)	0.23 (0.13)	0.36 (0.05)	0.17 (0.03)
Maternal additive (m^2 ± SE)	-	0.56 (0.03)	-
Dam permanent environment (c^2 ± SE)	0.10 (0.07)	-	0.02 (0.01)

4.4.2.1 Single-trait analyses of birth weight

Direct heritability (h^2) for birth weight was 0.21 ± 0.03 and 0.23 ± 0.13 for the Dormer and Merino Landsheep breeds respectively. The moderate estimates fell within the ranges reported for dual purpose, wool and meat sheep breeds worldwide (Lewer *et al*., 1994;Snyman *et al*., 1995; Hall *et al.,* 1995; Mortimer & Atkins, 1995; Vaez Torshizi *et al*., 1996; Yazdi *et al*.,1997; Al- Shorepy & Notter, 1998; Larsgard & Olesen, 1998; Bromley *et al*., 2000; Cloete *et al*., 2002; Duguma *et al*., 2002b; Hanford *et al*., 2002; Matika *et al*., 2003; Roden *et al*., 2003; Van Vleck *et al*., 2003). The estimates in the two breeds were also consistent with the averaged values across all breeds which were reported by Safari *et al*. (2005). In the review estimates were elucidated to be 0.21 ± 0.03, 0.19 ± 0.02 and 0.15 ± 0.02 for wool, dual-purpose and meat breeds respectively. The h^2 estimate for birth weight in the Ile de France breed was 0.31 ± 0.14. This high estimate was consistent with values that were reported in literature for divergent breeds (Tosh & Kemp, 1994; Jara *et al*., 1998; Wuliji *et al*., 2001; Lewer *et al*., 1994). Of particular interest are the reports by Tosh & Kemp (1994), who estimated h^2 of birth weight in Hampshire sheep at 0.39, and Jara *et al*. (1998), who derived an estimate of 0.32 ± 0.07 in Corriedale sheep. It is essential to mention that all these estimates heavily depended on the model that was utilized for the estimation of genetic parameters particularly the random effects that were incorporated.

The estimate of m^2 for birth weight in Ile de France sheep was 0.16 ± 0.05. This medium estimate was consistent with reports from literature (Maria *et al*., 1993; Tosh & Kemp; 1994; Mortimer & Atkins, 1995; Vaez Torshizi *et al*., 1996; Analla & Serradilla, 1998; Jara *et al*., 1998; Mousa *et al*., 1999; Janssens *et al.*, 2000; Bromley *et al*., 2000; Wuliji *et al*., 2001; Simm *et al*., 2002; Duguma *et al*., 2002b; Cloete *et al*; 2002; Hanford *et al*., 2002; Van Vleck *et al*., 2003; Safari *et al*., 2005). Maternal effects are very crucial especially for early growth traits of sheep. There are several reports that have shown inflated direct heritability (h^2) estimates and consequently inflated breeding values when maternal effects were not included in the model of analysis (Nashom & Danell, 1996; Vaez Torshizi *et al*., 1996; Maniatis & Pollott, 2003; Asadi Fozi *et al*., 2005). The importance of maternal effects in livestock species is well known. Such effects arise from the ability of the dam to produce the milk needed for growth of the offspring and other maternal behaviour during the post-natal phase. For birth weight, maternal effects are generally thought to be determined by the uterine capacity of the ewes. Genetic evaluation schemes therefore attempt to separate direct and maternal effects. However, accurate evaluation requires accurate estimates of genetic variances for direct and maternal effects and their correlations. Such estimates may differ according to breed or production systems (Robinson, 1995). Accounting for maternal effects also increases the accuracy of selection (Robinson *et al*., 1992a).

The dam permanent maternal environment effects (c^2) for birth weight were 0.15 ± 0.02, 0.09 ± 0.02 and 0.10 ± 0.07 in the Dormer, Ile de France and Merino Landsheep breeds respectively. These estimates were consistent with other estimates across breeds worldwide (Snyman *et al.*, 1995; Vaez Torshizi *et al.,* 1996; Analla & Serradilla, 1998; Al- Shorepy & Notter, 1998; Cloete *et al*., 1998; Bromley *et al*., 2000; Neser *et al*., 2001; Cloete *et al*., 2002a, b; Maniatis & Pollot 2002a; Duguma *et al.*, 2002b; Simm *et al*., 2002). It is of cardinal importance to stipulate that it was difficult to partition maternal effects into both m^2 and c^2 in the Dormer and Merino Landsheep breeds because of the lack of maternal genetic ties across generations in the data. Genetic linkages had been lost across the flocks due to the random entrance and exit of flocks into the scheme. The loss in genetic linkages resulted in too few granddam-dam-offspring relations. Permanent maternal environment effects for birth weight can be attributed to the uterine environment provided by the dam as well as the effect of multiple births (Neser *et al.*, 2001).

4.4.2.2 Single-trait analyses of pre-weaning weight

Pre-weaning weight had a low h^2 estimate of 0.09 ± 0.02 in the Ile de France breed. The estimate was consistent with some of those that were reported in literature (Tosh & Kemp, 1994; Cornington *et al*., 1995; Al-Shorepy &

Notter, 1996; Notter & Hough, 1997; Analla & Serradilla, 1998; Mousa *et al*., 1999; Rao & Notter 2000; Matika *et al*., 2003; Maniatis & Pollot, 2002b). Pre-weaning weight had a much higher h^2 estimate of 0.36 ± 0.05 in Merino Landsheep. This estimate was consistent with some reported in the literature (Maria *et al*., 1993; Analla *et al*., 1997; Neser *et al*., 2000). Of particular interest is the study of Neser *et al.* (2000), who obtained a h^2 estimate at 42 days of age of 0.37 ± 0.06 in the South African Mutton Merino breed. Most of the variation was accounted for by the dam permanent environmental effects (c^2) which had a moderate estimate of 0.26 ± 0.05 in Ile de France sheep. This estimate fell within the range of literature values (Tosh & Kemp, 1994; Conington *et al*., 1995; Rao & Notter 2000; Maniatis & Pollot, 2002b; Simm *et al*., 2002). The random entrance and exit of flocks from the NSIS resulted in loss of maternal genetic links across generations. This culminated in the difficulty in further partitioning maternal effects into its components, i.e. m^2 and c^2. Estimates of m^2 were high at 0.56 ± 0.03 in the Merino Landsheep breed. This estimate was probably inflated because maternal effects are normally partitioned into direct additive maternal effects, dam permanent environmental effects and dam temporary environmental (litter) effects. Maternal effects are very crucial especially in early growth traits in sheep. The interpretation of genetic parameters for traits that are influenced by maternal effects in an animal model context is dependent on both the structure and the model used in the analysis (Safari *et al*., 2005). It is essential to partition maternal environmental effects into across year dam effects and litter effects (within year common environmental effect unique to the litter) where multiple births are common.

4.4.2.3 Single-trait analyses of weaning weight

Direct heritability (h^2) estimates for weaning weight were 0.23 ± 0.02, 0.14 ± 0.003 and 0.17 ± 0.03 in Dormer, Ile de France and Merino Landsheep breeds respectively. These moderate estimates for the Dormer and Merino Landsheep fell within the ranges that were reported in the literature across breeds (Tosh & Kemp, 1994; Mortimer & Atkins, 1995; Fossceco & Notter, 1995; Vaez Torshizi *et al.*, 1996; Aslaminejah & Roden, 1997; Saatci *et al*., 1999; Neser *et al.*, 2001; Cloete *et al*., 2001; Duguma *et al*., 2002b; Safari *et al*., 2005). The low direct heritability (h^2) estimate obtained for Ile de France breeds concurred with several literature estimates (Van Wyk *et al*., 1993; Tosh & Kemp, 1994; Conington *et al*., 1995; Pitono & James, 1995; Nashom & Danell, 1996; Snyman *et al*.,1996; Notter & Hough, 1997; Yazdi *et al*., 1997; Larsgard & Olesen, 1998; Analla & Serradilla, 1998; Lewis & Beatson, 1999; Mousa *et al*., 1999; Rao & Notter 2000; Boujenane & Kansari, 2002; Matika *et al*., 2003). The dam permanent environmental effect (c^2) for weaning weight was estimated at 0.13 ± 0.02 and 0.02 ± 0.01 in the Dormer and Merino Landsheep breeds respectively. The estimates concur with many of those reported in literature (Mortimer & Atkins, 1995; Snyman *et al*., 1996; Yazdi *et al*., 1997; Analla & Serradilla, 1998; Al- Shorepy & Notter, 1998; Lewis & Beatson, 1999; Duguma *et al.*, 2002b; Matika *et al*., 2003; Van Vleck *et al*., 2003). The estimate of c^2 for weaning weight in the Ile de France breed amounted to 0.19 ± 0.02. This was in concordance with several literature estimates across the breeds (Tosh & Kemp, 1994; Conington *et al*., 1995; Hall *et al*., 1995; Cloete *et al*., 1998; Neser *et al*., 2000; Rao & Notter 2000; Maniatis & Pollot, 2002a). The estimate differed from the averaged estimates across breeds reported by Safari *et al*. (2005). Safari *et al*. (2005) reported an average c^2 estimate for meat breeds of 0.14 ± 0.02 and 0.07 ± 0.01 for dual-purpose breeds. The moderate estimate emanated as a consequence of the failure to partition maternal effects into the various components subsequent loss of genetic linkages across flocks as previously stated.

In contrast to some reports (Tosh & Kemp, 1994; Maniatis & Pollott, 2002a; Simm *et al*., 2002), a distinct increase in h^2 at later ages was not observed in the Ile de France breed (see Figure 4.4b). However, there was an increment in the h^2 between birth and the pre-weaning phase in the Merino Landsheep (see Figure 4.4c). A tendency for h^2 to rise with increasing age as observed in the Dormer breed (see Figures 4.4a) is frequently attributed to the inherent ability of the animal to grow, as derived from the genes it inherited from both parents and also the influence of the maternal milk supply on the variability of food intake and performance in the young lamb, although this trend is not always observed (Larsgard & Olesen, 1998).

