

A GENETIC STUDY OF EARLY GROWTH TRAITS AND EWE
PRODUCTIVITY IN MERINO SHEEP

by

GEMEDA DUGUMA JALETA

Thesis submitted in partial fulfilment of the requirements for the

Degree

Masters of Science (Agriculture)
(Animal Sciences)

University of Stellenbosch, South Africa

Supervisor:

Prof. S. J. Schoeman
Department of Animal Sciences
University of Stellenbosch

Co-supervisor:

Mr. S. W. P. Cloete
Animal Production Division
Elsenburg Agric. Development Center
South Africa

November 2001

DECLARATION

I hereby declare that the work in this thesis is my own original work and that it has not, as a whole or partially, been submitted for a degree at any other University.

Summary

A genetic study of early growth traits and ewe productivity in Merino sheep

Candidate : Gemedu Duguma Jaleta
Supervisor : Prof. S. J. Schoeman
Co-Supervisor : Mr. S. W. P. Cloete
Department : Animal Sciences
Faculty : Agricultural and Forestry Sciences
Degree : MSc Agric.

The objectives of this study were to investigate genetic parameters of early growth traits, lifetime ewe productivity (total number born, number weaned and weight weaned per ewe lifetime production) and testis measurements in the Merino flock maintained at the Tygerhoek Experimental Farm. Non-genetic fixed factors influencing these traits were evaluated by using appropriate models. The influence of non-genetic factors on preweaning lamb survival rate and the effect of scrotal circumference on ewe fertility was also studied. Fixed effect models were fitted to the data using either Procedure GLM or CATMOD in SAS (1996) depending on the parameters being estimated. Variance components were estimated by Restricted Maximum Likelihood (REML) procedures, fitting an animal model.

Records of 8310 lambs born from 2538 ewes and sired by 681 rams covering the period 1970 to 1998 were used in the analysis of birth weight (BW), weaning weight (WW) and preweaning average daily gain (ADG). All three traits were affected ($p < 0.001$) by type of birth of lambs (single, multiple), sex, year of birth of lambs, group of animals (selection, control) and age of dam at lambing (2- to 6-yr old). Male lambs and singles were heavier both at birth and weaning and grew faster ($p < 0.001$) than females and multiples, respectively. Non-selected animals were lighter than selected animals at birth and weaning with an inferior growth rate. BW increased with increasing dam age at lambing until a maximum of 3.7 kg was reached at 6-yr of age. However, WW and ADG reached a maximum at 4.5- and 4.2-yr of age, respectively.

Variance components for BW, WW and ADG were estimated using Restricted Maximum Likelihood (REML) procedures. Four different animal models were fitted, differentiated by

including or excluding maternal effects. The direct heritability estimates (h^2) ranged from 0.19 to 0.38, 0.25 to 0.40 and 0.26 to 0.40 for BW, WW and ADG, respectively. Estimates of direct heritability (h^2) were substantially higher when maternal effects were ignored. The direct heritability (h^2) estimate for BW decreased from 0.38 to 0.19 when both or either of the maternal effects, genetic or environmental, were fitted in the model. The h^2 estimate for WW was 0.36 when both maternal effects were ignored from the model and decreased to 0.29 and 0.25 when maternal effects were fitted. A similar trend was observed for ADG. The maternal heritability (m^2) for BW ranged from 0.38 to 0.41 when only maternal additive genetic effects were fitted in the model, and decreased to 0.25 and 0.27 when the maternal permanent environmental effect (c^2) was fitted. The m^2 for WW and ADG ranged from 0.02 to 0.11 and from 0.01 to 0.10, respectively. The respective c^2 estimates ranged from 0.05 to 0.10 and from 0.02 to 0.09. Moderate negative genetic correlations (r_{am}) between direct and maternal additive genetic effects were observed in BW, while close to zero estimates were obtained for WW and ADG. The direct additive genetic correlation estimates between BW and WW and BW and ADG were 0.16 and 0.04, respectively. The corresponding maternal additive genetic correlation estimates were 0.93 and 0.60. The direct and maternal additive genetic correlation estimates between WW and ADG were 0.99 and 0.85, respectively.

Data of 3272 lambing records collected on 818 ewes born from 689 dams and sired by 371 rams were used in the evaluation of ewe lifetime productivity (total number born, number weaned and total weight weaned). These records were collected from ewes born from 1969 to 1994 and gave birth from 1971 to 1999. Year of birth of ewe and ewe two-tooth liveweight affected ($p < 0.001$) the ewe reproduction traits investigated. Multiple born ewes were superior both in total number of lambs born and weaned than singles. Heritability estimates of 0.23, 0.17 and 0.20 were obtained for total number of lambs born (TLB), total number of lambs weaned (TLW) and total weight of lambs weaned per ewe lambing over four lambing opportunities (TWW), respectively. For total weight weaned per ewe lambing over the first lambing opportunity (TWW1) a heritability estimate of 0.02 was computed. Genetic correlation estimates of -0.10 , 0.57 and 1.00 were obtained between TWW1 and TLB, TWW1 and TLW and TWW1 and TWW, respectively. High and positive genetic correlations ranging from 0.61 to 0.92 were estimated between ewe lifetime reproduction traits.

Data from 1380 rams born from 1986 to 1998 were used to investigate genetic parameters for scrotal circumference (SC), testis diameter (TD) and two-tooth liveweight (LW). The other objective of this study was to estimate the magnitude of the effect of SC on ewe fertility. Year of birth, selection group and LW were significant ($p < 0.001$) sources of variation both for SC

and TD. Heritability estimates ranged from 0.29 to 0.40, 0.25 to 0.38 and 0.49 to 0.52 for SC, TD and LW, respectively. Adjustment for LW decreased heritability estimates of SC and TD by 11.0 and 8.0 %, respectively. The genetic correlation between SC and TD was unity. Rams with larger SC had a significant effect on ewe fertility (ewes lambing per ewe mated).

Average survival rate from birth to 100 days of age was 0.79 and was influenced by lamb birth weight, year of birth, age of dam at lambing, type of birth (single, multiple) and sex of lambs. Lambs with a liveweight between 4.0 to 4.9 kg at birth showed the highest survival rate while lambs with a liveweight of ≤ 2.0 kg showed the lowest survival rate.

Opsomming

‘n Genetiese studie van vroeë groei-eienskappe en ooiproduktiwiteit by Merinoskape.

Kandidaat	: Gameda Duguma Jaleta
Studieleier	: Prof. S.J. Schoeman
Mede-studieleier	: Mnr. S.W.P. Cloete
Departement	: Veekundige Wetenskappe
Fakulteit	: Landbou- en Bosbouwetenskappe
Graad	: MScAgric

Die doel van die studie was om genetiese parameters vir vroeë groei-eienskappe, ooileeftydproduksie (totale aantal gebore, aantal gespeen en totale gewig gespeen) en testismaatstawwe in die Merinokudde van die Tygerhoek Navorsingstasie te beraam. Nie-genetiese vaste effekte wat hierdie eienskappe beïnvloed, is met behulp van gepaste modelle geëvalueer. Die invloed van nie-genetiese faktore op voorspeense lamoorlewing en die invloed van skrotumomvang op ooi vrugbaarheid is ook ondersoek. Vaste-effek modelle is, afhange van die parameters wat beraam is, deur middel van of die GLM of CATMOD prosedures van SAS (1996) op die data gepas. Variansiekomponente is met behulp van die Beperkte Maksimum Aanneemlikheidsprosedure (REML), deur die passing van ‘n dieremodel, beraam.

Rekords van 8310 lammers wat tussen 1970 en 1998 van 2538 ooie gebore is en die nageslag van 681 ramme was, is vir die ontleding van geboortegewig (BW), speengewig (WW) en voorspeense daaglikse toename (ADG) gebruik. Al drie eienskappe is deur geboortestatus (enkeling, meerling), geslag, jaar van geboorte, groep (seleksie, kontrole) en ouderdom van die moeder met lamming (2- tot 6-jr oud) beïnvloed ($p < 0.001$). Ramlammers en enkelinge was met beide geboorte en speen swaarder en het vinniger ($p < 0.001$) as onderskeidelik ooilammers en meerlinge gegroei. Nie-geselekteerde lammers was ligter as dié van die seleksiegroep met beide geboorte en speen en het ook stadiger gegroei. BW het met toename in moederouderdom tot ‘n maksimum van 3.7 kg by 6-jr oud ooie gestyg. Maksimum WW en ADG is egter by 3- en 5 jr oud ooie onderskeidelik bereik.

Variansiekomponente vir BW, WW en ADG is met behulp van Beperkte Maksimum Aanneemlikheidsprosedures (REML) beraam. Vier verskillende modelle is gepas, waarin materne effekte óf in- óf uitgelaat is. Die direkte oorerflikhede (h^2) het van 0.19 tot 0.38, 0.25 tot 0.40 en 0.26 tot 0.40 vir BW, WW en ADG onderskeidelik gevarieer. Beramings van die direkte oorerflikheid (h^2) was aansienlik hoër waar die materne effekte geïgnoreer is. Die direkte oorerflikheidsberaming (h^2) vir BW het vanaf 0.38 tot 0.19 verlaag toe beide of een van die materne effekte, geneties of omgewings, in die model ingesluit is. Die h^2 beraming vir WW was 0.36 toe beide materne effekte geïgnoreer is en het tot 0.29 en 0.25 gedaal toe beide in die model gepas is. 'n Soortegelyke tendens is vir ADG waargeneem. Die materne oorerflikheid (m^2) van BW het vanaf 0.38 tot 0.41 gevarieer waar slegs die direkte materne effek gepas is maar tot 0.25 en 0.27 gedaal toe die materne permanente omgewingseffek (c^2) additioneel gepas is. Die m^2 vir WW en ADG het onderskeidelik van 0.02 tot 0.11 en van 0.01 tot 0.10 gewissel. Die ooreenstemmende c^2 beramings het vanaf 0.05 tot 0.10 en vanaf 0.02 tot 0.09 gewissel. Matige negatiewe genetiese korrelasies (r_{am}) tussen die direkte en materne genetiese effekte is vir BW gevind, terwyl bykans zero beramings vir beide WW en ADG gevind is. Die direkte genetiese korrelasies tussen BW en WW en tussen BW en ADG was onderskeidelik 0.16 en 0.04. Die ooreenstemmende materne genetiese korrelasies was 0.93 en 0.60. Die genetiese korrelasies tussen die direkte en materne genetiese effekte tussen WW en ADG was onderskeidelik 0.99 en 0.85.

Data van 3272 lamrekords van 818 ooie vanaf 689 moeders en 371 vaders is vir die evaluasie van ooileefstydproduktiwiteit (totale aantal gebore, aantal gespeen en totale speengewig) gebruik. Hierdie rekords is van ooie wat tussen 1971 en 1999 gelam het, versamel. Jaar van geboorte van die ooi en ooi-tweetandgewig het die reproduksie-eienskappe ondersoek, beïnvloed ($p < 0.001$). Meerlinggebore ooie was beter as enkelgebore ooie ten opsigte van aantal lammers gebore en gespeen. Oorerflikheidsberamings van onderskeidelik 0.23, 0.17 en 0.20 is vir aantal lammers gebore (TLB), totale aantal lammers gespeen (TLW) en totale gewig oor vier lamgeleenthede gespeen (TWW), gevind. Vir totale gewig per ooi met die eerste lamgeleentheid gespeen (TWW_1), is 'n oorerflikheidsberaming van 0.02 bereken. Genetiese korrelasies van -0.10, 0.57 en 1.00 is onderskeidelik tussen TWW_1 en TLB, TWW_1 en TLW en TWW_1 en TWW beraam. Hoë en positiewe genetiese korrelasies wat tussen 0.61 en 0.92 gevarieer het, is tussen ooileefstydreproduksie-eienskappe beraam.

Data van 1380 ramme wat tussen 1986 en 1998 gebore is, is gebruik om genetiese parameters van skrotumomvang (SC), testisdeursnee (TD) en tweetandgewig (LW) te beraam. 'n Ander doel van die ondersoek was om die effek van SC op oovrugbaarheid te ondersoek. Jaar van

geboorte, seleksiegroep en LW was betekenisvolle ($p < 0.001$) bronne van variasie vir beide SC en TD. Oorerflikheidsberamings het van 0.29 tot 0.40, 0.25 tot 0.38 en 0.49 tot 0.52 vir onderskeidelik SC, TD en LW gevarieer. Korrigerende vir LW het die oorerflikhede van SC en TD met onderskeidelik 11.0 en 8.0 % verlaag. Die genetiese korrelasie tussen SC en TD was een. Ramme met hoër SC het 'n betekenisvolle invloed op ooi vrugbaarheid (ooie gelam per ooie gepaar) gehad.

Die gemiddelde oorlewingstempo vanaf geboorte tot 100 dae was 0.79 en is deur geboortegewig van die lam, jaar van geboorte, ouderdom van die ooi, geboortestatus (enkeling, meerling) en geslag van die lam beïnvloed. Lammers met 'n geboortegewig van tussen 4.0 en 4.9 kg het die hoogste oorlewingstempo gehad, terwyl lammers met 'n geboortegewig van ≤ 2.0 kg die laagste oorlewingstempo gehad het.

DEDICATION

To my fathers Duguma Jaleta and Alemu Jaleta and to my mothers Ayane Dabalo and Wayyitu Mangasha who educated me.

ACKNOWLEDGMENT

First and foremost I thank my saviour, **LORD ALMIGHTY**, who has enabled me to accomplish the study.

My heartfelt gratitude is to:

The Oromia Agricultural Development Bureau, Oromia Agricultural Research Coordination Service and Bako Agricultural Research Center: for facilitating and funding this study and granting the study leave.

The Ethiopia Agricultural Research Organization and the Agricultural Research and Training Project: for invaluable support in facilitating this study.

Prof. S. J. Schoeman: for his guidance, invaluable comments and patience throughout the study period.

Mr. S. W. P. Cloete: for kind permission to use the data and his constructive comments.

Mrs. G. F. Jordaan: for assistance in data analysis and her patience with me during the course of the study.

My fathers: Duguma Jaleta and Alemu Jaleta and my mothers: Ayane Dabalo, Wayyitu Mangasha and Qanate Ofga'a: for the frequent visits they made to learn the well being of my wife and my son and words of encouragement they sent during the study period.

Dr. Waktola Wakgari and his family: for moral support and the home situation they have created for me.

Mr. Fufa Feyissa, Mr. Tesema Teshome and Mr. Desalegn Alemu: for their special concern for the success of the study and moral support.

Mr. Aliye Hussien, Fakadu Jalata, Nagash Galata, Tamasgen Tarafa, Solomon Abegaz, Wagari Kaba and Miss Selamawwit Tekalegn: who have helped my wife and my son and have made my communication with them simple.

Hailu Dadi, Haile Hatfaye, Jirenya Gindaba, Tadele Tefera, Teklemicael Debesay and Bezalgne Mohammed: for their cooperation in sharing views and valuable materials.

My father-in-law and mother-in-law: for the provision of shelter to my family and moral support.

In particular, my heartfelt gratitude is to Alganesh Alemu, my lovely wife: for shouldering all responsibilities, her understanding, endurance and encouragement during the course of the study.

Table of contents	Page
Summary.....	ii
Opsomming.....	v
Dedication.....	viii
Acknowledgment.....	ix
Chapter 1. General Introduction	1
Chapter 2. The influence of non-genetic factors on early growth traits in lambs ..	5
2.1. Introduction	5
2.2. Materials and methods.....	6
2.2.1. Location of the study area	6
2.2.2. Animals and management	6
2.2.3. Statistical Analysis	7
2.3. Results	9
2.4. Discussion.....	14
2.5. Conclusions	17
Chapter 3. The estimation of (co)variance components for early growth traits	18
3.1. Introduction	18
3.2. Materials and Methods	19
3.3. Results	21
3.3.1. Unitrait analyses	21
3.3.2. Multitrait analyses	24
3.3.3. Genetic and environmental trends	27
3.4. Discussion.....	29
3.4.1. Untitrait analyses	29
3.4.2. Multitrait analyses	32
3.4.3. Genetic and environmental trends	33
3.5. Conclusions	33
Chapter 4. Genetic parameter estimates for number and weight of lamb weaned	34
4.1. Introduction	34
4.2. Materials and Methods	35
4.3. Results	37

4.3.1. Fixed effects	37
4.3.2. Genetic parameters	38
4.4. Discussion.....	40
4.4.1. Fixed effects	40
4.4.2. Genetic parameters	42
4.5. Conclusions	43
Chapter 5. Testicular measurements in rams and its influence on ewe fertility	44
5.1. Introduction	44
5.2. Materials and Methods	45
5.3. Results	47
5.3.1. Non-genetic factors	47
5.3.1.1. Testis measurements.....	47
5.3.1.2. Ewe fertility	48
5.3.2. Genetic parameters	50
5.3.2.1. Testis measurements.....	50
5.4. Discussion.....	51
5.4.1. Non genetic factors.....	51
5.4.1.1. Testis measurements.....	51
5.4.1.2. Ewe fertility	51
5.4.2. Genetic parameters	52
5.4.2.1. Testis measurements.....	52
5.5. Conclusions	54
Chapter 6. The effect of non-genetic factors on preweaning lamb survival rate...	55
6.1. Introduction	55
6.2. Materials and methods.....	56
6.3. Results	56
6.4. Discussion.....	59
6.5. Conclusions	62
Chapter 7. General conclusion.....	63
References.....	65

Chapter 1

General Introduction

Genetic improvement through selection in a breeding programme depends on the accuracy of identifying genetically superior animals. This requires that environmental factors influencing the accuracy of predicted breeding values be either controlled experimentally or eliminated statistically (Van Wyk *et al.*, 1993a). Correction for some of these factors might be achieved through the use of adjustment factors or by placing animals that are treated differently or that produce under different environmental circumstances in different contemporary groups (Bourdon, 2000; Notter, 2000). Inaccuracies inherent in breeding value estimation, where there is confounding between genetic and environmental effects, will inevitably lead to substantial inefficiencies (Lewer *et al.*, 1994). Environment evidently can affect genotype, preventing consistent results from a specific breeding program (Tosh & Kemp, 2000).

Performance of animals is influenced by direct and maternal additive genetic effects (Lewis & Beatson, 1999). Maternal influences are evident early in the life of lambs, while it tends to disappear with an increase in age (Snyman *et al.*, 1995). Maternal influences can be derived from the genotype of the dam (maternal additive genetic effects) and those consistent between lambings but not genetic in origin, also referred to as maternal permanent environmental effects (Lewis & Beatson, 1999). In mammalian species, maternal effects influence growth traits, particularly preweaning growth rate (Bradford, 1972; Meyer, 1992; Swalve, 1993; Albuquerque & Meyer, 2001). Maternal effects imply an impact of the mother on her offspring other than a simple half of the genes she transmits to it. It arises from the mother's ability to produce milk needed for growth of the lambs as well as her general maternal behaviour (Bradford, 1972). The confounding of this dual contribution of the dam and the possibility of a negative correlation between direct and maternal effects have led to the investigation of the magnitude of these effects (Willham, 1980). Selection progress in a maternally influenced trait can sometimes be inaccurately predicted from direct heritability estimates alone. This could be as the result of a negative correlation between direct and maternal influences, which in turn may result in a lower total heritability. Moreover, some inconsistency was observed in the genetic correlations for direct and maternal additive genetic estimates in sheep, which even included a change of sign. Published values ranged from

moderately positive (Yazdi *et al.*, 1997) to very high negative (Maria *et al.*, 1993; Fadili *et al.*, 2000). Since a negative genetic correlation implies an antagonism in selection programmes trying to improve both direct and maternal performance, it is important to clarify the “true” size and sign of this biological relationship (Lewis & Beatson, 1999). In addition to these, the occurrence of multiple births in sheep, as opposed to cattle, poses the question of what the influence of a permanent environmental effect of the dam would be on the traits such as birth and weaning weight (Snyman *et al.*, 1995). Therefore, maternal effects have to be considered when carrying out genetic evaluations of early growth traits, in addition to direct genetic effects.

High productivity is achieved through the optimisation of reproduction of ewes, as well as survival and growth of their lambs. Snyman *et al.* (1998b) reported that among others, reproduction and survival rates are traits that are universally important in any environment or livestock production system. Other traits vary in importance and can, in some situations, be of little or no value. Land *et al.* (1983) indicated that no discussion of increasing lambing rates would be complete without the mentioning of lamb survival after birth.

Reproductive traits are difficult to measure and are strongly influenced by management decisions, but are also of paramount economic importance (Notter, 2000). A high reproductive rate in ewes increases both flock incomes from surplus stock and selection pressure in choosing replacements (Meyer & Clarke, 1982). Furthermore, reproductive performance is the primary contributor to mutton production. In South Africa, though Merino sheep are pre-eminently wool producers, 50 to 60 % of their income is generated through mutton production (Snyman *et al.*, 1998c). This same study reported that until recently, reproductive performance has, for various reasons, to a large extent been ignored in selection programmes. One of the main reasons is that genetic differences in reproductive performance are difficult to measure due to technical problems of recording and analysing reproduction data under extensive field conditions. Furthermore, early selection for reproduction based on own performance is not possible, as it can only be measured at a relatively late stage in life.

In the past, emphasis has mostly been given to the individual components of ewe productivity, such as fertility, litter size, lamb survival rate and lamb weaning weight (Fogarty, 1995; Snyman *et al.*, 1997). However, recently emphasis has been placed on the composite traits. The weight of lamb weaned per ewe mated is a composite trait representing total production per ewe. Snyman *et al.* (1997) reported that selection for total weight of lamb weaned would result in a correlated genetic increase in weaning weight of the individual lambs. However, selection for litter size alone would not increase the individual weaning weight of each lamb,

which is just as important as the number of lambs weaned (Snyman *et al.*, 1996). In addition, under harsh, extensive conditions and in wool producing sheep breeds high lambing percentages may lead to the production of a high quantity of lambs, but the quality of these lambs are in many instances not acceptable (Snyman *et al.*, 1997). Selection for increased reproductive performance in such flocks should be aimed at increasing the quality and monetary value of the product in terms of weight and carcass quality. Thus, the primary objective of lamb production under extensive conditions is to produce lambs that can be marketed as soon as possible after weaning, without the need for supplementary feeding.

Reproduction traits typically have large environmental variances, substantial non-additive genetic variance and low additive genetic variance. As a result, most female reproductive traits are lowly heritable, so little improvement through selection is expected (Smith *et al.*, 1989b). As an alternative to direct selection, substantial gains can be achieved by indirect selection for a correlated trait when the heritability of the trait under selection is higher than that of the trait of interest and the genetic correlation between the two traits is high (Walkley & Smith, 1980; Bourdon, 2000). Following the finding by Land (1973), emphasis was placed on scrotal circumference as an indirect selection criterion to improve reproduction performance of related females. Given the beneficial attributes and moderate heritability estimates (0.08 to 0.50) of scrotal circumference (Fogarty, 1995), testis measurements would be useful indirect selection criteria for the improvement of flock fertility.

In males, testicular size is the most likely criterion considered from a physiological, genetic and practical perspective to improve reproductive performance of related females (Land, 1973; Walkley & Smith, 1980). The expression of sexual traits in the female and male is related by basically similar physiological control mechanisms (Land, 1973; Purvis *et al.*, 1988). Before formulating a viable breeding plan for the Tygerhoek Merino flock, it is important to investigate the effect of testis size of service sires on the reproduction performance of ewes. Venter *et al.* (1984) also proposed that minimum scrotal circumference standards at a certain age should be established for individual breeds. Above all, literature estimates of genetic correlations between testicular traits and female reproductive performance are contradictory. Results reported by Purvis *et al.* (1988) suggest that selection for testis size would indirectly improve female reproduction. Kritzinger *et al.* (1984b) who have evaluated data sets of ram lambs of two breeds (Dorper and Mutton Merino) failed to demonstrate any positive association between prepubertal testis diameter of ram lambs and reproduction performance of their female relatives.

The objectives of this study were to determine genetic and non-genetic factors influencing early growth traits, ewe lifetime production (total number born, number weaned and weight weaned) and testis measurements in a flock of Merino sheep maintained at the Tygerhoek Experimental Farm. Non-genetic factors influencing preweaning lamb survival rate were also evaluated. The influence of testis size of service sires on ewe fertility (ewe lambing per ewe joined) and the genetic correlations between total weaning weight in the first parity and ewe lifetime reproduction traits were also investigated. The reason for investigating the genetic correlations between total weaning weight in the first parity and ewe lifetime reproduction traits was to try to determine whether the former one could be used as an efficient indicator of ewe lifetime productivity if selection is based on it.

Chapter 2

The influence of non-genetic factors on early growth traits in lambs

2.1 Introduction

The profitability of a sheep production enterprise is determined both by fertility and production traits (Nagy *et al.*, 1999). Of the production traits, the individual weaning weight of lambs and the preweaning weight gains are important components of market lamb production. Snyman *et al.* (1997) also indicated that the aim with the slaughter lamb production is to produce slaughter lambs that can be marketed as soon as possible after weaning without the need for supplementary feeding. This is of particular importance in South Africa where the Merino constitutes a large part of the total sheep population and this breed supplies the majority of the lamb and sheep carcasses marketed in the Republic (Heydenrych *et al.*, 1984).