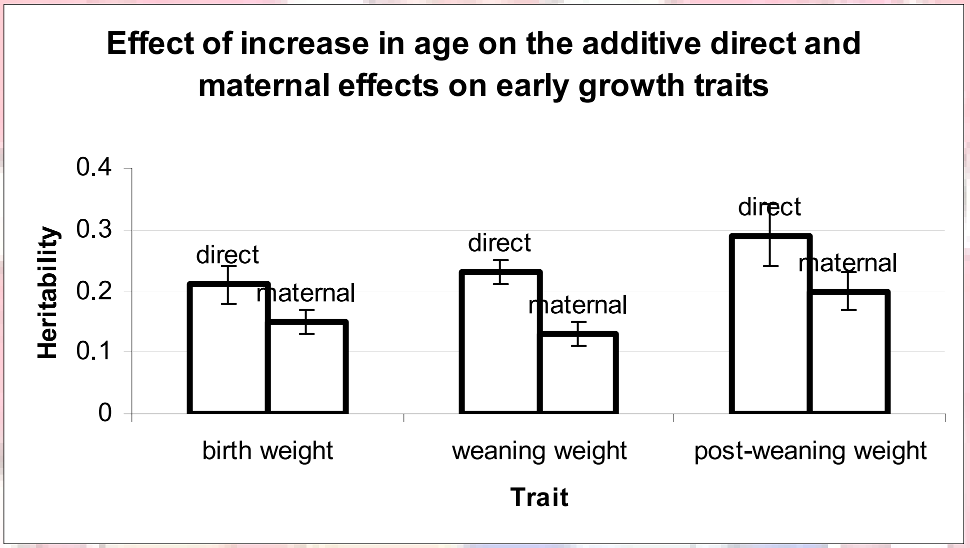

Figure 4.4a Trends in h^2 and m^2 respectively for the Dormer breed with an increase in the age at which weights were recorded. Vertical bars around the observed means denote standard errors

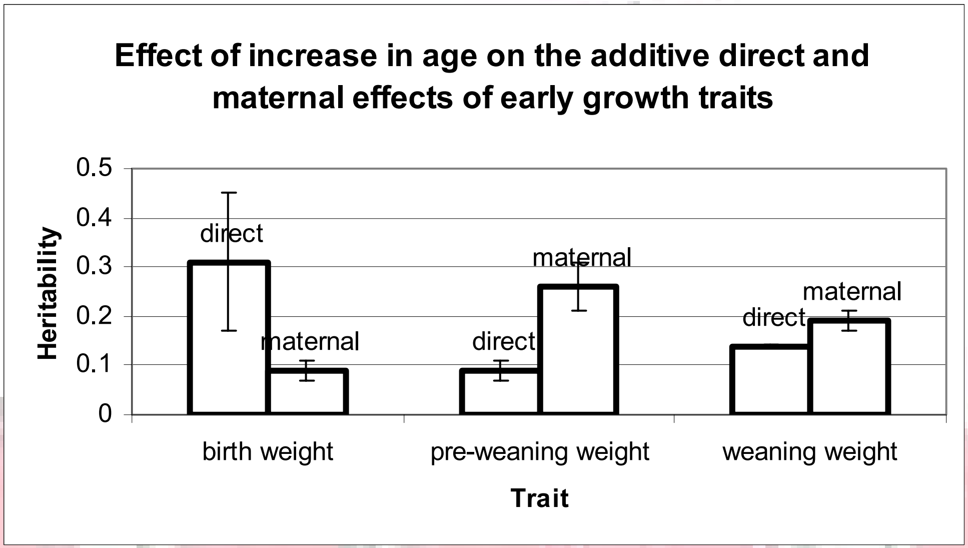

Figure 4.4b Trends in h^2 and m^2 respectively for the Ile de France breed with an increase in the age at which weights were recorded. Vertical bars around the observed means denote standard errors

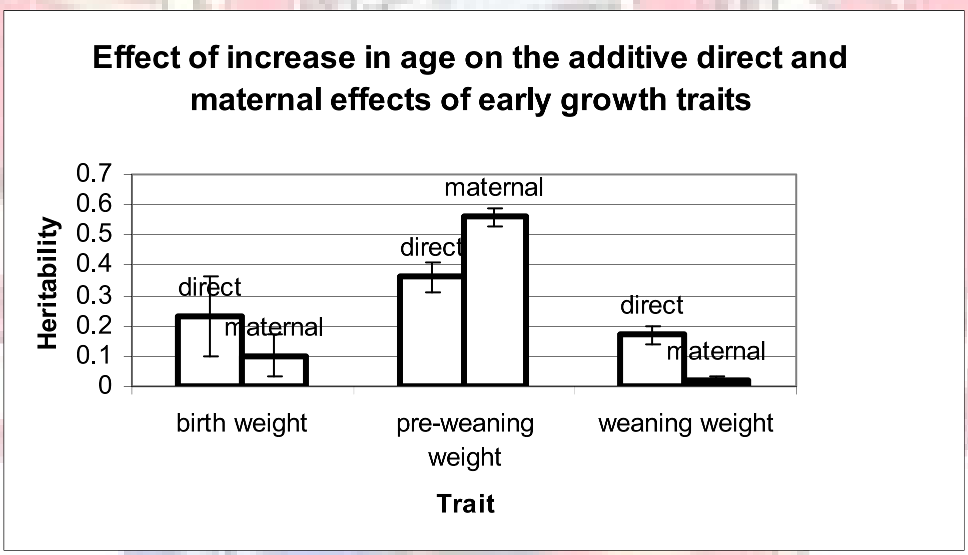

Figure 4.4c Trends in h^2 and m^2 respectively for the Merino Landsheep breed with an increase in the age at which weights were recorded. Vertical bars around the observed means denote standard errors

The contribution of the dam to early growth (as depicted through c^2 or m^2 depending on modeling), remained fairly constant in the Dormer breed (Figure 4.4a). It tended to increase from birth weight to pre-weaning weight in the Ile de France and Merino Landsheep breeds, while it tended to decline subsequently. In general a decline in the maternal componenet is expected, particularly for post-weaning weight (Snyman *et al.*, 1995).

4.4.2.4 Single-trait analyses of post-weaning weight

The direct heritability (h^2) of post-weaning weight was 0.29 ± 0.05 in the Dormer breed. This estimate was consistent with literature values obtained across sheep breeds worldwide (Atkins, 1991; Brash *et al*., 1992; Waldron *et al*., 1992; Lewer *et al.*, 1994; Swan & Hickson, 1994; Fossceco & Notter, 1995; Vaez Torshizi *et al*., 1996; Yazdi *et al*., 1997; Cloete *et al*., 1998; Nagy *et al*., 1999; Lee *et al*., 2002; Maniatis & Pollot, 2002; Ingham *et al*., 2003). This estimate unanimously concurred with the averaged estimates obtained by Safari *et al*. (2005) across breeds of 0.28 ± 0.03 and 0.22 ± 0.02 in dual-purpose and meat breeds respectively. The dam permanent environmental effect (c^2) of post-weaning weight was (0.20 ± 0.03), indicating that the importance of maternal effects remained to this stage in this breed. The poor population structure as previously mentioned prevented the further partitioning of maternal effects into their components. The medium estimate was generally higher than literature values, and consistent with only a few estimates in the literature (Lewis & Beatson, 1999; Maniatis & Pollot, 2002a). Dam permanent environmental effect (c^2) is usually low for post-weaning weight across breeds as confirmed by Safari *et al*. (2005). It is universally accepted that maternal effects diminish with age. The data structure in the present study could have biased the estimate to an extent. It is noteworthy that the post-weaning weights were taken on an age range between 129 days and 399 days. The mean age was 221 days. This large range, as well as a lower average age at recording, probably contributed to the medium dam permanent environment effect. There was also a marked erosion of data from weaning to post-weaning because only 17 % of the data records that were utilized for weaning weight were available at the post-weaning stage (Table 3.3a), which could have resulted in the overestimation. The estimates obtained from the single-trait analyses clearly indicate that stud breeders should be encouraged not only to keep more records, but also to be precise. If records from more studs were available, more accurate parameters and breeding values can be estimated and this would assist selection decisions. The results of this study confirm the importance of implementing the correct model pertaining to random effects for the estimation of genetic parameters. Exclusion of important components in the genetic analyses obviously has the effect of inflating the remaining parameter estimates and possibly biasing the breeding values obtained from such analyses.

4.4.3 Three-trait analyses on the Dormer breed

A three-trait analysis was conducted for birth weight (BW), weaning weight (WW) and post-weaning weight (PWW). According to log likelihood ratio tests, the most appropriate animal model for the three-trait analysis incorporates additive genetic effects as well as the maternal permanent environmental effects. The data set for this analysis had to be reduced owing to missing records on a number of occasions. The smaller data set contained only 3 050 animals with complete weight records. At this juncture it is worth mentioning that the thorough editing probably resulted in the loss of genetic links across the flocks. The correlations among traits and variance ratios obtained in the three-trait analysis are presented in Table 4.4g and Table 4.4h.

Table 4.4g Estimates (SE in brackets) of genetic (above diagonal), and phenotypic (below diagonal) correlations and direct heritability estimates (h^2) (on diagonal) using a three-trait analysis in the Dormer breed

	Birth weight	**Weaning weight**	**Post-weaning weight**
Birth weight	**0.28 (0.04)**	0.25 (0.07)	0.31 (0.10)
Weaning weight	0.25 (0.02)	**0.55 (0.06)**	0.43 (0.05)
Post-weaning weight	0.16 (0.02)	0.47 (0.16)	**0.35 (0.04)**

Table 4.4h Estimates (SE in brackets) of environmental (r_e) (above diagonal) correlations, dam permanent environmental correlations (r_{pe}) (below diagonal) and dam permanent environmental effects (c^2) (on diagonal) using a three-trait analysis in the Dormer breed

	Birth weight	**Weaning weight**	**Post-weaning weight**
Birth weight	**0.32 (0.02)**	0.28 (0.06)	0.08 (0.06)
Weaning weight	0.50 (0.07)	**0.37 (0.04)**	0.56 (0.05)
Post-weaning weight	0.67 (0.11)	0.91 (0.05)	**0.21 (0.06)**

The direct heritability (h^2) estimates obtained for birth weight and post-weaning weight using the three-trait analysis were fairly similar to the estimates obtained using single-trait analysis (0.28 ± 0.04 versus 0.21 ± 0.03 and 0.35 ± 0.04 versus 0.29 ± 0.05) respectively. The moderate estimate for birth weight was similar to the ones reported in literature across all breeds (Lewer *et al*., 1994; Snyman *et al*., 1995; Hall *et al*., 1995; Mortimer & Atkins, 1995; Vaez Torshizi *et al*., 1996; Yazdi *et al*.,1997; Al- Shorepy & Notter, 1998; Larsgard & Olesen, 1998; Bromley *et al*., 2000; Cloete *et al*., 2002; Duguma *et al*., 2002b; Hanford *et al*., 2002; Matika *et al*., 2003; Roden *et al*., 2003; Van Vleck *et al*., 2003). The estimate was accepted, based on the argument given by Gilmour *et al*. (2002) that statistical modeling becomes complicated as the number of traits increases. There may be variation for a specific trait, but the matrix may not be positive definite due to the variances being too big. When undertaking REML estimation, ASREML needs to invert each matrix. For this the program requires that the matrices be negative definite or positive definite. The matrices may not be singular. Negative definite estimates will have negative elements on the diagonal of the matrix and/or its inverse. The h^2 estimate for the post-weaning weight was also consistent with literature estimates (Brash *et al*., 1992; Lewer *et al*., 1994; Hickson *et al*., 1995; Mortimer & Atkins, 1995; Fossceco & Notter, 1995; Yazdi *et al*., 1997; Cloete *et al*., 2001; Lee *et al*., 2002).