A large number of non-genetic factors influence lamb weights and preweaning weight gains. The effects of year of birth, sex, type of birth and dam age on early growth traits of lambs have been well documented (Heydenrych, 1975; Fourie & Heydenrych, 1982; Fahmy, 1989; Boujenane & Kerfal, 1990; Bunge *et al.*, 1990; Schoeman, 1990; Sinha & Singh, 1997). Milk production also has a direct effect on weight gain of lambs (Hanrahan, 1976; Njwe & Manjeli, 1992). Postnatal factors account for 75 % of the maternal influence on weaning weight and are largely mediated through milk production (Bradford, 1972). Schoeman (2000) also reported that variation in pre-weaning weight might be due to poor milk production, composition, or the environmental conditions under which the animal is maintained. The effect of dam age on early growth of lambs is also well documented (Heydenrych, 1975; Fourie & Heydenrych, 1982; Fahmy, 1989; Van Wyk *et al.*, 1993a). The effect of dam age on postnatal growth of lambs may be indirect through milk production in that mature ewes may produce more milk than young ewes.

Selection of genetically superior individuals to be parents of the next generation is complicated by non-genetic factors that tend to mask the actual breeding values of the individuals being selected (Eltawil *et al.*, 1970). Identifying those non-genetic factors could help to look for appropriate ways to eliminate biases that may be caused by them; and therefore, more accurate estimation of breeding values would be possible. Van Wyk *et al.* (1993a) indicated that the specification of a model to describe the biological processes that

influence the specific trait requires the study of non-genetic sources of variation, so that a model can be found which (according to the available data) best describes the biological processes concerned. Moreover, most estimates of genetic variances in any livestock species are probably biased because of missing pedigree information jointly affected by fixed effects in the model and non-random selection of parents (Schenkel & Schaeffer, 2000). Knowledge of the non-genetic factors on production traits of sheep allows a more accurate assessment of breeding values and increases the rate of response to selection (Napier & Jones, 1982).

The purpose of the present study was to investigate some non-genetic factors influencing early growth traits in a Merino flock maintained at the Tygerhoek Experimental Farm. This was done to fit the appropriate operational model for the estimation of genetic parameters in a follow-up investigation.

2.2 Materials and methods

2.2.1 Location of the study area

The experimental animals originated from a selection experiment on the Tygerhoek Experimental Farm of the Department of Agricultural Development that was started in 1969. The farm is situated in the southern coastal area of the Western Cape province, about 150 km east of Stellenbosch at an altitude of approximately 168 m above sea level (34° 08' S, 19° 54' E). The area has an average annual rainfall of 429 mm, 60 % of which is recorded in winter (April – September). The average maximum (minimum) summer and winter temperatures are approximately 22°C (15°C) and 12°C (5°C), respectively.

2.2.2 Animals and management

Originally, 800 ewes were stratified according to wool production at 18 months within age groups of 1.5 to 5.5 years, and randomly allotted to five equal groups of 160 breeding ewes each. Twenty-six randomly chosen rams sired the progeny born in 1969. During the 1969 mating season, 20 available rams were allocated at random to each experimental group in sets of four rams per group. Selection of breeding rams in groups 1 and 3 was based on the highest uncorrected clean fleece mass at 18 months, provided that they had a fibre diameter lower than the average of their contemporaries. Replacement ewes were selected on clean fleece mass at 18 months of age in group 1 and corrected 42-day body mass in group 3 (Heydenrych *et al.*, 1984). Both groups consisted of 160 breeding ewes and 6 rams up to 1976, when they were pooled and reduced to 150 breeding ewes and 6 rams. This decision was based on preliminary findings (Heydenrych, 1977; as cited by Cloete *et al.*, 1992) and other reasons. Later selection of this group was predominantly based on uncorrected clean fleece mass at 18

months in both sexes but with a restriction on fibre diameter in rams. The size of the breeding flock ranged from 150 to 160 breeding ewes and 6 to 8 breeding rams. For the progeny groups born during the period 1986 to 1989, the prerequisite for breeding rams to grow wool with a lower fibre diameter than the mean of their contemporaries was relaxed to include individuals up to 2 μm stronger than their contemporaries.

Group 5 (hereafter called control group for the purpose of this study) served as a genetically stable Control Group for the assessment of selection progress in the selected lines. It originally consisted of 160 breeding ewes and 16 rams, but was allowed to increase to 200 breeding ewes and 20 breeding rams each year from 1976. Rams for the Control Group were chosen at random in such a way that each ram was replaced by a son, which was used for one season only. Ewes were normally replaced by a second daughter reaching joining age, thereby retaining the same age structure as in the selection groups (Heydenrych *et al.*, 1984).

Selection Group and Control Group individuals were maintained in a single flock. Males and females were kept separately. These flocks grazed mainly dryland lucerne pastures and occasionally small grain pastures or crop residues, when available (Cloete *et al.*, 1992).

2.2.3 Statistical Analysis

After editing, records of 8310, 7997 and 7997 lambs born from 1970 to 1998 were used in the analysis for birth weight (BW), weaning weight (WW) and preweaning average daily gain (ADG), respectively. The lambs were the progeny of 2538 ewes and 681 sires. Total number of records used and means for all traits are presented in Table 2.1. Records with missing or incomplete information, those found suspect due to duplicate animal identifications and other irreconcilable inconsistencies were eliminated from the data. Those lambs deviating more than three standard deviations from the mean weight for BW and WW were excluded. Lambs were weaned at approximately 120 days of age from 1970 to 1982, and at about 100 days of age thereafter, and before fitting the models WW was adjusted accordingly for all lambs. The few triplets (12 records) were pooled with twin lambs. After running a preliminary analysis, ewes above 6-yr-old age were pooled with 6-yr-old ewes due to their small numbers and no differences ($p > 0.05$) between the two sub-classes for any of the traits.

Fixed effects fitted were lambing year (1970 to 1998), sex (male, female), birth type (single, multiple), dam age (2 to 6-yr old age), group of animals (group of animals selected for increased clean fleece weight and unselected control group), lambing year by group interaction and lambing year by type of birth interaction. The analyses were first carried out fitting a full model including all main effects and interactions using the General Linear Model

(GLM) procedures of SAS (1996) to determine whether any of the effects or their interactions have an influence on the traits ($p < 0.05$). Those having no effect ($p > 0.05$) were subsequently omitted using a step-down procedure. The reduced models were then refitted for each variable.

Table 2. 1. Number of records, means and standard deviations for BW, WW and ADG

	BW	WW	ADG
No. records	8310	7997	7997
No. dams	2538	2538	2538
No. sires	681	681	681
Weight*			
Mean	3.6	22.9	192
s.d.	0.8	4.8	46.4
Dam age (yr)			
2	1527	1460	1460
3	1851	1782	1782
4	1900	1835	1835
5	1662	1607	1607
6	1370	1313	1313
Sex			
Male	4031	3862	3862
Female	4279	4135	4135
Type of birth			
Single	4946	4860	4860
Multiple	3361	3137	3137
Group of animals			
Selection	4238	4096	4096
Control	4072	3901	3901

*BW and WW in kg; ADG in g

The following model was fitted:

$$Y_{ijklmn} = \mu + Y_i + S_j + T_k + G_l + A_m + (YG)_{il} + (YT)_{ik} + e_{ijklmn}$$

where:

Y_{ijklmn} = record of the n^{th} animal

μ = the overall mean

Y_i = the fixed effect of the i^{th} birth year ($i = 1970, 1971, \dots, 1998$)

S_j = the fixed effect of the j^{th} sex ($j = 1$ or 2 ; $1 =$ male, $2 =$ female)

T_k = the fixed effect of the k^{th} type of birth ($k = 1$ or 2 ; $1 =$ single, $2 =$ multiple)

G_l = the fixed effect of the l^{th} group of animals ($l = 1$ or 2 ; $1 =$ selection group, $2 =$ unselected control)

A_m = the fixed effect of m^{th} ewe age ($m = 2, 3, 4, 5$ or 6 -yr-old)

$(YG)_{il}$ = interaction effect between i^{th} birth year and l^{th} group

$(YT)_{ik}$ = interaction effect between i^{th} birth year and k^{th} type of birth

e_{ijklmn} = the residual effect

2.3 Results

Analysis of variance for BW, WW and ADG is presented in Table 2.2, while least-squares means (\pm S.E.) for the same traits are shown in Table 2.3. The effects of all environmental factors were significant ($p < 0.001$) for all three traits, except for the birth year by type of birth interaction that was only significantly related to BW. The analyses of variance showed that the fixed effect models accounted for 39.8, 38.2 and 38.4 % of the variances in BW, WW and ADG, respectively. Of these, type of birth was of paramount importance for BW, and year of birth for both WW and ADG.

The effect of sex of lambs was significant ($p < 0.001$) for BW, WW and ADG. Male lambs were by 6.3 % (0.2 kg) and 8.2 % (1.9 kg) heavier at birth and weaning than females, respectively. They also grew approximately 9 % (17 g/day) faster from birth to weaning than female lambs. The effect of sex accounted for about 1.9 and 3.8 % of the variation in BW and WW, respectively.

Table 2.2. Analysis of variance for BW, WW and ADG

Fixed effects	df	Mean Square and significance level		
		BW	WW	ADG
Year	27	28.928***	1428.583***	161941.943***
Sex	1	102.828***	6991.854***	543823.467***
Type of birth	1	971.439***	15233.934***	856388.743***
Group of animals	1	85.369***	7782.480***	622206.758***
Ewe age	4	39.490***	190.818***	8069.298***
BY*GR	27	1.205***	86.056***	7149.017***
BY*TB	27	0.702**		
Error degrees of freedom	8218		7935	7935
Error mean square		0.403	14.42	1337.07
R ² (R-square %)		39.82	38.24	38.42
C.V.		17.46	16.61	19.05

** p < 0.01; *** p < 0.001; BY*GR=birth year by selection group interaction; BY*TB=birth year by type of birth interaction

Table 2.3. Least squares means (\pm S.E.) for BW, WW and ADG

Fixed effects	BW (kg)	WW (kg)	ADG (g)
Overall mean	3.6	22.9	192
Sex			
Male	3.7 \pm 0.01 ^a	23.8 \pm 0.06 ^a	202 \pm 0.60 ^a
Female	3.5 \pm 0.01 ^b	21.9 \pm 0.06 ^b	184 \pm 0.60 ^b
Type of birth			
Single	3.9 \pm 0.01 ^a	24.4 \pm 0.06 ^a	204 \pm 0.55 ^a
Multiple	3.2 \pm 0.01 ^b	21.4 \pm 0.07 ^b	182 \pm 0.68 ^b
Group of animals			
Selection	3.7 \pm 0.01 ^a	23.9 \pm 0.06 ^a	202 \pm 0.62 ^a
Control	3.5 \pm 0.01 ^b	21.8 \pm 0.06 ^b	184 \pm 0.61 ^b

^{a,b} denotes significant differences in columns within effects

Year of birth had a significant ($p < 0.001$) effect on live weights and growth rates up to weaning. WW was more affected by year differences than BW (Figure 2.1). BW was relatively stable throughout the study period except for the sudden increase in 1983. It

increased by 1.0 kg in this particular year. The WW performance of this flock was, however, decreasing in the early years of the study from 1970 to 1986, whereafter it increased. About 14.2 and 20.8 % of the weight differences for BW and WW were due to year of birth, respectively.

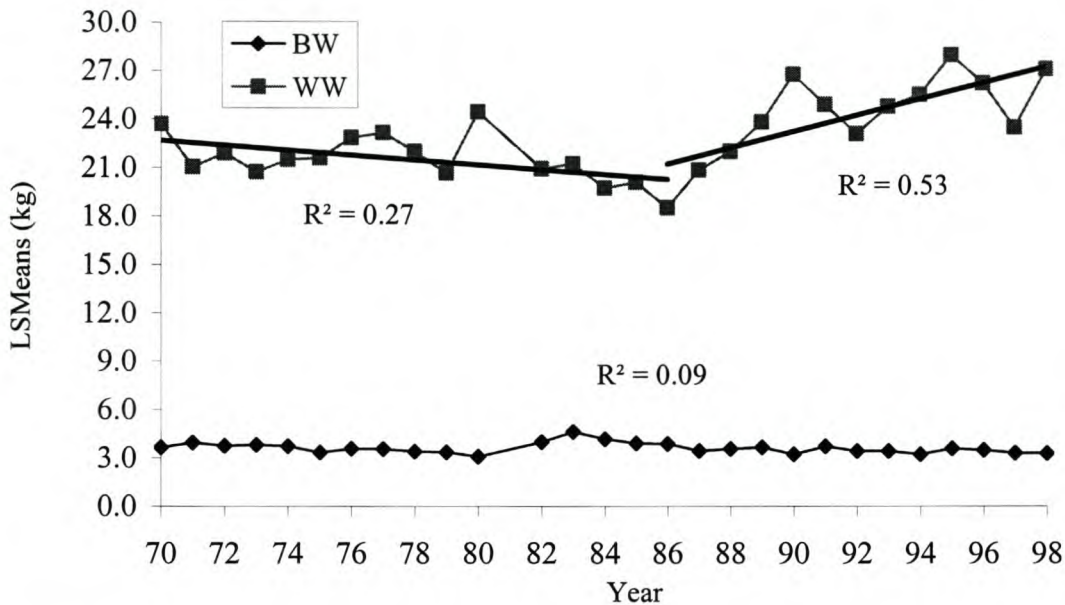


Figure 2.1. The effect of year of birth on BW and WW

Type of birth also had an effect ($p < 0.001$) on early weight traits of lambs. Single born lambs were by 20.6 % (0.8 kg) and 13.0 % (3.0 kg) heavier at birth and weaning than those born as multiples, respectively. They also grew faster at approximately 22 g/day than multiple born lambs. The effect of type of birth decreased with an increasing age of the lamb. As seen from the analysis of variance, type of birth accounted for 17.7 and 8.2 % of the liveweight variation at birth and at weaning, respectively.