The direct heritability (h^2) estimate obtained for weaning weight was more than double the one that was obtained using a single-trait analysis (0.55 ± 0.06 versus 0.23 ± 0.02). Although comparable very high h^2 estimates for weaning weight are occasionally found in the literature (Brash *et al*., 1994; Aslaminejad & Roden, 1997), it is not a common feature in sheep breeding. This anomaly can be explained by the specification of variance structures in ASREML when conducting multiple-trait analysis. A more sophisticated error structure is required when compared to single-trait analysis. In multiple trait analyses, the error structure for the residual must be specified as two-dimensional with independent records and an unstructured variance matrix across traits. This is done because records may have observations missing in different patterns and these are handled internally during the analysis. This is further exacerbated by finding initial values to commence the iteration sequence and in some cases ASREML is coded to obtain starting values from the data (Gilmour *et al*., 2002).

The dam permanent environmental effect (c^2) obtained for birth weight using three-trait analyses was slightly more than double that value obtained by single-trait analysis (0.32 ± 0.02 versus 0.15 ± 0.02). However, it fell within the range reported in literature (Tosh & Kemp, 1994; Conington *et al*., 1995; Hall *et al*., 1995; Al- Shorepy & Notter, 1998; Roden *et al*., 2003). The high estimate probably resulted because the power in the data was not adequate to partition maternal effects into their components (m^2 and c^2). The high estimate is indicative of the importance of maternal effects on early growth traits of sheep. During the peri-natal period and the post-natal period, the ability of the dam to provide sufficient milk for its growing lambs is of cardinal vitality. The significance of maternal effects can therefore not be overemphasized at this stage. The dam permanent environmental effect (c^2) obtained for post-weaning weight was similar to the one obtained in the single-trait analysis (0.21 ± 0.06 versus 0.20 ± 0.03). It is however worth mentioning that the usage of more information and computational challenges associated with multi-trait analysis causes anomalies in genetic parameter estimations.

The first step in genetic improvement of production efficiency in a population is to identify suitable selection criteria. However other knowledge is also essential. Apart from h^2 estimates and variation of each trait, knowledge of how selection for one trait will influence others is needed (Van Wyk *et al*., 1993d). This is important since unfavourable correlated responses could render improvement in a specific trait undesirable as far as total economic merit is concerned. Also, if genetic improvement in a trait does not increase the efficiency of production, this improvement is of no economic consequence. The phenotypic, genetic and environmental correlations between live weights were found to be positive and medium to high. At this juncture it is worth mentioning that genetic correlations are strongly influenced by genes common to the traits under consideration. Because selection changes the frequencies of these genes, genetic correlations can change after a few generations of selection (Bohren *et al*., 1969).

The genetic correlation (r_g) between birth and weaning weight was 0.25 ± 0.07. This correlation is consistent with other estimates that have been reported across breeds although much lower than the average value of 0.47 reported in a review across breeds by Safari *et al*. (2005). From the published literature available, r_g estimates between birth and weaning weight range from -0.33 to 0.81 (Lewer *et al*., 1994; Vaez Torshizi *et al*., 1996; Yazdi *et al*., 1997; Jara *et al*., 1998; Mousa *et al*., 1999; Neser *et al*., 2001; Wuliji *et al*., 2001; Duguma *et al*., 2002b; Hanford *et al*., 2002; Simm *et al*., 2002; Boujenane & Kansari, 2002). Interestingly, Neser *et al*. (2001) obtained a genetic correlation of 0.27 ± 0.24 between birth weight and weaning weight at 100 days in Dorper sheep. All estimates of r_g depend on the models that were utilized, particularly the random effects that were incorporated during model construction. It is worth mentioning that genetic correlation estimates are notorious for their inconsistency and associated large standard errors (Tallis, 1959; Snyman *et al*., 1998). This result and the available literature suggests that selection for high birth weights will result in a significant improvement in weaning weight. Selection for exceedingly high birth weights is alleged to result in other negative outcomes such as a high incidence of lambing problems. The phenotypic and environmental correlations between birth weight and weaning weight were positive but low (0.25 ± 0.02 and 0.28 ± 0.06) respectively. These estimates were consistent with those reported in previously cited literature. The genetic correlation between birth weight and post-weaning weight was moderate (0.31 ± 0.10) indicating that selecting for high post-weaning weight will result in higher birth weights. However, the phenotypic correlation between birth weight and post-weaning weight was low (0.16 ± 0.02) and the environmental correlation was also low (0.08 ± 0.04). The genetic, phenotypic and environmental correlations between weaning weight and post-weaning weights were moderate (respectively 0.43 ± 0.05, 0.47 ± 0.16 and 0.56 ± 0.05). These estimates were consistent with those reported in the literature (Lewer *et al*., 1994; Al-Shorepy & Notter, 1996; Vaez Torshizi *et al*., 1996; Yazdi *et al*., 1997; Wuliji *et al*., 2001; Simm *et al*., 2002). The dam permanent environmental correlation (r_{pe}) was high and positive between all early growth traits as depicted in Table 4.4h. These high and positive correlations were in agreement with the estimates in previously cited literature. This study and available literature explicitly indicate that selecting for high weaning weights will result in significant increases of post-weaning weight. Of particular interest is the estimate by Al-Shorepy & Notter (1996) who had a genetic correlation estimate of 1.00 in a Composite breed of sheep. The absence of genetic antagonisms between the growth traits indicates that none of the traits should be affected adversely by selection in the South African Dormer breed. Contrary to the case with improved livestock, where a policy of guarding against high birth weights is generally recommended, genetic improvement of birth weight, also because of its high correlation with later weights, should not be avoided in Dormer sheep until an optimum is reached. It has to be stated that genetic correlations not different from unity between weaning weight and post-weaning weight are commonly reported in the literature. However, the present estimates for all breeds are thus uncharacteristically low.

4.4.4 Three-trait analyses in the Ile de France breed

A three-trait analysis was carried out using a smaller data set with all the complete records for birth weight, pre-weaning weight and weaning weight. The model that was utilized included additive direct effects and the dam permanent environmental effects. Only 5 239 records were used in this particular analysis. Direct and maternal heritability estimates and correlations among traits are presented in Table 4.4i and Table 4.4j. The direct heritability (h^2) estimate obtained using the three-trait analysis for birth weight was fairly similar to the one obtained with single-trait analysis (0.37 ± 0.04 versus 0.31± 0.14). The high estimate was consistent with those reported in literature across sheep breeds throughout the world (Lewer *et al*., 1994; Tosh & Kemp, 1994; Jara *et al*., 1998; Wuliji *et al*., 2001). The direct heritability (h^2) estimates for pre-weaning weight and weaning weight from multivariate analyses differed from those obtained with single-trait analysis (0.23 ± 0.05 and 0.37 ± 0.23 ± 0.05 versus 0.09 ± 0.02 and 0.14 ± 0.003 versus 0.37 ± 0.03 respectively). These differences could probably be explained by the differences in the sizes of the data sets.

Table 4.4i Estimates (SE in brackets) of genetic (r_g) (above diagonal), phenotypic (r_p) (below diagonal) correlations and direct heritabilities (h^2) (on diagonal) using a three-trait analysis in the Ile de France breed

	Birth weight	**Pre-weaning weight**	**Weaning weight**
Birth weight	**0.37 (0.04)**	0.19 (0.06)	0.33 (0.06)
Pre-weaning weight	0.29 (0.01)	**0.23 (0.05)**	0.57 (0.03)
Weaning weight	0.27 (0.02)	0.71 (0.01)	**0.37 (0.03)**

Table 4.4j Estimates (SE in brackets) of environmental (r_e) (above diagonal) correlations, dam permanent environmental correlations (r_{pe}) (below diagonal) and dam permanent environmental effects (c^2) (on diagonal) using a three-trait analysis in the Ile de France breed

	Birth weight	**Pre-weaning weight**	**Weaning weight**
Birth weight	**0.03 (0.01)**	0.39 (0.04)	0.24 (0.03)
Pre-weaning weight	0.69 (0.05)	**0.18 (0.02)**	0.86 (0.03)
Weaning weight	0.64 (0.07)	0.82 (0.09)	**0.10 (0.01)**

Although the estimates were different, they still fell within the ranges reported in literature because medium to high direct heritability estimates are a common phenomenon across sheep breeds. As expected, maternal effects influenced early growth traits in sheep as already reported in the single-trait analysis. Estimates for dam permanent environmental effects (c^2) using multi-trait procedures for birth weight, pre-weaning weight and weaning weight were 0.03 ± 0.01, 0.18 ± 0.02 and 0.10 ± 0.01 respectively. Although the estimates differed from those obtained using single-trait analyses they still fell within the ranges reported from the single-trait analyses. They differed from those reported in the single-trait analysis, probably because there was data erosion and a loss of genetic links across flocks during the editing process in order to pave way for a meaningful multiple trait analyses.

The genetic correlation between birth weight and pre-weaning weight was 0.19 ± 0.06. The estimate differed from the few that were reported in literature. Analla *et al.* (1997) reported a genetic correlation between birth weight and 45 day weight of 0.59 in Segurena sheep, Mousa *et al*. (1999) reported a genetic correlation between birth weight and 7-week weight of 0.45 in a composite breed of sheep and Neser *et al*. (2001) derived an estimate of 0.51 ± 0.12 in Dorper sheep. It is crucial to note that a negative correlation of -0.33 ± 0.11 was also reported by Simm *et al*. (2002) between birth weight and 56-day weight. The estimates that were reported in this study and those in literature heavily depended on the models that were used. The phenotypic correlation between birth weight and pre-weaning weight was 0.29 ± 0.01. This low estimate differed from the few that were reported in literature. Mousa *et al*. (1999) reported a phenotypic correlation between birth weight and 7-week weight of 0.43 in a composite breed of sheep, Neser *et al.* (2001) derived an estimate of 0.48 in Dorper sheep and Simm *et al*. (2002) reported a phenotypic correlation between birth weight and 56-day weight of 0.53 ± 0.02. The environmental correlation between birth and pre-weaning weight was moderate (0.39 ± 0.04) and slightly lower than the one reported by Analla *et al*.(1997) in Segurena sheep of 0.51.

The genetic correlation (r_g) between birth weight and weaning weight was moderate and positive at 0.33 ± 0.06. This estimate was consistent with other values reported in literature (Vaez Torshizi *et al*., 1996; Yazdi *et al*., 1997; Jara *et al*., 1998; Wuliji *et al*., 2001; Hanford *et al*., 2002). The phenotypic correlation (r_p) was low (0.27 ± 0.02) and identical to the estimate obtained by Lewer *et al*. (0.27 ± 0.02) in Merino sheep. Boujenane & Kansari obtained an almost similar estimate of 0.28 using 10 370 records from Timahdite sheep. The environmental correlation (r_e) between birth weight and weaning weight was moderate (0.24 ± 0.03). This moderate estimate was similar to the estimate reported by Vaez Torshizi *et al*. (1996) of 0.21 (using 3 701 records of Merino sheep) and also by Jara *et al*. (1998) of 0.21 ± 0.08 (using 1 880 records in Corriedale sheep). The genetic, phenotypic and environmental correlation between pre-weaning weight and weaning weight were moderately positive (0.57 ± 0.03, 0.71 ± 0.01 and 0.86 ± 0.03 respectively). These estimates are consistent with those reported in literature (Al-Shorepy & Notter, 1996; Analla *et al*., 1997; Nagy *et al*., 1999; Simm *et al*., 2002). The dam permanent environmental correlations (r_{pe}) amongst the early growth traits were positive and high as depicted in Table 4.4j. These high and positive correlations were in concurrence with literature values (Yazdi *et al*., 1997; Mousa *et al*., 2000; Bromley *et al*., 2000; Neser, 2001; Duguma, 2002b). The estimates from this study and those reported in literature confirmed that it should be feasible to genetically improve pre-weaning weight and weaning weight at the same time.