Selection group also had an effect ($p < 0.001$) on BW, WW and ADG. Animals from the group selected for clean fleece weight were by 5.8 % (0.2 kg) and 9.0 % (2.1 kg) heavier at birth and weaning than the unselected control, respectively. They also grew faster than the unselected control group. A difference of about 18 g/day was observed between the selected group and the unselected control. Three distinct time periods are observed. In the first few years (1969 to 1979), the WW of the selected group increased while those of the control group slightly decreased (Figures 2.2 and 2.3). A sharp drop was observed in both groups between 1979 and 1985, followed by an increase in both since 1986. Selection group accounted for 1.6 and 4.2 % of the variation in BW and WW, respectively.

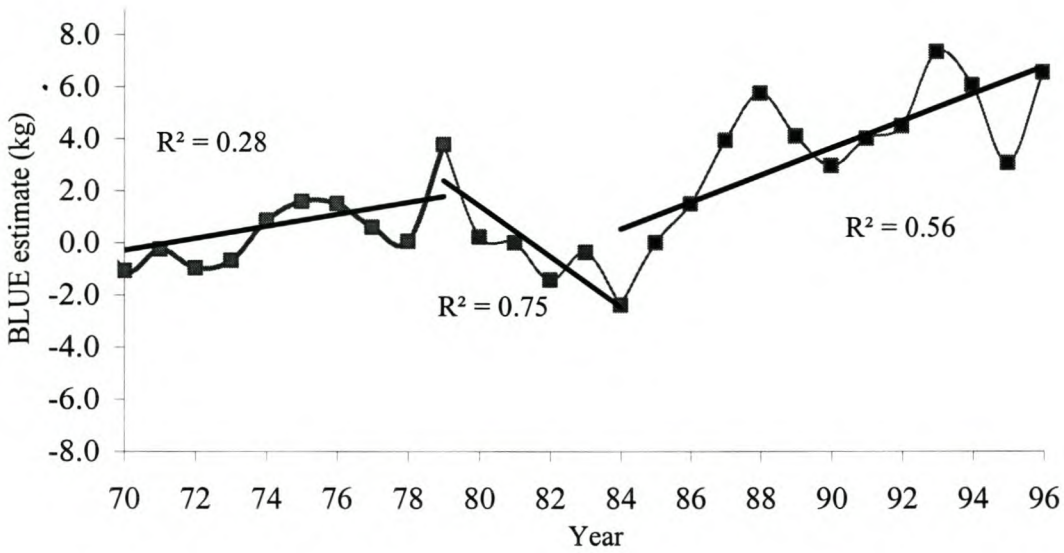


Figure 2.2. Phenotypic trends of WW for the selected group

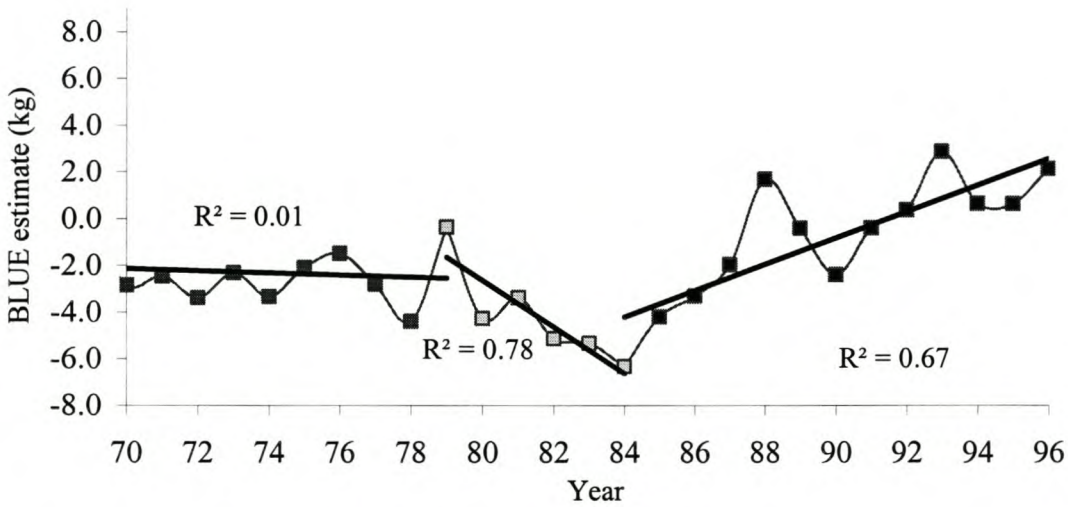


Figure 2.3. Phenotypic trends of WW for the control group

The age of dam effect was significant ($p < 0.001$) for all weight traits. Its effect followed the expected patterns for BW (Figure 2.4). It increased with increasing dam age until the maximum of 3.7 kg was reached at 6-yr of age. However, the lack of an adequate number of records on ewes older than 6-yr of age in the present data set prevented the estimation of age effects at older ages. Unlike BW, maximum WW and ADG were obtained for those lambs born to 4-yr-old ewes (Figures 2.5 and 2.6), whereafter it declined. Quadratic regressions of WW and ADG on age of dam reached a maximum at about 4.5 and 4.2-yr of age, respectively. Lambs born from maiden and older ewes grew slower and had lower liveweights

at weaning as compared to lambs from middle-aged ewe groups (3 to 5-yr-old ewes). The effect of dam age decreased with increasing age of lambs. Dam age accounted for about 2.9 and 0.4 % of liveweight variation at birth and at weaning, respectively.

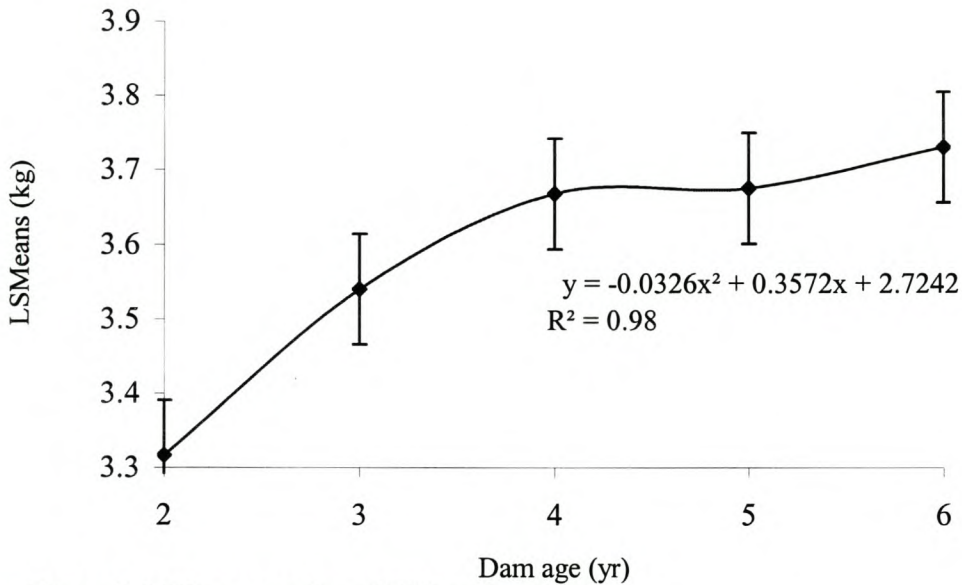


Figure 2.4. The regression of BW on dam age

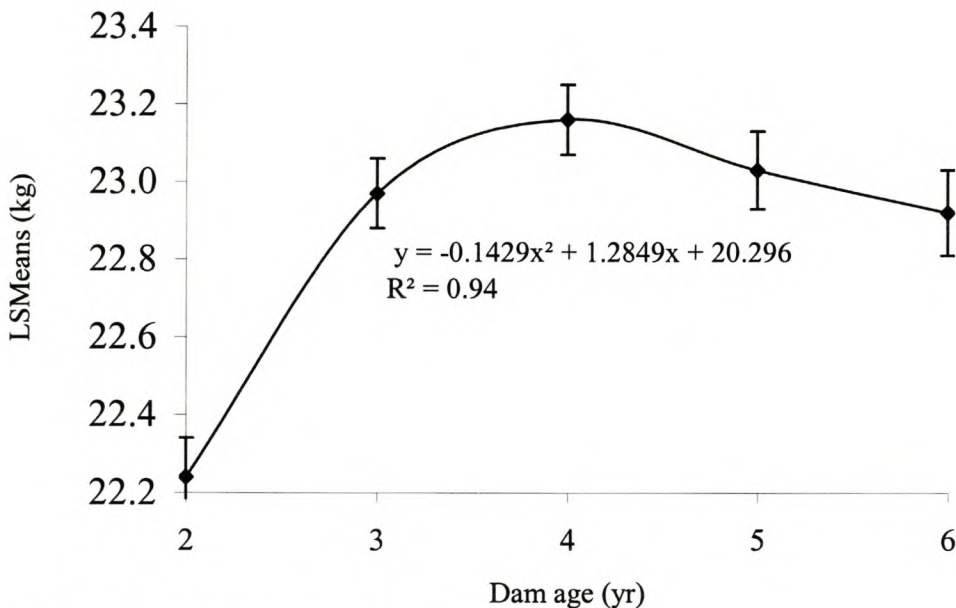


Figure 2.5. The regression of WW on dam age

For all three traits, the lambing year by group interaction was also significant ($p < 0.001$). Nevertheless, it accounted only for about 0.6 to 1.3 % variation in the three traits. The lambing year by birth type interaction was only significantly ($p < 0.001$) related to BW.

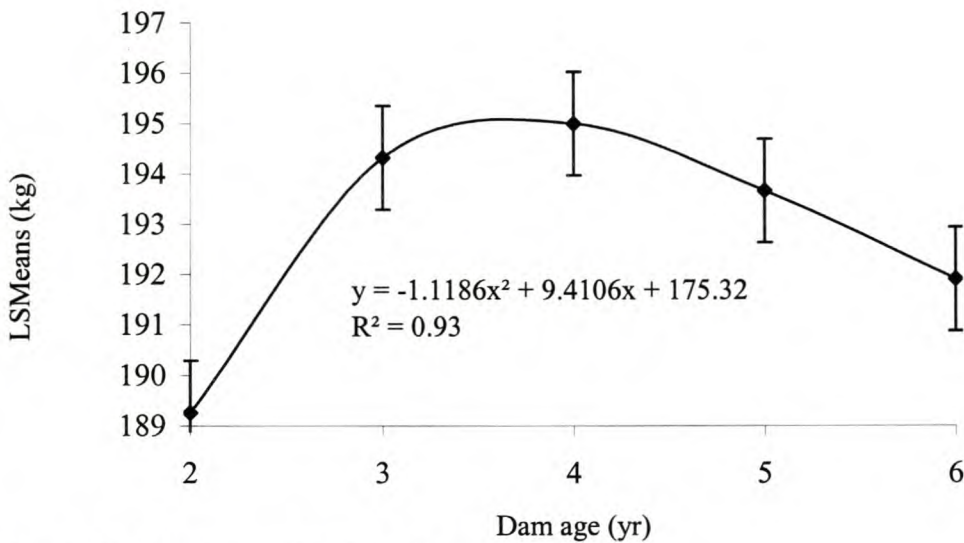


Figure 2.6. The regression of ADG on dam age

2.4 Discussion

The effect of environmental factors such as year, sex, type of birth and ewe age observed in the current study is in general agreement with those reported in the literature (Heydenrych, 1975; Fourie & Heydenrych, 1982; Boujenane & Kerfal, 1990; Schoeman, 1990; Van Wyk *et al.*, 1993a). Under arid conditions, the above-mentioned environmental fixed factors are known to predominate in determining sheep productivity (Eltawil *et al.*, 1970).

Very few reports have been reported for BW in Merino sheep of South Africa. It was only analysed in a previous study conducted with this flock (Heydenrych, 1975) and one recently reported by Cloete *et al.* (2000) with a Merino flock in the Swartland region. It is, however, a trait of potential economic importance through its effects on lamb survival rate in this flock, in that very large and small lambs were at risk of preweaning death (Chapter 6). Mean BW found in the present study was lower than those reported by Heydenrych (1975) based on part of the same data. This might be due to the smaller data set used in the previous study. It was, however, in accordance with that reported by Cloete *et al.* (2000). The mean WW obtained was also in agreement with these authors, but higher than those reported in the Carnarvon Merino flock (Snyman *et al.*, 1996). It was, nevertheless, lower than results reported for several other breeds by Schoeman (2000). The mean ADG found in the current study was in good agreement with those reported for Baluchi sheep (Yazdi *et al.*, 1998).

Male lambs were heavier at birth and at weaning than female lambs. They also grew faster than female lambs. This is in general agreement with reports in the literature (Heydenrych,

1975; Fourie & Heydenrych, 1982; Schoeman, 1990; Van Wyk *et al.*, 1993a; Mavrogenis, 1996; Gojjam *et al.*, 1998; Abegaz & Duguma, 2000). The heavier WW of ram lambs than their female contemporaries may be due to greater birth weights and growth rate of male lambs. According to Eltawil *et al.* (1970), lambs with a heavier BW, which might be due to being males, singles and/or from mature ewes, tend to achieve higher weights at weaning, partly because of the positive correlations between traits. The influence of sex on liveweight increased with an increase in age, and agreed with results reported by Fourie & Heydenrych (1982) and Nagy *et al.* (1999). Such differences might be attributed to different physiological functions in the two sexes (Rajab *et al.*, 1992).

In the current study, year had an effect ($p < 0.001$) on weights and growth rate up to weaning. Differences observed in weights between years may be a reflection of differences in feed availability between years, caused by variation in total annual precipitation and the distribution of rainfall. The southern Cape area is subjected to dry years with limited feed availability. Similar results of the effects of year on production traits are well documented (Eltawil *et al.*, 1970; Blackburn & Cartwright, 1987; Rajab *et al.*, 1992; Mavrogenis, 1996).

Differences in early growth traits were observed between the selected group and the unselected control. This could possibly be explained through the positive genetic correlation between liveweight and fleece weight. Heydenrych (1975), Heydenrych *et al.* (1984) and Cloete *et al.* (1992; 1998b) reported that selection for clean fleece weight resulted in a correlated increase in liveweight due to this positive genetic correlation between fleece weight and body weight. In general, three time periods (1969 to 1979, 1980 to 1985 and 1986 to 1995) are evident in the phenotypic trends for WW in both groups. In the first, the selected group showed a substantial increase and in the second and the third both followed the same direction. The increase in the selected group during the first decade might be due to the fact that animals with a higher genetic level entered the selection line. The decrease and an increase in the second and third phases, respectively, may be due to environmental factors since animals were kept mainly on pastures. The third phase might possibly have had better years than the second phase. In addition, different people managed the flocks over the period of 25 years that might have contributed to certain unexplained fluctuations.

Type of birth also affected liveweight and growth rates of this flock. Single born lambs were heavier and grew faster than multiple born lambs. This accord with results reported by Heydenrych (1975) for the same flock, Fourie & Heydenrych (1982) in Döhne Merino and several other breeds (Galal & Awgichew, 1981; Boujenane *et al.*, 1991; Rajab *et al.*, 1992; Abegaz *et al.*, 2000). Part of the type of birth differences on WW might be due to the carry-

over of the heavier weight of singles at birth. Differences due to type of birth may be more important under arid conditions than under intensive sheep production systems (Eltawil *et al.*, 1970). The difference of 0.8 kg found in the present study for BW corresponds to the 0.7 kg reported by Yazdi *et al.* (1998) for Baluchi sheep. However, a 1.8 kg higher WW for singles than multiples reported by Yazdi *et al.* (1998) for the Baluchi breed was slightly less than the current result. Generally, in the current study, the effect of type of birth decreased as lambs became older. Fourie & Heydenrych (1982) reported similar results. According to Bradford (1985), environments with scarce forage that are highly variable among seasons and years, and where supplemental feed is scarce and uneconomic, would only support sheep with single births. However, if such environments permit supplementation at critical times, twinning from mature ewes could be tolerated. The Tygerhoek Merino sheep grazed mainly dryland lucerne pastures unless occasionally supplied with grain pastures or crop residues when available (Cloete *et al.*, 1992).

The average weight of lambs at birth increased with an increasing ewe age up to the maximum age (6-yr) considered in this study. Three other South African studies observed an increase in BW up to 5- to 7-years of age in both Döhne Merino and Dormer sheep (Fourie & Heydenrych, 1982; Van Wyk *et al.*, 1993a; Schoeman, 1990). An increase in BW was observed up to an age of five years (fourth parity) in Horro sheep of western Oromia, Ethiopia (Abegaz & Duguma, 2000), seven years of age in Baluchi sheep of northeast Iran (Yazdi *et al.*, 1998) and in Romanov sheep of Canada (Fahmy, 1989). The reasons for the differences may be attributed to differences in production environments and management levels (Schoeman, 2000). It might also be due to breed effects, in that earlier maturing breeds may reach their peak earlier than the late maturing breeds.

The influence of age of dam on growth traits of offspring was greatest at birth and lessened, as the animal grew older, at weaning. Lambs out of 2-yr-old ewes were lighter ($p < 0.001$) at birth and weaning than were lambs out of older ewes. This might be explained by the fact that young dams that had not reached adult size continued to grow during pregnancy and thus competed with the fetus for available nutrients. Moreover, maiden ewes as first-time lambers may produce less milk than average. Abegaz & Duguma (2000) indicated that maiden ewes may put their lambs at disadvantage in two possible ways. They produce lambs with lower body weight and their mothering ability is poor as a result of lack of experience and a poorly developed udder. According to Snyman *et al.* (1996), problems related to young ewes may be carried over to the second and perhaps even to the third parities. Although 6-yr-old ewes had lambs that were heavier at birth than all other age groups, their lambs were lighter at weaning

than those reared by 3- to 5-yr-old ewes. The general trend for the effect of age of ewe on WW and ADG was curvilinear. Maximum liveweight and growth rate of lambs were obtained from ewes of intermediate age groups and lower liveweight and inferior growth rate performance from lambs of very young and old aged ewes. Therefore, the dam age effect observed on BW of lambs from 6-yr-old ewes might be a manifestation of an age effect on pre-natal environment and that of WW and ADG of lambs from middle-aged ewes could be brought about by a higher milk production in the middle-aged ewes. An animal's WW is mostly a function of the milk production and mothering ability of its dam (Ercanbrack & Knight, 1998; Bourdon, 2000). It is also interesting to note that maximum WW and ADG were attained approximately at an age at which ewes of this flock attain their mature liveweight. In the Tygerhoek Merino flock breeding ewes reached their maximum liveweight at their fourth mating when they are 4.5-yr-old (Heydenrych, 1975). The superiority of lambs born to middle aged ewes in WW obtained in the current study agreed with the findings of Rajab *et al.* (1992), Van Wyk *et al.* (1993a) and Abegaz & Duguma (2000). In contrast, Schoeman (1990) found non-significant ewe age differences on 100-day body weight in Döhne Merino's (which is the same age as the current weaning age). The difference might be due to management practices.

2.5 Conclusions

In this study, several non-genetic fixed factors have a significant influence on early growth traits. Male lambs and singles were heavier both at birth and weaning and grew faster than females and multiples, respectively. Non-selected animals were lighter than selected animals at birth and weaning with inferior growth rates. The trend in this study for BW was an increase with an increase in age of dam up to 6-yr of age. However, the age of dam effects on WW and ADG were curvilinear. The heaviest lambs were from 3-to 5-yr-old dams and the lightest from 2- and 6-yr-old dams. Therefore, the heavier BW of lambs from 6-yr-old ewes may be due to a better pre-natal environment, while not providing as much milk to support preweaning growth level. Thus, it becomes more profitable to keep a larger proportion of the middle-aged ewes (between 3-to 5-yr-old ewes) to improve productivity of this flock.

Chapter 3

The estimation of (co)variance components for early growth traits

3.1 Introduction

In mammals, growth is influenced by the genes of the individual for growth, by the environment provided by the dam and other environmental effects (Lewis & Beatson, 1999; Albuquerque & Meyer, 2001). In young animals, the milk supply of the dam (Bradford, 1972; Meyer, 1992; Lewis & Beatson, 1999) 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 greater relative variation in litter size in sheep and the competition between lambs on their mother's milk supply. It incorporates both similarities between twins and similarities between lambs born to the same ewe in different years (Snyman *et al.*, 1995). The dam, therefore, contributes to the phenotypic value of her offspring, not only by a sample half of her genes, but also through her genes responsible for the expression of her maternal performance.

The confounding of the maternal effect of the dam and her genetic contribution to the phenotypic value of her offspring and the possibility of a negative genetic correlation between the direct and maternal effect are the two most important problems in selection programmes (Willham, 1980). Thus, in order to decide upon a feasible selection strategy, estimation of the genetic parameters and the correlations between direct and maternal additive genetic effects are necessary. The recent statistical and computational developments have made routine analyses to estimate these parameters by Restricted Maximum Likelihood (REML), fitting an animal model, conceptually straightforward and technically feasible. Further, a multitrait genetic evaluation by best linear unbiased prediction (BLUP) fitting an animal model requires partitioning of the phenotypic variances and covariances into their direct genetic, maternal genetic, maternal permanent environmental and residual components (Meyer, 1993).

The primary objective of animal breeding is to maximize genetic improvement in economically important traits through selection. To determine the effectiveness of genetic selection, genetic trends in the population under consideration can be monitored (Van Wyk *et al.*, 1993c). According to Wilson & Willham (1986), trend lines may be used to compare

alternative methods of selection or management and to reinforce the selection and management established. So far, no genetic and environmental trends have been estimated for early growth traits in the Merino flock at the Tygerhoek Experimental Farm. However, a graphic historical perspective of a breeding programme using phenotypic, genetic and environmental trend lines can convey a quick assessment of a breeder's selection success in previous generations (Wilson & Willham, 1986).

The objectives of this study were to estimate (co)variance components for birth weight, weaning weight and average daily gain to weaning and to estimate genetic and environmental trends for these traits in the Tygerhoek Merino flock.

3.2 Materials and Methods

Records of 8310 lambs born from 2538 ewes and sired by 681 rams, raised over the period from 1970 to 1998 were used in this study. The general management of the flock and description of the study area are described in Chapter 2. Liveweight at birth (BW), weaning (WW) and preweaning average daily gain (ADG) were the growth traits investigated. The environmental effects having an effect ($p < 0.05$) on the traits (Chapter 2) were fitted in the models to estimate the genetic parameters. The model used included birth year (1970 to 1998), sex (male, female), birth type (single, multiple), dam age (2- to 6-yr old) and group (group of animals selected for increased clean fleece weight and the unselected control) as fixed effects.

Variance components were estimated by Restricted Maximum Likelihood procedures (REML) applying the VCE 4.2.5 package of Groeneveld (1998). Genetic correlations among growth traits were obtained by multitrait analyses. An animal model including maternal additive genetic and maternal permanent environmental effects as additional random effects was fitted for all three traits. Both the unitrait and multitrait genetic analyses were conducted under all models for all three traits. By using estimated (co)variance components, direct heritabilities (h^2), maternal heritabilities (m^2), maternal permanent environmental variances (c^2) and the correlations between the direct and maternal additive genetic effects (r_{am}) were obtained. Total heritabilities (h^2_{total}) were calculated as defined by Willham (1972) for those analyses where maternal genetic effects were obtained. All models involved the same fixed effects in both the unitrait and multitrait analyses. In order to assess the importance of different random effects, four models of analysis differing in the random effects were fitted.

The models were:

$$1. Y = X\mathbf{b} + Z\mathbf{a} + e \quad (\text{Model 1})$$

$$2. Y = X\mathbf{b} + Z\mathbf{a} + P\mathbf{c} + e \quad (\text{Model 2})$$

$$3. Y = X\mathbf{b} + Z\mathbf{a} + M\mathbf{m} + e \quad \text{Cov}(\mathbf{a}, \mathbf{m}) = A\sigma_{am} \quad (\text{Model 3})$$

$$4. Y = X\mathbf{b} + Z\mathbf{a} + M\mathbf{m} + P\mathbf{c} + e \quad \text{Cov}(\mathbf{a}, \mathbf{m}) = A\sigma_{am} \quad (\text{Model 4})$$

where:

Y = the vector of records

\mathbf{b} = the vector of fixed effects

X = the matrix that associates \mathbf{b} with Y

\mathbf{a} = the vector of breeding values for direct additive genetic effects

Z = the matrix that associates \mathbf{a} with Y

\mathbf{m} = the vector of breeding values for maternal genetic effects

M = the matrix that associates \mathbf{m} with Y

\mathbf{c} = the vector of permanent environmental effects due to dam

P = the matrix that associates \mathbf{c} with Y

e = the vector of residual effects.