Due to very few records being available for analyses as depicted in Table 3.3c, only single-trait analyses are reported for the Merino Landsheep. However, a series of bivariate analyses of different trait combinations were attempted using ASREML (Gilmour, *et al.,* 2002) but convergence was not achieved, probably due to a loss of genetic links as well as data erosion during editing.

4.5 Conclusion

Estimates of direct heritability (h^2) for early growth traits from different models ranged from moderate to moderately high. This study also investigated the effect of implementing different models on the estimation of genetic parameters and concluded that failure to include a measure of maternal variation in the analyses will culminate in biased estimates of direct genetic variance. The data structure in all breeds mostly did not allow the partitioning of m^2 and c^2 effects as well as the estimation of r_{am} These limitations should be addressed as more and better structured data become available.

The positive moderate to high correlations among early growth traits in all the three terminal sire sheep breeds studied indicated that these traits can be improved simultaneously during selection programs. The Dormer, Ile de France and Merino Landsheep breeds have got the capacity to improve meat production if they are used as terminal sires in crossbreeding programs. However, breeding objectives in sheep production systems are becoming more complex because in recent years there has been a trend towards increasing the economic value for meat production relative to wool and a greater need for products, both meat and wool. It was crucial to estimate the genetic parameters that influenced weaning weight because weaning weight records are considered to be instrumental in the improvement of reproduction by the South African National Small Stock Improvement Scheme for wool producing and dual-purpose breeds (Olivier, 1993). It is crucial to note that the use of direct breeding values for early growth traits is very essential in terminal sire sheep breeds. It is more important in the context of this study than the usage of weaning weight to assess reproduction. It is also fair to say that maternal genetic or dam permanent environment is also of somewhat lesser importance in the context of the present study where the application of sires in terminal crossbreeding is contemplated. Stud breeders should be encouraged not only to keep more records, but also to be precise. If records from more flocks were available, more accurate parameters and breeding values could have been estimated that could have greatly assisted selection decisions. An across-flock breeding value estimation, entailing the entire breed should be the goal of all breeders (Neser *et al*., 2001). Finally, although the results obtained in these studies can be utilized in the interim, they should be verified when more and better linked data become available. Efficient and reliable selection indices should then be constructed.

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Chapter 5

GENETIC AND PHENOTYPIC TRENDS IN SOUTH AFRICAN TERMINAL SIRE SHEEP BREEDS

5.1 Abstract

Genetic and phenotypic trends were constructed for early growth traits in the Dormer, Ile de France and Merino Landsheep breeds. The traits that were considered were birth weight, pre-weaning weight, weaning weight and post-weaning weight. However, pre-weaning weights were available for the Ile de France and Merino Landsheep breeds only and post-weaning weights were available only for the Dormer breed. The Dormer exhibited significant improvement in the phenotypic and genetic aspects of early growth traits during the 17 years of evaluation (1990-2007). The average predicted direct breeding values of birth weight decreased by 0.055 % during the evaluation period. The predicted direct breeding value for weaning weight increased by 0.12 % per annum during the 17 year period. Post-weaning weight mean annual predicted breeding value improved by 0.32 % per annum. The Ile de France registered an increase in the predicted direct breeding value of birth weight which amounted to 0.025 % per annum. Direct breeding value for pre-weaning weight increased at an annual rate of 0.23 %. and that of weaning weight increased by 1.21 %. In the Merino Landsheep the predicted direct breeding value for birth weights decreased by 0.04 % per annum and pre-weaning and weaning weights increased by 0.36 % and 0.10 % per annum respectively. The latter trends were obviously biased due to inconsistencies in data structure and very few records available for analysis in this breed. The results suggest that worthwhile genetic progress is feasible in all breeds.

Keywords: predicted breeding value, regression coefficient, evaluation, least square mean, significant.

5.2 Introduction

The primary goal of animal breeders is to maximize the rate of genetic improvement through selection (Van Wyk, 1992). In meat sheep enterprises, this implies maximizing the genetic improvement of meat production. Sheep breeding enterprises must be evaluated on a regular basis to determine their effectiveness (Van Wyk *et al*., 1993; Swanepoel, 2006). Genetic trends reflect the amount of genetic improvement (or lack thereof) in a population over time. Accurate genetic parameters for a breed are required before changes are made to selection criteria. Selection on best linear unbiased prediction (BLUP) of breeding values obtained by Henderson’s mixed model methodology is recommended for livestock improvement since the correlation between the predicted and the true breeding value is maximized (Olivier *et al*., 1995). The primary objective of a breeding programme for livestock species is to maximize the rate of genetic progress for economically important traits through selection (Van Wyk *et al*., 1993). The heritability of and genetic relationship between traits are needed for planning an efficient breeding system and for the development of an effective genetic evaluation strategy. REML procedures based on a derivative-free or average information algorithm are normally used for the estimation of variance and covariance components under an animal model in which the additive genetic effect of the individual is fitted as a random effect (Torshizi *et al.,* 1996; Gilmour *et al*., 2002). The difference in profitability of sheep breeds remains one of the most controversial issues among sheep producers (Snyman *et al*., 1995). Farmers continuously change from one breed to the other mainly due to short-term financial reasons and current trends and fluctuations in wool and meat prices. Profitability in sheep production for meat depends to a great extent on lamb weight, therefore selection objectives concentrate on this trait (Tosh & Kemp, 1994). Genetic parameters are needed to estimate breeding values and to compare responses obtained from different selection programmes. Genetic improvement of livestock depends on defining breeding objectives, the estimation of genetic parameters and the accurate identification of the most suitable animals to be used for future breeding. Genetic and phenotypic trends in South African terminal sire sheep flocks have not been reported. Knowledge of these is essential to effectively implement selection criteria. Against this background, the objectives of this study were (i) to obtain estimated breeding values for early growth traits in the Dormer, Ile de France and Merino Landsheep breeds, and (ii) to construct genetic and phenotypic trends in the same breeds.

5.3 Materials and Methods

Data came from complete records that were used in single-trait analyses of early growth traits in the Dormer, Ile de France and Merino Landsheep, as already reported in previous chapters. Direct breeding values were derived for each trait by using the data from the most appropriate single trait animal model in ASREML (Gilmour *et al*., 2002). Maternal breeding values were excluded based on the reasoning that direct genetic trends are more important in the terminal sire breeds as sires of these breeds are expected to pass on good genes for growth to their crossbred progeny. Genetic trends were calculated as the regression of average predicted breeding value on year of birth. The phenotypic trends were calculated as the regressions of average phenotypic values on year of birth. The trends were constructed using direct breeding values of flocks that were consistently submitting information from the NSIS. It is crucial to explicitly report at this stage that genetic links across the flocks were constantly being broken due to random entrance and exit into the scheme. This resulted in few links being available between granddam-dam-offspring relations. The few linkages also resulted in the failure to partition maternal effects into m^2 and c^2. The number of flocks that contributed direct breeding values for the construction of genetic and phenotypic trends have already been reported in section 3.3.2.

5.4 Results and Discussion

5.4.1 Genetic and phenotypic trends in the Dormer breed

The genetic and phenotypic trends for birth weight, weaning weight and post-weaning weight are shown in Figures 5.4a-5.4f:

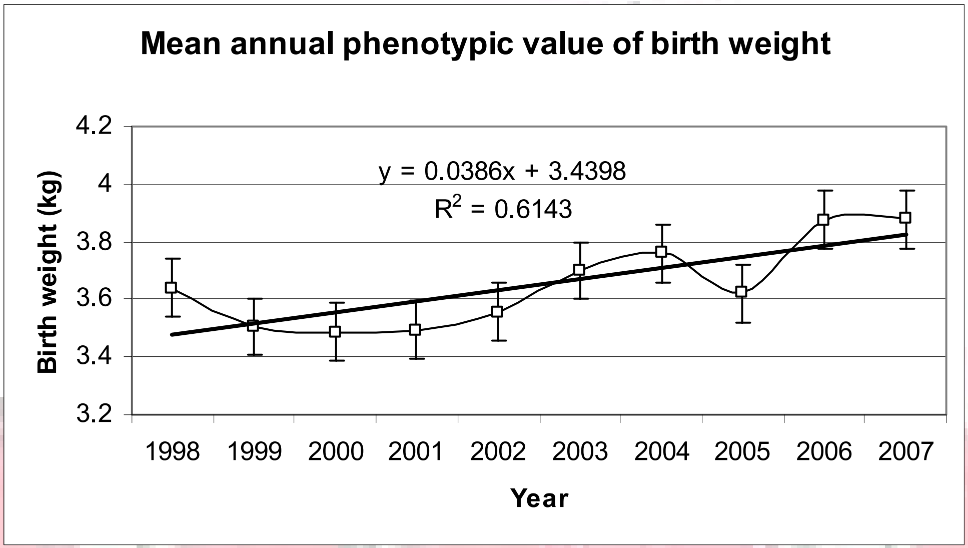

Figure 5.4a Phenotypic trends in birth weight for the Dormer breed. Annual means are accompanied by the relevant standard error

Birth weight of the Dormer breed decreased from 3.65 to 3.5 kg between 1998 and 2001 on the phenotypic level (Figure 5.4a). It then increased from 3.5 to 3.75 kg between 2001 and 2004. Birth weight dropped to 3.6 kg in 2005 and later on increased to the highest average level of 3.85 kg in 2007. The regression coefficient for the linear regression of the phenotypic values of birth weight on years of birth was 0.0386 ± 0.011 kg per annum and the goodness of fit amounted to 61%. Expression of the regression coefficient (b) as a percentage of the least square mean for birth weight (3.83), inferred an annual phenotypic increase in birth weight of 1.006 % between 1998 and 2007. This positive trend could have resulted from environmental and husbandry factors such as an improved plane of nutrition.