Further, with A the numerator relationship matrix between animals, I_n an identity matrix with order the number of animals and I an identity matrix with order the number of records, the (co)variance structure of the random effects in the analysis can then be described as:

$V(\mathbf{a}) = \sigma_a^2 \mathbf{A}$, $V(\mathbf{m}) = \sigma_m^2 \mathbf{A}$, $V(\mathbf{c}) = \sigma_c^2 \mathbf{I}_n$, $V(e) = \sigma_e^2 \mathbf{I}$ and $\text{Cov}(\mathbf{a}, \mathbf{m}) = A\sigma_{am}$, where σ_a^2 is the additive genetic variance, σ_m^2 , the maternal additive genetic variance, σ_c^2 , the maternal permanent environmental variance, σ_e^2 , the residual variance and σ_{am} , the direct and maternal genetic covariance. It was assumed that all effects in the models are independent with the exception of the direct and maternal additive genetic effects.

In estimating the genetic and environmental trends, breeding values of BW and WW, both for the direct and maternal additive genetic, estimated from Model 3, were used. Aggregate breeding values, which is the sum of the direct and maternal breeding values (Azzam & Nielson, 1987), were calculated for both traits. The aggregate breeding values of animals born

within specific years (age contemporaries) were averaged. The back solutions (BLUE estimates) of the year effects were considered as the estimate of environmental trends. Thus, the aggregate breeding values for BW and WW and the back solutions for the year effect were regressed on years to illustrate the genetic and environmental trends over years, respectively.

3.3 Results

3.3.1 Unitrait analyses

Estimates of (co)variance components, direct (h^2) and maternal (m^2) heritabilities, values for the maternal permanent environmental effects (c^2) and the correlations between the direct and maternal additive genetic effects (r_{am}) for each trait are shown in Table 3.1. For comparisons, published heritability estimates for BW and WW are summarised in Tables 3.2 and 3.3, respectively. Standard errors of heritability estimates were unavailable for the variance components estimated with Models 3 and 4. Standard errors of heritability estimates obtained from Models 1 and 2 were low, ranging from 0.01 to 0.02. For each trait, estimates of σ^2_p were comparable for all models.

The log likelihood values obtained under the four different models of analysis are shown for each trait in Table 3.1. According to Groeneveld (1998), the model with the smallest log likelihood would best fit the data set under consideration. Thus, in all three traits, Model 2, where the maternal permanent environmental effect were fitted as the only random effect in addition to the direct additive genetic effect, best fit the data. In this study, fitting the maternal additive genetic effects as the only random effect in addition to the direct additive genetic effect resulted in larger log likelihood than in Models that ignored the maternal additive genetic effects. The estimates of m^2 were also larger than both h^2 and c^2 estimates for BW. For WW and ADG, both m^2 and c^2 estimates were smaller than h^2 estimates, while they were almost equal in model (Model 4) that included both simultaneously.

The h^2 estimates for BW ranged from moderate to moderately high. In Model 1, where maternal effects were ignored, h^2 estimates were higher and most likely biased upwards. However, fitting either or both of the maternal effects reduced the σ^2_a and h^2 estimates from 0.16 to 0.08 and 0.38 to 0.19, respectively. Likewise, failure to take account of maternal permanent environmental effects (c^2) resulted in higher maternal genetic variances (σ^2_m) and the corresponding m^2 estimates. Thus, when the maternal permanent environmental effect (c^2) was ignored, the total variance was attributed to the maternal genetic variance (σ^2_m), probably resulting in an overestimation of m^2 .

Table 3.1. Estimates of (co) variance components, genetic parameters and heritability estimates for early growth performances from univariate analyses

Model	σ^2_a	σ^2_c	σ^2_m	σ_{am}	σ^2_e	σ^2_p	h^2	c^2	m^2	r_{am}	h^2_t	Log L
BW												
M1	0.16				0.26	0.42	0.38				0.38	9629.90
M2	0.08	0.11			0.22	0.41	0.19	0.27			0.19	9078.86
M3	0.08		0.15	-0.03	0.23	0.43	0.19		0.38	-0.23	0.26	14821.99
M4	0.07	0.04	0.10	-0.02	0.22	0.41	0.19	0.10	0.25	-0.22	0.22	14799.42
WW												
M1	5.25				9.52	14.77	0.36				0.36	9604.73
M2	4.31	1.51			8.83	14.65	0.29	0.10			0.29	9509.85
M3	3.73		1.64	0.04	9.34	14.75	0.25		0.11	0.02	0.31	15334.04
M4	3.83	0.92	0.78	0.08	9.05	14.66	0.26	0.06	0.05	0.05	0.30	15317.49
ADG												
M1	458.37				904.31	1362.68	0.34				0.34	9606.44
M2	384.71	124.27			844.85	1353.83	0.28	0.09			0.28	9530.81
M3	355.05		136.05	-11.85	882.19	1361.44	0.26		0.10	-0.05	0.30	15362.81
M4	362.20	85.91	55.85	-4.25	854.50	1354.21	0.27	0.06	0.04	-0.03	0.28	15345.38

σ^2_a , direct additive genetic variance; σ^2_c , maternal permanent environmental variance; σ^2_m , maternal additive genetic variance; σ_{am} , direct-maternal genetic covariance; σ^2_e , residual variance; σ^2_p , phenotypic variance; Log L, log likelihood; h^2 , direct heritability; c^2 , ratio of maternal permanent environmental effect; m^2 , maternal heritability; r_{am} , direct-maternal genetic correlation; h^2_t , total heritability; $h^2_t = (\sigma^2_a + 0.5 \sigma^2_m + 1.5 \sigma_{am}) / \sigma^2_p$.

Table 3.2. Parameter estimates for BW reported in the literature

Breed	h^2	m^2	c^2	r_{am}	References
Chios	0.13 to 0.38	0.13 to 0.33	0.16 to 0.28	0.00 to -0.44	Ligda <i>et al.</i> (2000)
Various breeds	0.19 to 0.34	0.30 to 0.65		-0.18 to -0.74	Burfening & Kress (1993)
Horro	0.18 to 0.32	0.10 to 0.26		-0.64	Abegaz & Duguma (2000)
Elsenburg Dormer	0.16 to 0.42	0.43		-0.35	Van Wyk <i>et al.</i> (1993b)
Romanov	0.04	0.22	0.10	-0.99	Maria <i>et al.</i> (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	Näsholm & Danell (1996)
Afrino	0.22	0.09	0.12		Snyman <i>et al.</i> (1995)
Baluchi	0.14	0.12		0.18	Yazdi <i>et al.</i> (1997)
Australian Merino	0.30	0.29		-0.43	Torshizi <i>et al.</i> (1996)
Döhne Merino	0.04	0.10	0.17		Cloete <i>et al.</i> (1998a)
Moroccan Timahdit	0.18	0.59		-1.00	Fadili <i>et al.</i> (2000)
Dorper sheep	0.11	0.10	0.12	0.35	Neser <i>et al.</i> (2001)

Table 3.3. Parameter estimates for WW reported in the literature

Breed	h^2	m^2	c^2	r_{am}	References
Chios	0.15 to 0.29	0.05 to 0.16	0.08 to 0.12	-0.22 to -0.26	Ligda <i>et al.</i> (2000)
Various breeds	0.09 to 0.22	0.07 to 0.48		-0.41 to -0.88	Burfening & Kress (1993)
Elsenburg Dormer	0.13 to 0.34	0.20		-0.16	Van Wyk <i>et al.</i> (1993b)
Horro	0.10 to 0.26	0.19 to 0.24		-0.42	Abegaz & Duguma (2000)
Romanov	0.34	0.25	0.00	-0.97	Maria <i>et al.</i> (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	Näsholm & Danell (1996)
Afrino	0.33	0.17			Snyman <i>et al.</i> (1995)
Baluchi	0.19	0.03		0.51	Yazdi <i>et al.</i> (1997)
Australian Merino	0.28	0.41		-0.59	Torshizi <i>et al.</i> (1996)
Moroccan Timahdit	0.50	0.24		-0.94	Fadili <i>et al.</i> (2000)
S. A. Mutton Merino	0.19	0.09	0.10	-0.55	Neser <i>et al.</i> (2000)
Dorper sheep	0.20	0.10	0.08	-0.58	Neser <i>et al.</i> (2001)

In both Models 3 and 4, where the maternal additive genetic effects were fitted, m^2 estimates were larger than both h^2 and c^2 values. In Model 2, when maternal additive genetic effects were ignored, the c^2 value was larger than the h^2 estimate. The estimate of the total maternal effect ($m^2 + c^2 + 1/4h^2 + \sqrt{h^2} * \sqrt{m^2} * r_{am}$) was 0.35, which indicated that the maternal effect is more important than the direct additive effect. It is also evident that the relative values of h^2 and m^2 were greatly influenced by the model used in the analysis. Estimates of the correlations between the direct and maternal additive genetic effects (r_{am}) were negative and moderate in magnitude.

As in BW, h^2 estimates for WW decreased when either of the maternal effects were fitted in the model. When the maternal permanent environmental effects (c^2) were fitted in the model, the variance due to maternal additive genetic effects (σ_m^2) and the corresponding estimate of m^2 decreased. As opposed to BW, both maternal additive genetic and maternal permanent environmental effects were smaller than the direct additive genetic effects under all Models. The correlations between direct and maternal additive genetic effects (r_{am}) were nearly zero and positive in sign.

For ADG, the estimates for the direct and maternal additive genetic and maternal permanent environmental variances followed the same pattern as for WW, and they were of approximately similar magnitude. The correlations between direct and maternal additive genetic effects (r_{am}) were nearly zero and negative in sign.

3.3.2 Multitrait analyses

The (co)variance estimates from multitrait analyses (Models 3 and 4) are shown in Table 3.4, while the variance component and genetic parameter estimates from Model 4 are in Table 3.5. The h^2 estimates obtained for BW were of similar magnitude with estimates from the unitrait analysis. As in the unitrait analysis, when maternal effects were ignored in the model, h^2 increased and were most likely biased upwards. When maternal effects, either genetic or environmental, were fitted in the model, h^2 was decreased. The m^2 estimate obtained from Model 3, where maternal permanent environmental effect was ignored in the model, was also high. When maternal permanent environmental effects (c^2) were fitted in the model, the maternal genetic variance (σ_m^2) and the m^2 estimate declined by 21.1 and 14.0 % respectively, indicating that exclusion of maternal permanent environmental effects (c^2) resulted in an inflation of m^2 .

Table 3.4. Estimates of variance components and genetic parameters from multitrait analyses (Model 3 and Model 4) of BW, WW and ADG

Item	BW	WW	ADG
Model 3			
Variance components			
σ^2_a	0.168	3.823	346.534
σ^2_m	0.356	0.706	20.438
σ_{am}	-0.014	0.161	-0.022
σ^2_e	0.363	7.491	644.509
σ^2_p	0.873	12.181	1011.459
Genetic parameters			
h^2	0.20	0.31	0.34
m^2	0.41	0.06	0.02
r_{am}	-0.06	0.10	0.00
h^2_t	0.37	0.36	0.35
e^2	0.42	0.61	0.64
Model 4			
Variance components			
σ^2_a	0.113	8.703	850.667
σ^2_m	0.145	0.331	6.129
σ_{am}	-0.003	-0.170	-11.711
σ^2_c	0.024	0.377	23.057
σ^2_e	0.256	12.979	1264.205
σ^2_p	0.535	22.220	2132.347
Genetic parameters			
h^2	0.21	0.40	0.40
m^2	0.27	0.02	0.01
r_{am}	-0.02	-0.10	-0.16
h^2_t	0.34	0.39	0.39
c^2	0.05	0.02	0.01
e^2	0.48	0.59	0.60

As in BW, for WW and ADG, the estimates of h^2 were most likely inflated when maternal effects were ignored in the model; and that of maternal additive genetic effects were also biased when maternal permanent environmental effects were ignored. Nevertheless, the h^2 estimates were larger than both m^2 and c^2 estimates. The h^2 estimates obtained from multitrait analyses were slightly larger than those obtained from unitrait analyses for both traits.