The mean annual predicted direct breeding value for birth weight declined from 0.018 to 0 kg between 1998 and 2001 (Figure 5.4b). The averaged breeding values decreased steadily during the evaluation period despite minor fluctuations that were probably caused by haphazard data structures due to the inconsistency in record keeping amongst breeders over the years or alternatively from the selection decisions that were taken by studs contributing to the national flock. The regression coefficient of the predicted breeding value for birth weight on birth year was -0.0021 ± 0.001 kg per annum and the corresponding R^2 was 0.421. The average predicted direct breeding values of birth weight decreased by 0.055 % during the evaluation period (1998 to 2007) when expressed relative to the overall mean. An annual decrease in the breeding value of birth weight of 0.055 % indicated that selection objectives with regards to birth weight were reasonably implemented. There are not numerous studies to compare these results with. In contrast to the present study Van Wyk *et al*. (1993) reported an annual increase in birth weight of 0.023 kg per year in the Elsenburg Dormer stud, whilst Duguma. (2001) also reported an increment in the mean direct breeding value for birth weight in the Tygerhoek Merino flock. Results of increases in birth weight should be treated with caution because if they are excessive they will result in negative consequences such as difficulties in lambing. It is furthermore a stated breed objective of Dormers to maintain birth weight as part of the application of the breed as a terminal sire (Dormer Breeders' Society, 2005).

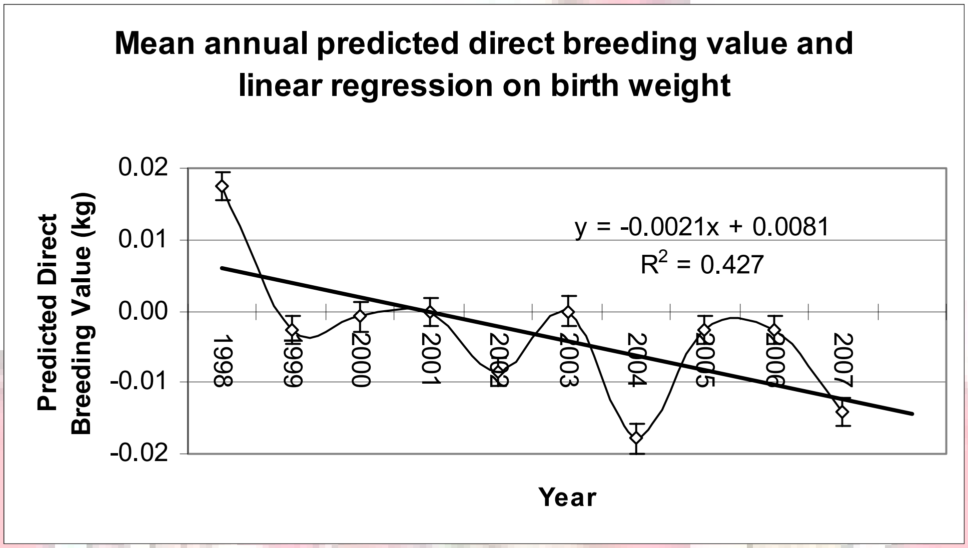

Figure 5.4b Genetic trends in birth weight for the Dormer breed. Annual means are accompanied by the relevant standard error

Mean phenotypic values of weaning weight in Dormer sheep did not fluctuate much during the evaluation period as presented in Figure 5.4c. Weaning weight increased from approximately 30 kg to 35 kg between 1990 and 2007. The regression coefficient (b) for depicting the regression of averaged breeding value on birth year of weaning weight amounted 0.0406 ± 0.01 kg per annum with an observed R^2 of 0.90. Expression of the coefficient of regression as a percentage of the least square mean of weaning weight (33.06) yielded an annual increment in weaning weight of 0.12 %. A genetic improvement of 0.12 % per annum in a terminal breed of sheep is quite low although reasonable. The annual genetic gain differed from the figure obtained by Van Wyk *et al*. (1993) in the Elsenburg Dormer stud, i.e 1.04 % per year. The result obtained clearly indicates that genetic improvement in weaning weight through selection is feasible. Since weaning weight is a good indicator of early growth, it was concluded that the Dormer breed is structuring itself to fulfill a demand for terminal sires in crossbreeding programs, where rapid early growth is a prerequisite. However, there is still room for improvement, as faster genetic gains of up to 2% should be achievable.

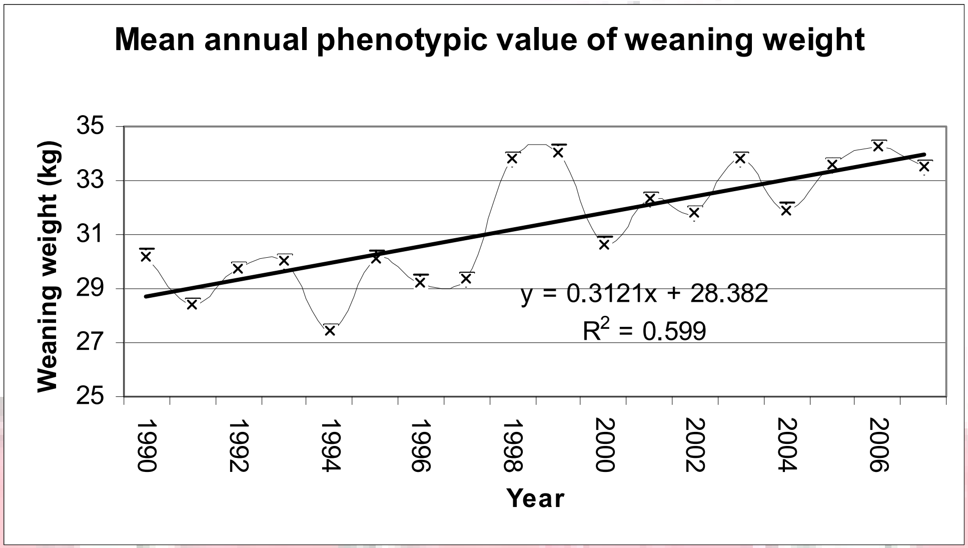

Figure 5.4c Mean phenotypic values for weaning weight in the Dormer breed. Annual means are accompanied by the relevant standard error

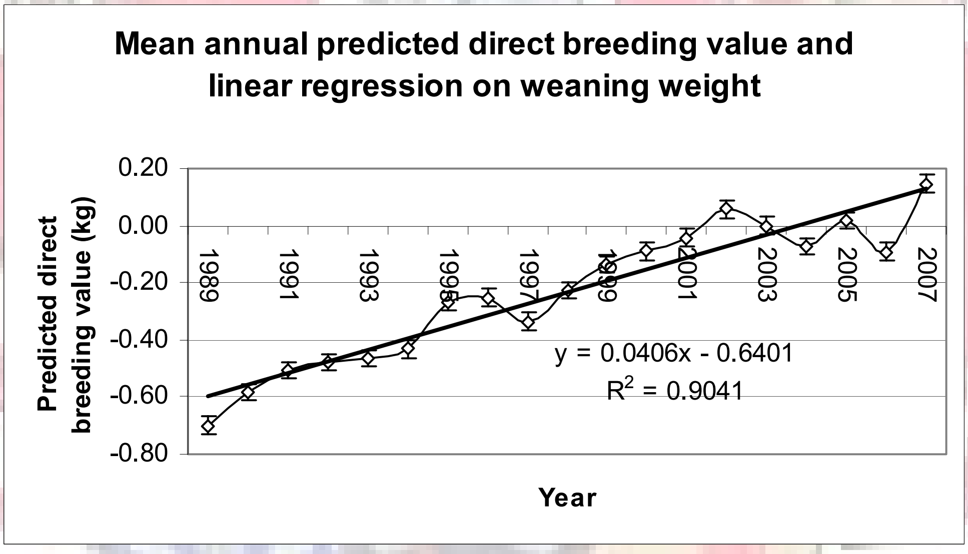

Figure 5.4d Mean predicted breeding values for weaning weight in the Dormer breed. Annual means are accompanied by the relevant standard error

Post-weaning weight increased from 40 to 60 kg between 1990 and 2007 on the phenotypic level. The regression coefficient for average post-weaning weight on birth year amounted to 1.0237 ± 0.300 kg per annum and R^2 was 0.414 (Figure 5.4e). The least square mean of post-weaning weight was 53.06 kg. Therefore the mean annual phenotypic increase in post-weaning weight amounted to 1.93 %. This figure therefore indicates quite significant progress in post-weaning weights. In contrast, the average breeding values for post-weaning weight was improved by 0.32 % per annum (Figure 5.4f). It was concluded that post-weaning weight exhibited substantial genetic improvement during the evaluation period. However, the genetic change only contributed a portion of the attained phenotypic response. The major share of the response was presumably driven by nutritional and managerial interventions during the period of study.

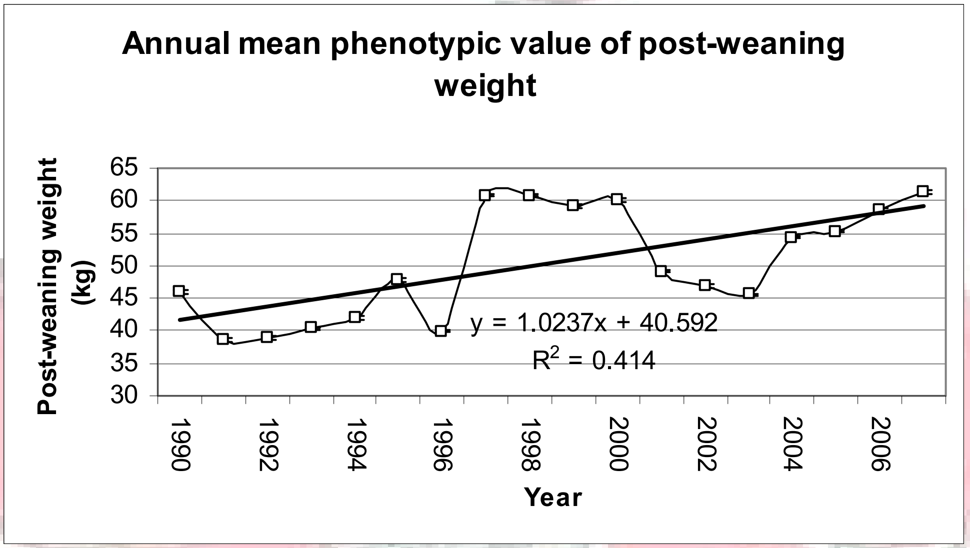

Figure 5.4e Mean phenotypic values for post-weaning weight in the Dormer breed. Annual means are accompanied by the relevant standard error

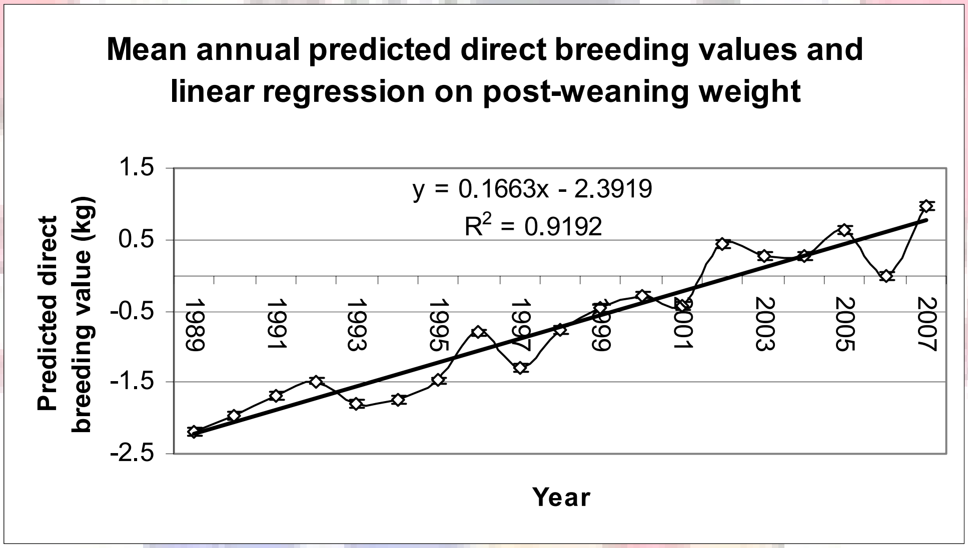

Figure 5.4f Mean predicted breeding values for post-weaning weight in the Dormer breed. Annual means are accompanied by the relevant standard error

5.4.2 Genetic and phenotypic trends in the Ile de France breed.

The genetic and phenotypic trends for birth weight, pre-weaning weight and weaning weight are shown (Figures 5.4g-5.4l):

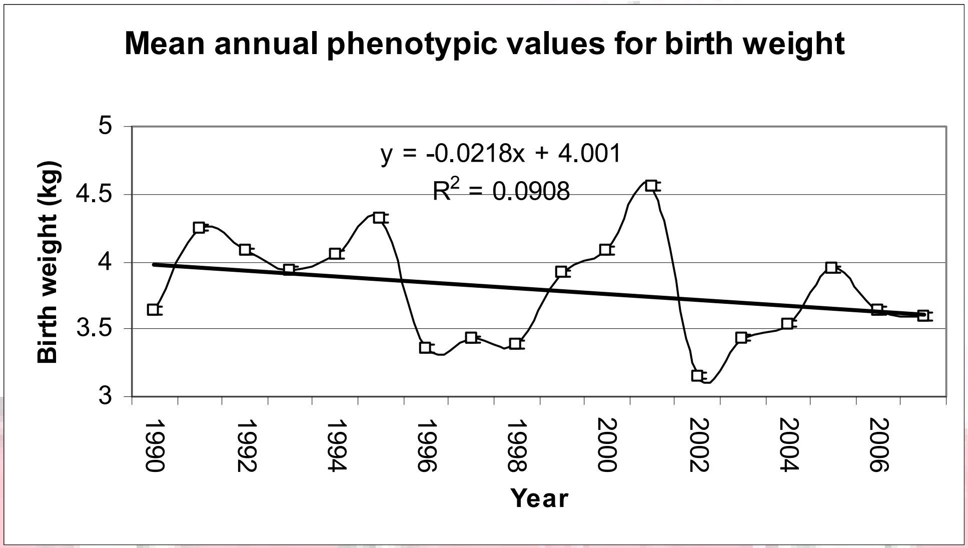

Figure 5.4g Mean annual phenotypic values for birth weight in the Ile de France breed. Annual means are accompanied by the relevant standard error

Birth weight decreased from approximately 4.0 to 3.5 kg between 1990 and 2007 in Ile de France sheep. The coefficient of regression was -0.021 ± 0.017 kg per annum and the least square mean for birth weight was 3.99 kg. Therefore the mean annual decrease in birth weight amounted to 0.53 %. The mean annual predicted breeding values for birth weight (Figure 5.4h) decreased from 0.024 kg in 1991 to approximately 0 kg in 1992 and in 1998. The overall regression coefficient of regression was 0.001 ± 0.0008 kg per annum indicating an average annual increase in breeding value of 0.025 %. The average annual pre-weaning weight increased steadily during the evaluation period (Figure 5.4i). The mean breeding value of pre-weaning weight increased from -0.3636 to 0.1203 kg between 1990 and 2007 (Figure 5.4j). The predicted breeding value of pre-weaning weight increased by 0.23 % per annum during the 17 years period of evaluation. This positive trend indicates reasonable genetic progress in terms of pre-weaning weight.

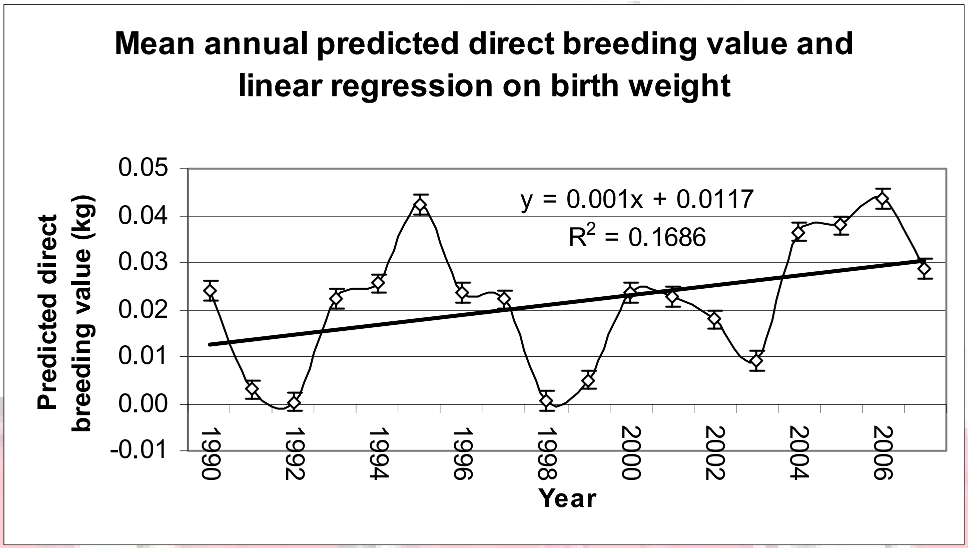

Figure 5.4h. Mean annual predicted breeding values for birth weight for the Ile de France breed. Annual means are accompanied by the relevant standard error

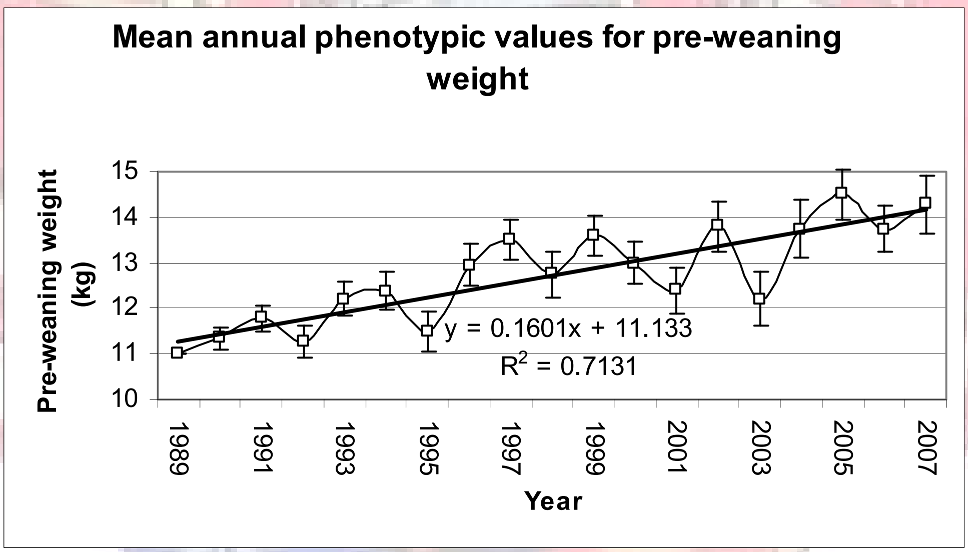

Figure 5.4i Mean annual phenotypic values for pre-weaning weight in the Ile de France breed. Annual means are accompanied by the relevant standard error

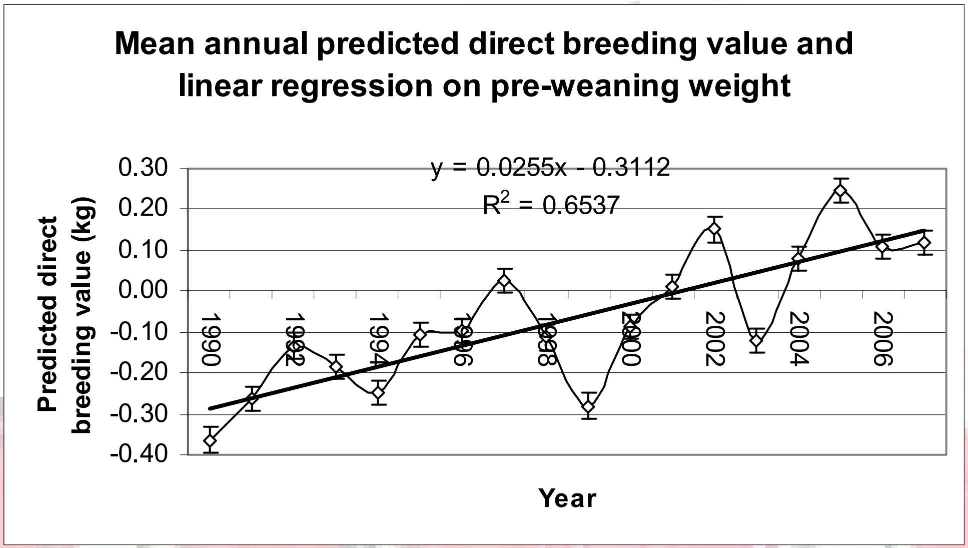

Figure 5.4j Mean annual predicted breeding values for pre-weaning weight in the Ile de France breed. Annual means are accompanied by the relevant standard error

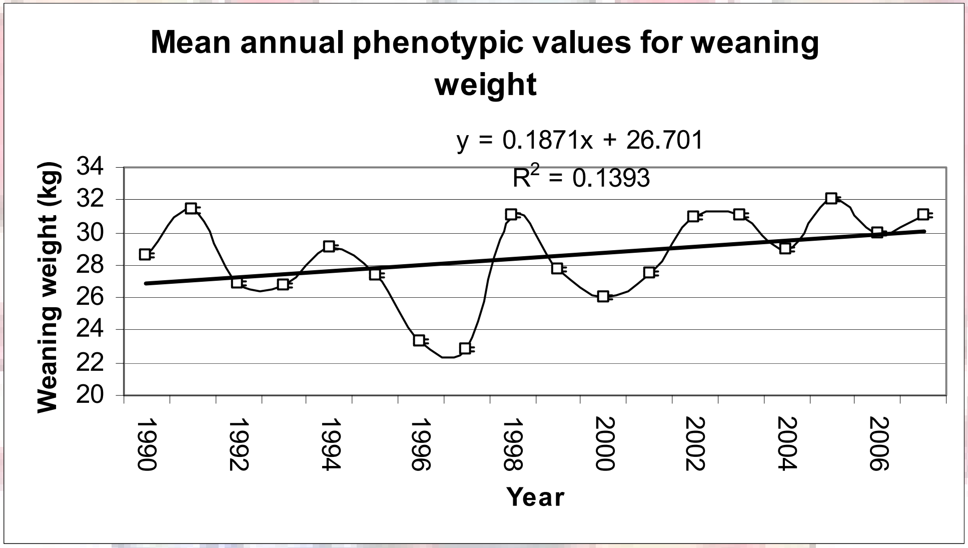

Figure 5.4 k Mean annual phenotypic values for weaning weight in the Ile de France breed. Annual means are accompanied by the relevant standard error