Direct genetic correlations between BW and WW and between BW and ADG were small positive, while that between WW and ADG was almost unity. The maternal genetic correlations between BW and WW, BW and ADG and WW and ADG were all high positive. The maternal permanent environmental correlation estimates between the different weight traits were positive and high.

Table 3.5. Estimated direct genetic, maternal genetic, maternal permanent environmental and residual correlations (above diagonal) and the corresponding covariances (below diagonal) between BW, WW and ADG from multitrait analyses (Model 4)

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

3.3.3 Genetic and environmental trends

The mean, standard deviations, maximum and minimum estimated breeding values (kg) for BW and WW are presented in Table 3.6. The estimated mean direct breeding value of WW was larger than that of the maternal breeding values. The differences between the maximum and minimum direct breeding values were also larger than the maternal breeding values for WW. In case of BW, the differences between the maximum and minimum maternal breeding values were large as compared to that of the direct. In general, mean maternal breeding values for both traits were negative while that of the direct and aggregate breeding values were positive (Table 3.6).

Table 3.6. Mean, maximum and minimum estimated breeding values (kg) for BW and WW

Trait	Records (no.)	Mean (Std. Dev.)	Maximum	Minimum
BW	8310			
Maternal		-0.011 (0.217)	1.153	-1.001
Direct		0.006 (0.170)	0.760	-0.528
Aggregate		0.055 (0.266)	1.226	-1.068
WW	7991			
Maternal		-0.001 (0.555)	2.251	-2.204
Direct		0.742 (1.536)	6.510	-6.549
Aggregate		0.741 (1.821)	7.840	-6.620

The estimated average maternal and direct genetic trends are presented in Figures 3.1 and 3.2 for BW and WW, respectively. Linear regressions produced R^2 values of 0.51 for BW direct and 0.58 for BW maternal genetic trends. The corresponding values for WW were 0.46 and 0.37. Environmental trends for both traits are also shown in Figure 3.3. Both maternal and direct breeding values increased throughout the study period, except for 1985 and 1996 when a sudden drop in mean maternal breeding values was observed in BW. In the latter year, a sharp increase in mean direct breeding value for BW was evident (Figure 3.1), while a sharp decrease was evident in WW (Figure 3.2). The aggregate breeding values followed more or less the same trend as the direct breeding values during most of the study period particularly for WW, and for this reason they were not plotted. This may be explained by the large direct genetic effect for WW. Maternal breeding values of WW in 1970 and 1971 were slightly

higher than the direct breeding values (Figure 3.2). Other than these, the direct breeding values were higher than the maternal breeding values in both BW and WW. For BW, in 1983, 1987 to 1988 and 1991 to 1995, when both direct and maternal breeding values increased, the estimated aggregate breeding values were larger than the direct breeding values (not shown).

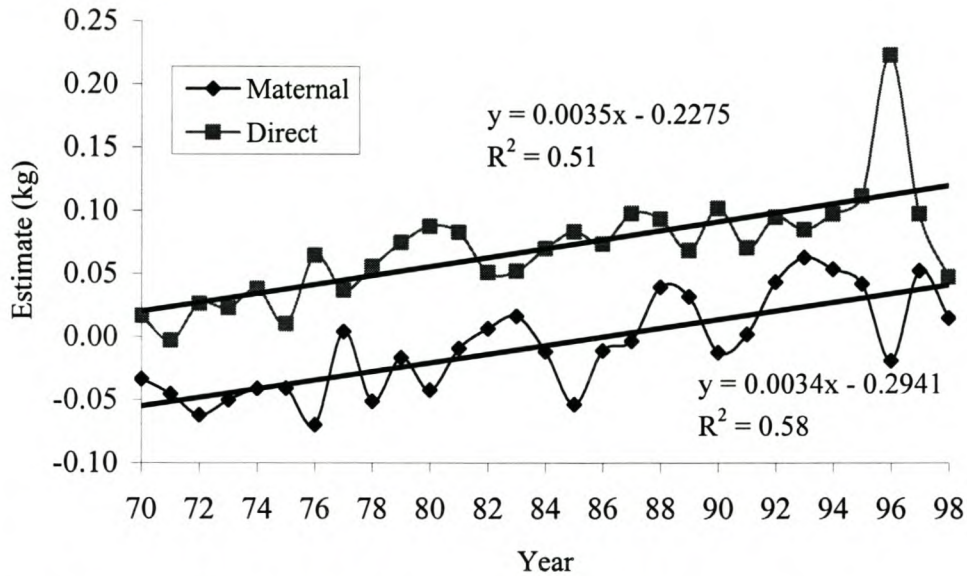


Figure 3.1. Regression of estimated breeding values of BW on year

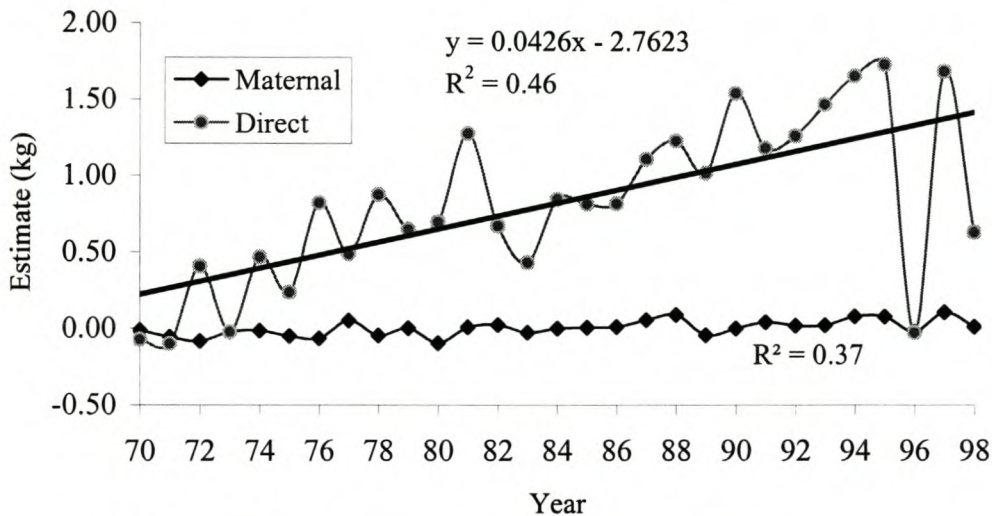


Figure 3.2. Regression of estimated breeding values of WW on year

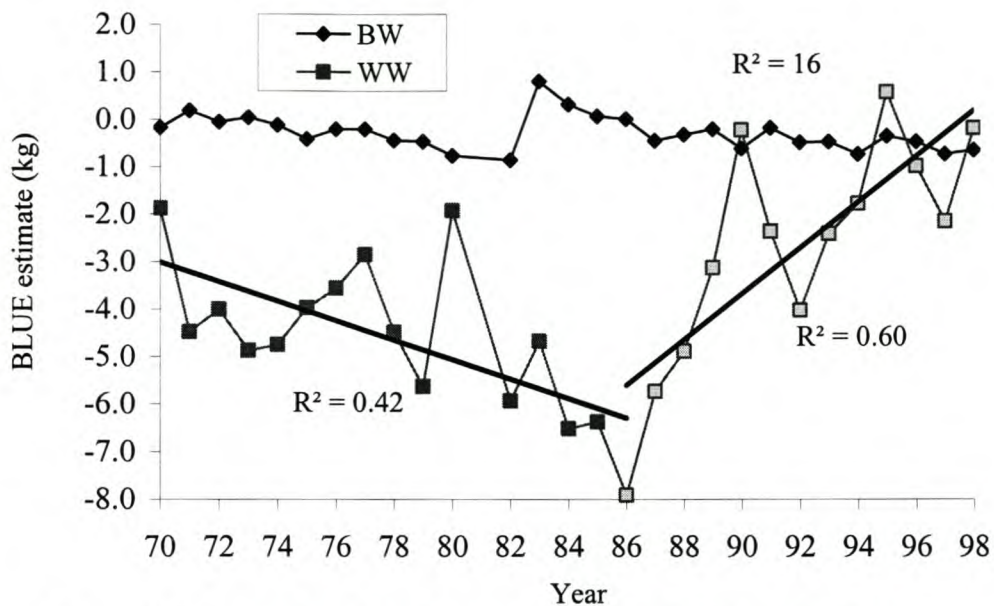


Figure 3.3. Regression of environmental effects of BW and WW on year

The environmental trends had R^2 value of 0.16 for BW and values ranging from 0.42 to 0.60 for WW. The environmental trends for BW remain relatively stable throughout the study period except for a sudden increase in 1983. Although the trend for WW was characterised by large year-to-year variation, two distinct periods (1970 to 1986 and 1987 to 1998) were evident. During the first, WW decreased while in the second it increased (Figure 3.3).

3.4 Discussion

3.4.1 Untitrait analyses

Estimates of h^2 for BW obtained in the present study are within the range of the animal model estimates, which varied from 0.04 (Cloete *et al.*, 1998a) to 0.42 (Van Wyk *et al.*, 1993b; Table 3.2). Estimates of h^2 for WW obtained from the different models were also within the literature ranges. The h^2 estimates for WW in the literature ranged from 0.09 (Burfenig & Kress, 1993) to 0.50 (Fadili *et al.*, 2000; Table 3.3). The estimates for ADG ranged from 0.19 (Yazdi *et al.*, 1997) to 0.42 (Fadili *et al.*, 2000). The estimates also corresponds to those reported by Heydenrych (1975), which was based on part of the same data set as was used in the present study but using sib analysis.

In all three traits, estimates of h^2 ranging from 0.19 to 0.29 were computed after maternal effects were taken into account. In contrast, failure to take account of these effects gave estimates ranging from 0.34 to 0.38. This indicates the extent to which estimates of h^2 can be biased if maternal effects, either genetic or environmental, are ignored using an animal model.

The h^2 of BW in particular was halved when either or both of the maternal effects were fitted compared to the estimate obtained under Model 1 (0.38). Several corresponding results have been reported in the literature (Torshizi *et al.*, 1996; Ligda *et al.*, 2000; Al-Shorepy, 2001). Snyman *et al.* (1995) reported that ignoring maternal effects, if these effects have a significant influence, leads to the over-estimation of direct as well as total heritabilities.

In the present study, the magnitude of m^2 estimates obtained for BW were substantial, being greater than both the h^2 and c^2 estimates. The m^2 estimates, however, were lower than h^2 estimates for WW and ADG. Yazdi *et al.* (1997) found comparable results and indicated that this was presumably due to poor quality of pasture that prevented the genetic ability of ewes to provide sufficient milk for her lamb(s) to be expressed. Thus, inadequate milk yield could mask the expression of the maternal ability of ewes. In general, the values for m^2 in the present study were of low to medium magnitude and are in general in agreement with most of the literature cited (Tables 3.2 and 3.3). Burfening & Kress (1993) found m^2 estimates ranging from 0.30 to 0.65 depending on the model applied for BW in Rambouillet, Targee and Columbian breeds. Van Wyk *et al.* (1993b) also reported a m^2 value of 0.43 for BW in a Dormer stud without considering the effect of maternal permanent environmental effects. In the present study, m^2 was accounting for about 0.38 of the phenotypic variance when maternal permanent environmental effect was ignored from the model. However, it was reduced to 0.25 when the latter was fitted in the model. Thus, the high m^2 values reported by Burfening & Kress (1993) and Van Wyk *et al.* (1993b), might have been including effects due to the permanent environmental effects of the dam. Snyman *et al.* (1995) also indicated that the exclusion of the maternal permanent environmental effect, when it has a significant influence, could cause estimates of m^2 to be biased upwards.

The maternal permanent environmental effect (c^2) for BW (Model 2) was larger than the direct genetic effect (h^2), which is in accordance with results of several other studies (Table 3.2). The c^2 estimates computed, agreed with some of the estimates reported for WW by Naser *et al.* (2000; 2001) and the literature cited (Table 3.3). The exception is a zero c^2 estimate reported by Maria *et al.* (1993). Both Snyman *et al.* (1995) and Naser *et al.* (2001) reported an estimate of 0.12 while Cloete *et al.* (2001) found an estimate of 0.07 for the permanent environmental effect of the dam in BW. They ascribed this value to the permanent environmental effect of the uterus and the effect of multiple births. Likewise, Maria *et al.* (1993) indicated that the permanent environmental effect is due to uterine capacity, feeding level during late gestation and the maternal behaviour of the ewe. Maternal behaviour is likely to be associated with the rearing ability of a dam. Relatively large c^2 estimates for WW and

ADG most likely reflected the rearing ability of a dam that might be influenced by environmental fluctuations between years or her birth/weaning status. Literature results indicated that early growth of a ewe has an effect on the amount of milk she gives to her lambs during her early life (Gould & Whiteman, 1975).