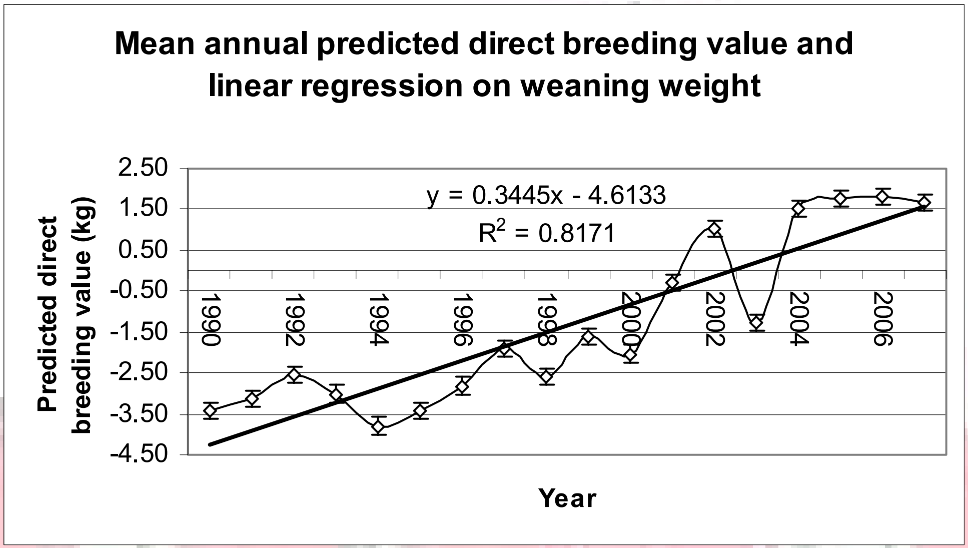

Figure 5.4 l Mean annual predicted breeding values for weaning weight in the Ile de France breed. Annual means are accompanied by the relevant standard error

Phenotypic means for weaning weight were fluctuating between 22 and 31 kg in the period from 1990 to 2007. The regression of animal breeding values on year of birth (b) amounted to 0.3445 ± 0.02 kg per annum and the least square mean of weaning weight was 28.47 kg. Expressing the regression coefficient as a percentage of the least square mean gave a predicted breeding value increase of 1.21 % per annum. The increase in annual breeding value was significant genetic progress for a terminal sire breed of sheep.

5.4.3 Genetic and phenotypic trends in the Merino Landsheep breed

The genetic and phenotypic trends for birth weight, pre-weaning weight and weaning weight are shown in Figures 5.4m-5.4r. The birth weight decreased from approximately 5.4 to 4.6 kg between 1999 and 2005 in Merino Landsheep. The coefficient of regression was -0.0923 ± 0.046 kg per annum and the corresponding R^2 was 0.449. The overall least square mean for birth weight was 3.91 ± 0.20 kg. Expressing the coefficient of regression as a percentage of the least square mean gave a mean annual decrease in birth weight of 2.36 %. The figure was probably biased because only 673 records from the original data set of 7 772 records had the trait recorded. The average annual predicted breeding value of birth weight decreased from 0.0163 kg in 1999 to -0.0028 kg in 2008 (Figure 5.4n). The breeding value of birth weight decreased by 0.04 % per annum. This figure was probably biased because very few records were available for analysis. Pre-weaning weight of Merino Landsheep lambs did not vary much between 1999 and 2007 (Figure 5.4o). The coefficient of regression of the overall predicted breeding values on the birth year amounted to 0.0733 ± 0.025 kg per annum and the least square mean for pre-weaning weight was 20.56 ± 0.19 kg. Therefore pre-weaning weight increased at a rate of 0.36 % per annum between 1999 and 2008.

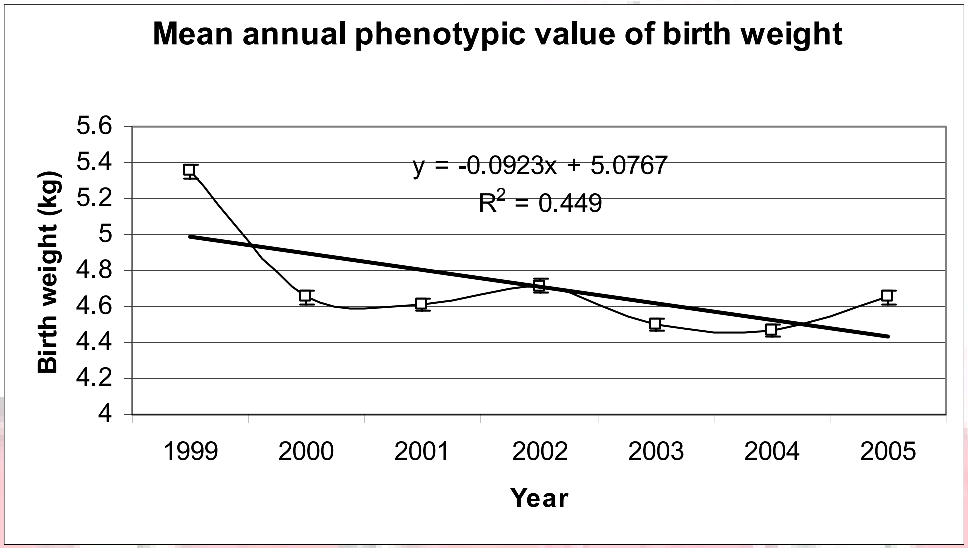

Figure 5.4m Mean phenotypic values for birth weights in the Merino Landsheep breed. Annual means are accompanied by the relevant standard error

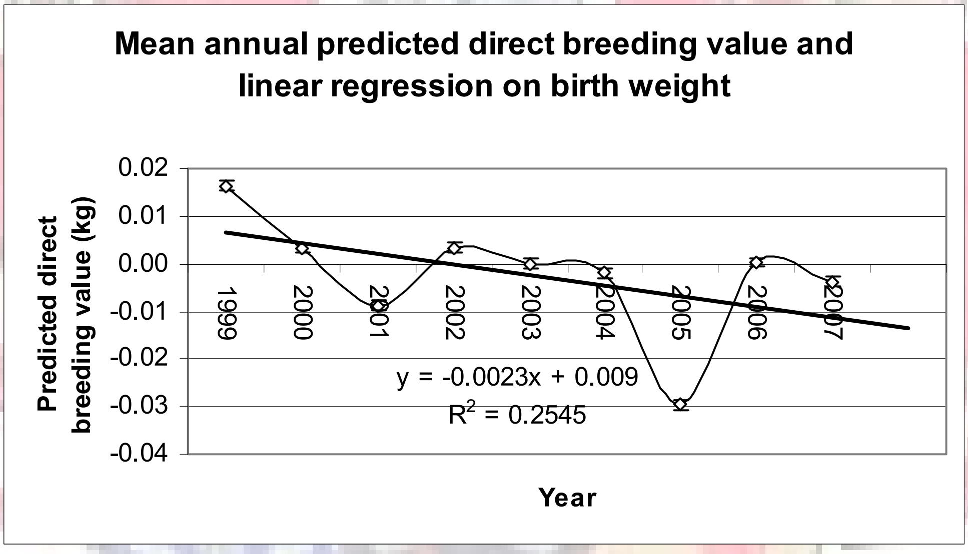

Figure 5.4 n Mean annual predicted breeding values for birth weight in the Merino Landsheep breed. Annual means are accompanied by the relevant standard error

The mean phenotypic value of weaning weight fluctuated between 25 and 40 kg prior to 1996. It then stabilized in 1996 at about 30 kg. The mean weaning weight of about 30 kg was maintained up to the end of the genetic evaluation period in 2007 (Figure 5.4q). The annual predicted direct breeding value for weaning weight increased by 0.10 % per annum between 1990 and 2007 (Figure 5.4r). These results were probably biased due to limited records available for analysis.

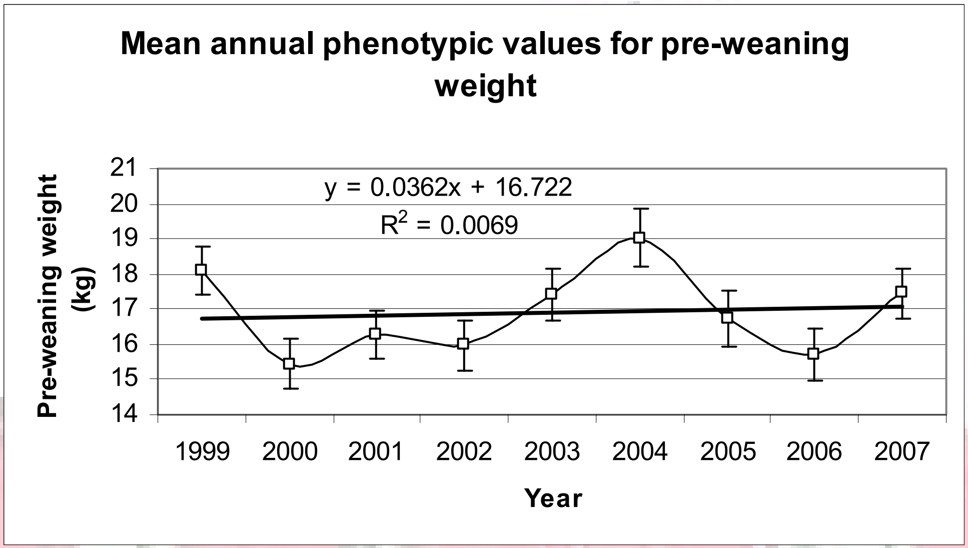

Figure 5.4o Mean phenotypic values for pre-weaning weights in the Merino Landsheep breed Annual means are accompanied by the relevant standard error

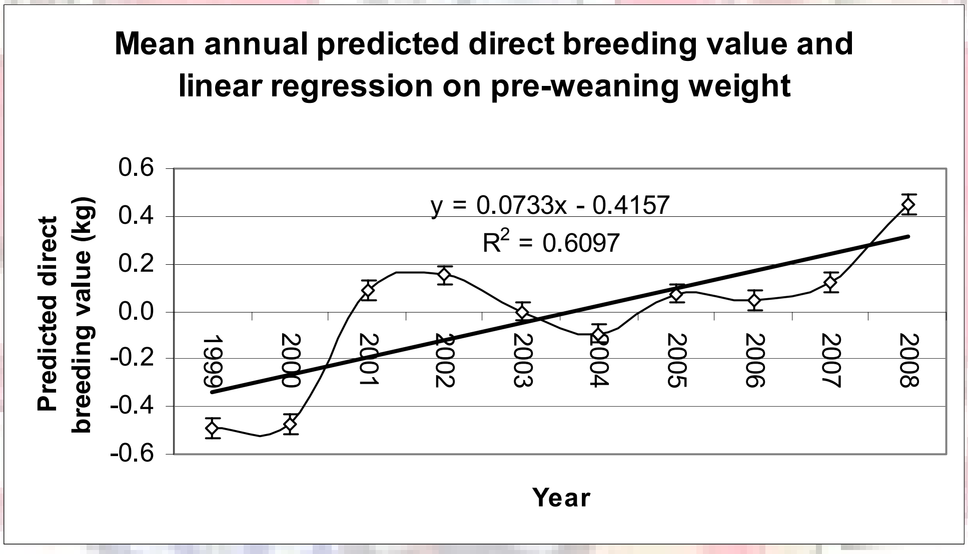

Figure 5.4p Mean annual predicted breeding values for pre-weaning weight in the Merino Landsheep breed. Annual means are accompanied by the relevant standard error

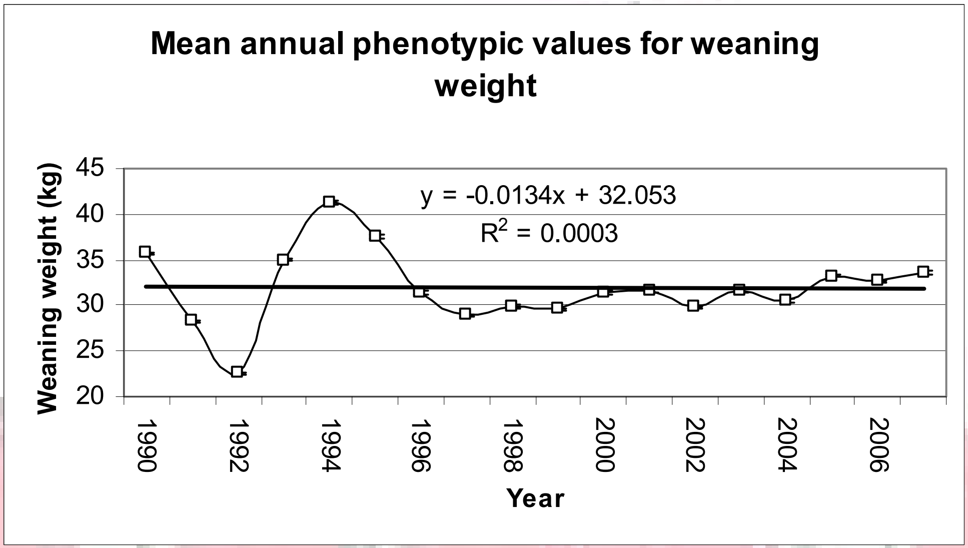

Figure 5.4q Mean phenotypic values for weaning weights in the Merino Landsheep breed. Annual means are accompanied by the relevant standard error

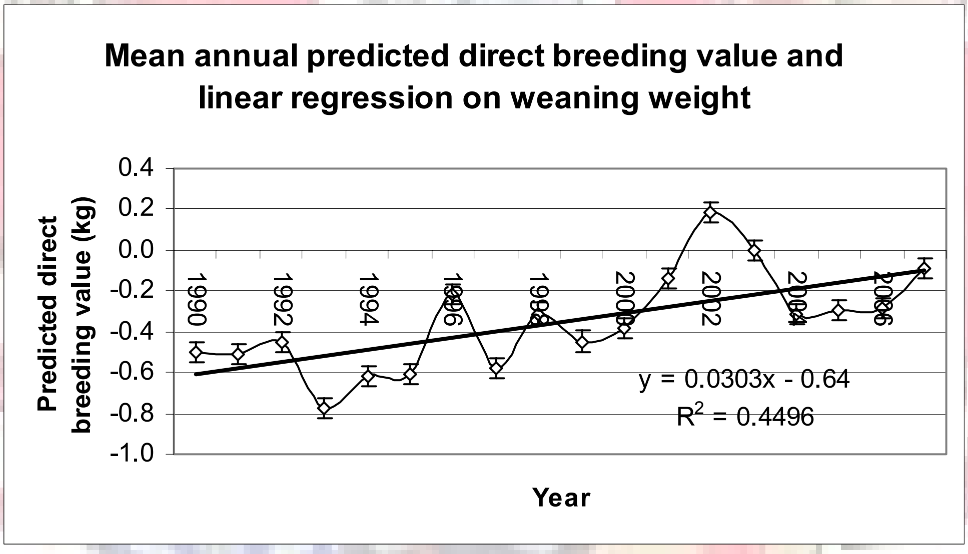

Figure 5.4r. Mean annual breeding values for weaning weight in the Merino Landsheep breed. Annual means are accompanied by the relevant standard error

5.5 Summary of response to selection in South African terminal sire sheep breeds

The overall response per annum to selection for early growth traits in South African Terminal sire sheep breeds is presented in Table 5:

Table 5 Response per annum to selection for early growth traits in South African Terminal sire sheep breeds expressed as a percentage of the respective overall least-squares. Corresponding values reported by Olivier *et al*. (2004) in brackets

	Birth weight	Pre-weaning weight	Weaning weight	Post-weaning weight
Dormer	-0.055%	-	+0.12%(0.22%)	+0.32%
Ile de France	+0.025%	+0.23%(0.12%)	+1.21%	-
Merino Landsheep	-0.04%	+0.36%	+0.10%(0.09%)	-

5.6 Conclusion

The genetic and phenotypic trends obtained in the study indicated that significant and sustained genetic progress in the desired direction has been achieved in early growth traits in the Dormer between 1990 and 2007. However, it needs to be conceded that faster progress would theoretically be feasible. The results obtained in this study therefore provide an important perspective on the selection objectives of this breed. The Dormer is thus well positioned for utilization as a terminal sire in crossbreeding programs with the objective of prime lamb production. Compared to the Dormer, genetic progress in the Ile de France breed between 1990 and 2007 was commendable, particularly for weaning weight. The Ile de France thus has much potential in improving early growth traits when it is utilised as a terminal sire in crossbreeding programmes (Table 5). In the interim the results of the study may be used but future analyses are supposed to be conducted when more well-structured data are available There was very minimal response in weaning weight to selection in the Merino Landsheep between 1990 and 2008, possibly because of a lack of clearly defined selection objectives. This possibly stems from a lack of genetic parameter estimates. However, the Merino Landsheep still has the potential to be utilized as a terminal sire in crossbreeding programs with the objective of prime lamb production. The attained trends should be updated when sufficient data becomes available.

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Chapter 6

GENERAL CONCLUSIONS

Individual chapters contained in this thesis already contain abstracts. Therefore only the most important conclusions are presented in this chapter. It was obvious that results pertaining to the fixed effects that were assessed (sex, age at which weights were recorded, dam age and birth type) were consistent with reports in the literature. Significant year and contemporary group effects were also found, but these were of limited practical importance.

The genetic parameters obtained in this study using single-trait analyses were consistent with those reported in literature from various breeds across the world. However, care should be taken when interpreting results from scientific analyses because accuracy and validity depend on a number of factors. In these studies the genetic parameters estimated depended on the models that were utilized. Some animal models contained maternal factors partitioned into their various components such as additive maternal effects and dam permanent environmental effects. However, for most traits in all the three breeds it was difficult to partition maternal effects into m^2 and c^2 due to the poor population structures in the data. This limitation emanated from the random entrance and exit of flocks into the NSIS. This random movement resulted in the loss of genetic linkages between granddam-dam-offspring relations. The significance of being consistent in contributing information to the NSIS and the benefits arising thereof can, however, not be overemphasized. In view of the stated complications in the data structure, the correlation between direct effects and maternal effects (r_{am}) was excluded from all the analyses. In the event that the direct-maternal correlation (r_{am}) had been included in the analyses, uncharacteristically high negative correlations were found. It is possible that these correlations may have been related to sampling issues and instead of underlying biological principles. However it needs to be stated that the additive effects are the most important traits to consider in the selection of crossbred sires. These estimates were presumably estimated with little bias, and it can be used in both straight breeding and crossbreeding programmes.

The heritability estimates for early growth traits in terminal sire sheep breeds were moderate to high. This means success can be achieved when breeds are selected for traits of economic importance in terminal crossbreeding programs for prime lamb production. Breeders can confidently incorporate early growth traits in their selection indices for meat and carcass traits. There were no antagonistic correlations amongst early growth traits in the Dormer and Ile de France breeds. This means that selection for any of the traits will result in favourable correlated responses in other growth traits. Positive genetic correlations of later weights with birth weight may be a cause of concern in all breeds, as increases in birth weight could be associated with an increase in the incidence of difficult births and resultant dystocia cases. This is of particularly importance when it is considered that it is advantageous for maternal dam lines not to grow out to a heavy mature live weight (Roux, 1992).

Genetic and phenotypic trends indicated favourable responses to selection for weaning weight and post-weaning weight in the Dormer. A corresponding positive trend in birth weight may be a cause of concern, for reasons outlined above. Genetic trends in the Ile de France and Merino Landsheep were mostly positive and reasonable. However markedly better responses to selection should be attainable in all the three terminal sire sheep breeds when proper selection objectives and strategies are designed in future after the utilization of the genetic parameters obtained in this study.The reason for the current suboptimal genetic progress in these breeds is difficult to quantify. It may be that the respective breed societies lack well-defined selection objectives. Alternatively, a lot of emphasis may be placed on subjective conformation. It has recently been shown that subjective conformation scores are not always favourably related to important production traits in the Dorper breed (Olivier & Cloete, 2006). A lack of a clear, industry wide selection objectives may also contribute to the less than optimal attained responses.

Finally, although the results obtained in these studies may be utilized in the interim, a number of recommendations have to be made. More accurate genetic parameter estimates should be estimated in future when more data become available, and the data structure is improved. To achieve this, a serious effort should be made to increase the level of recording in all three breeds, but particularly in the Ile de France and Merino Landsheep breeds. There should be an active effort to increase the number of genetic ties between flocks in all three breeds through the use of common sires across flocks. Efforts for an improvement of the data structure pertaining to dams for the accurate partitioning of maternal genetic and permanent environmental effects should also receive attention. If this can be accomplished, future analysts may be in a position to obtain reliable estimates of the direct-maternal correlation in early growth traits for all three breeds. In order to achieve cutting edge terminal sire breeding, genetic parameters for meat and carcass traits together with their correlations with early growth traits, feed intake, wool traits and disease resistance should be estimated using more sophisticated and non-invasive methodology such as X-ray computer tomography, video image analysis and ultrasonography (Sehested, 1984; Young *et al*., 1996). Finally, more research on the use of sires from the respective breeds in the terminal crossbreeding situation is needed, to accurately quantify the level of heterosis attained, as well as the benefits of sexual dimorphism (Roux, 1992). Animal resources used for these studies should be thoroughly linked to the NSIS database, to ensure representivity. Such studies will play a major role in placing terminal crossbreeding in the South African small stock industry on a sound scientific basis.

6.1 References

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