Generally, results showed a trend for increasing direct additive but decreasing maternal variance ratios from birth to weaning at 100 days of age. Other studies reported a similar pattern (Maria *et al.*, 1993; Burfening & Kress, 1993; Tosh & Kemp, 1994; Fadili *et al.*, 2000). This is, however, in contrast to results reported in beef cattle by Albuquerque & Meyer (2001). The increasing h^2 of lamb weight at weaning is most likely caused by an increased expression of genes with direct additive effects on body development (Yazdi *et al.*, 1997). This also confirms the idea of Robison (1981) and Snyman *et al.* (1995), who concluded that maternal effects in mammals diminish with age. In general, results of this study showed that maternal effects, genetic and environmental, are important for BW and need to be considered in any selection programme.

The estimates of correlations obtained between direct and maternal additive genetic effects (r_{am}) for BW are lower than in most of the estimates reported in the literature cited (Table 3.2). The estimate of 0.35 reported by Nesor *et al.* (2001) for BW opposed the negative estimates found in this study. This same study reported a high negative correlation estimate in WW. In the present study, the signs of these estimates for WW agree with Näsholm & Danell (1996), Snyman *et al.* (1996) and Yazdi *et al.* (1997). However, the positive genetic correlations ranging from 0.18 to 0.57 reported by these authors were higher than those of the present estimates, which were very small, ranging from 0.02 to 0.05. This suggested that selection for increased liveweight of the lamb would not negatively affect the maternal ability of the ewe. Cloete *et al.* (2001) also found no significant correlation between the direct additive and maternal additive effects in Merino flock. A negative estimate of the direct and maternal additive genetic covariance has mostly been observed in field data while it has by and large been absent in experimental data sets (Meyer, 1997). She has indicated that this could have been attributed to factors like more uniform management and lack of preferential treatment. Alternatively, it may also reflect better identification of contemporary or management groups.

Early growth traits in sheep are mostly characterised by negative r_{am} estimates (Tables 3.2 and 3.3). These estimates may be considerable and could be affected by small data sets (Maria *et al.*, 1993; Fadili *et al.*, 2000; Al-Shorepy, 2001), the models fitted or poor pedigree structure that is inadequate for obtaining estimates of both direct and maternal heritabilities

and the genetic correlations between animal effects (Kominakis *et al.*, 1998; Lee *et al.*, 2000). The effects of management practices on the direct and maternal genetic correlations have also been indicated. Both Meyer (1992) and Swalve (1993) suggested that environmental covariances between dam and offspring that is not accounted for may bias the direct and maternal genetic correlation downwards. The antagonism between the effects of an individual's genes for growth and those of its dam for a maternal contribution may also be due to natural selection for an intermediate optimum (Garrick *et al.*, 1989; Tosh & Kemp, 1994). According to Koots *et al.* (1994), negative genetic correlations between direct and maternal effects for the same trait suggests either a statistical effect of partitioning the effects or negative pleiotropy of the effect of alleles on the animal's own performance and their effect on maternal performance. The difficulty of statistically separating the direct and maternal component (Meyer, 1992), and the design of fixed effects were also suggested as a factor that could have a strong influence on the reliability of the estimation of the direct and maternal additive genetic correlation (Gerstmayr, 1992). In beef cattle, Robinson (1996) indicated that the negative correlation between direct and maternal genetic variances could result from other effects in the data rather than a true negative genetic relationship.

3.4.2 Multitrait analyses

As in the unitrait analyses, exclusion of maternal effects resulted in an overestimation of h^2 estimates. Likewise, the exclusion of maternal permanent environmental effects most likely resulted in an inflation of m^2 . Thus, it is evident from these that the direct additive genetic variances included maternal additive genetic variances when the maternal genetic effects were excluded from the models. The maternal additive genetic variances also included variances due to permanent environmental effects of the dam when the latter was excluded from the model. This is in general agreement with the suggestion of Meyer (1992) and Snyman *et al.* (1995).

Genetic correlations between growth traits of the Tygerhoek Merino lambs were positive and varied from low to high. The low direct genetic correlations between BW and WW might be beneficial for avoiding lambing difficulties, which could result in loss of lambs and dams. A significant reduction in survival rate of lambs was observed in this flock as lambs became heavier at birth (Chapter 6). The nearly zero, but positive correlations observed between direct and maternal additive genetic effects for WW and the high maternal genetic correlations between WW and other traits could indicate the likely response to selection on individual weight performance.

3.4.3 Genetic and environmental trends

As seen from the standard deviations estimated (Table 3.6), the direct breeding values of WW were more variable than the maternal breeding values. Thus, the relatively high variability of the direct breeding values and the nearly zero genetic correlations observed between the direct and the maternal additive genetic effects in this trait are probably showing the opportunity to base selection on individual WW. In the present study, the cause for the either sudden drop or rise of direct and maternal additive genetic effects in 1996 could not be explained, but may be related to poor pedigree structure.

3.5 Conclusions

Heritability estimates of early growth traits from the different models ranged from moderate to moderately high. Results showed a trend for increasing direct additive and decreasing maternal variance ratios from birth to weaning at 100 days of age. With these data, ignoring maternal effects, both maternal genetic and environmental, lead to an overestimation of the h^2 estimates. Likewise, exclusion of maternal permanent environmental effects of the dam resulted in overestimation of m^2 estimates, particularly for BW. Thus, they need to be considered when carrying out genetic evaluations of early growth traits, in addition to direct genetic effects. The genetic antagonisms between direct and maternal additive genetic effects obtained were not large enough to prevent genetic improvement if selection is based on individual weight performance.

Chapter 4

Genetic parameter estimates for total number born, number weaned and weight of lamb weaned

4.1 Introduction

Improved ewe productivity continues to be a major objective in the local sheep industry. This could be achieved in part by increasing the number of lambs born, lambs weaned and weight of lambs weaned per ewe per year. These traits are important since most sheep are raised for mutton production. In South Africa, though Merino sheep are pre-eminently wool producers, 50 to 60 % of their income is generated through mutton production (Snyman *et al.*, 1998b). Schoeman (2000) reported that sheep production, which was until recently primarily aimed towards wool production, has changed owing to *inter alia* the high demand for mutton and lamb, the meat vs. wool price structure and input costs.

Until recently emphasis has mostly been given to the individual component traits of reproduction such as fertility, litter size, lamb survival rate and number of lambs born and weaned per ewe joined. Ewe productivity, defined as number or total weight of lambs weaned per ewe joined, which is dependent upon the component traits (Fogarty *et al.*, 1985) has received much less attention (Fogarty, 1995). Lifetime production of total number of lambs born, lambs weaned and weight of lambs weaned per ewe are traits of great interest to sheep producers, but few estimates of genetic parameters for lifetime production of these traits in sheep are available.

Total weight of lamb weaned per year is the best single measure of a flock's productivity (Snyman *et al.*, 1997). It is a function of the number of lambs born, their survival and the individual lamb weight at weaning (Boujenane *et al.*, 1991). According to Snyman *et al.* (1997), there is a relatively large phenotypic variation in total weight of lamb weaned regardless of the reproductive rate of the flock. They indicated that this variation may have a genetic basis and could therefore be exploited to genetically increase lifetime reproductive efficiency in any flock. Selection for total weight of lamb weaned would result in a correlated genetic increase in weaning weight of individual lambs. However, selection for litter size alone would not increase the individual weaning weight of each lamb, which is just as important as the number of lambs weaned (Snyman *et al.*, 1996). Total weight of lamb weaned is determined by litter size as well as several other factors, such as mothering ability,

milk production of the ewe and growth potential of the lamb (Snyman *et al.*, 1997). Moule (1971) reported that the total number of live lambs a ewe produces in her lifetime is a direct expression of her fecundity, but it depends on the number of parturitions.

The objective of this study was to estimate genetic parameters for total number of lambs born, lambs weaned and total weight of lambs weaned in a Merino flock at the Tygerhoek Experimental Farm. Genetic correlations between total weight weaned in the first parity and total lifetime production of ewes were also investigated. Prediction of genetic correlations between total weight weaned in the first parity and total lifetime production so as to make either early culling or selection decisions are prerequisites for maximizing production efficiency.

4.2 Materials and Methods

Lifetime production records for number born, number weaned and weight of lambs weaned were studied in the Merino flock of the Tygerhoek Experimental Farm. After editing, a total of 818 ewes with 3272 lambing records from 1971 to 1999 were used in this study. The ewes were the progeny of 689 dams and sired by 371 rams. Traits studied were total number of lambs born per ewe lambing over four lambing opportunities (TLB), total number of lambs weaned per ewe lambing over four lambing opportunities (TLW), total weight of lambs weaned per ewe lambing over four lambing opportunities (TWW), as well as total weight of lambs weaned per ewe lambing at first parity (TWW1). The first four lambings of a ewe were taken as an indication of lifetime reproduction. Thus, only data of ewes with four consecutive lambings (only those ewes which gave birth for four consecutive lambings) were used in this analysis.

Total weight of lamb weaned for each ewe was computed by adding weaning weights of all the lambs weaned by the ewe in a specific lambing year. Total weaning weight over four consecutive lambings was calculated by adding the total weight of lambs weaned per ewe for the first, second, third and fourth lambings. Weaning weight of lambs was recorded at about 120 days of age from 1970 to 1982 and at about 100 days of age thereafter, and it was adjusted accordingly.

The traits, TLB and TLW were considered as continuous for this study. This was justified due to the fact that these traits are a combination of four separate lambings, which increased the number of categories. All ewes were bred to lamb for the first time at 2-yr of age. In all cases, ewe ages ranged from 2 to 6 year.

Different models for analysing the data were used depending on the parameters being estimated. The fixed models were initially applied to the data using Procedures GLM in SAS (1996). In general, model selection and fitting involved two stages: choosing the fixed effects to include in the genetic model; and estimating the (co)variance for each random effect with the significant ($p \leq 0.05$) fixed effects. The fixed part of the model of analyses for TLB and TLW included ewe type of birth and ewe birth year as fixed effects. For TWW, ewe birth year was fitted as fixed effect. The model of analysis for TWW1 included group (selection and control group), ewe birth year and type of lambing as fixed effects. In all cases ewe two-tooth liveweight was fitted as a covariable. The analyses were first carried out fitting all possible effects to determine whether any of the effects have an influence on the traits ($p < 0.05$). Those having no effect ($p > 0.05$) were excluded from the final analysis.

Variance components were estimated by Restricted Maximum Likelihood procedures (REML) applying the VCE 4.2.5 package of Groeneveld (1998). An animal model including the random additive animal effects was used to estimate variance components. Initially, maternal permanent environmental effect was also fitted as an additional random effect with that of the direct additive genetic effect. Nevertheless, it was estimated to be zero in all cases, thus only the model with the direct additive genetic effect was used. By using the estimated variance components, direct heritabilities (h^2) were computed. Following completion of the unitrait analysis, a series of two trait analyses was conducted to estimate the genetic correlations between traits.

The model fitted was:

$$Y = X\mathbf{b} + Z\mathbf{a} + \mathbf{e}$$

where

\mathbf{y} = vector of observations

\mathbf{b} = vector of fixed effects

\mathbf{a} = vector of random animal effects

X = the matrix that associates \mathbf{b} with Y

Z = the matrix that associates \mathbf{a} with Y

\mathbf{e} = vector of random residual effects

4.3 Results

4.3.1 Fixed effects

The overall means, analyses of variance and significance of the fixed effects for reproduction traits are shown in Tables 4.1 and 4.2. Least squares means for TLB, TLW and TWW1 are also presented in Table 4.3. The analyses of variance showed that the fixed models accounted for about 14.4 to 17.5 % of the variances in TLB and TLW and 13.9 % in TWW. It accounted for 40.6 % of the variances in TWW1. The R^2 value for TWW1 is higher than for the other traits possibly due to the inclusion of type of lambing effects in the model. Of the different effects considered, two-tooth liveweight of the ewe was of paramount importance for TWW, TLB and TLW followed by ewe type of birth for the latter two traits (Table 4.1). On average, ewes bore and weaned 1.31 and 1.02 lambs per lambing over four lambing opportunities.

Ewe two-tooth liveweight, ewe birth year, type of lambing and group (selection and control group) had significant ($p < 0.001$) effects on TWW1 (Table 4.2). Ewes from the group selected for clean fleece weight produced 6.2 % (1.5 kg) higher TWW1 than ewes in the control group. Multiple bearing ewes weaned 22.3 % (5.4 kg) more weight of lambs than those which gave birth to singles.

Ewe type of birth had a significant effect ($p < 0.001$) on both TLB and TLW. Multiple born ewes bore 7.6 % (0.40) more lambs than singles. They also weaned 7.4 % (0.30) more lambs than the latter (Table 4.3).

Table 4.1. Overall mean and analysis of variance for TLB, TLW and TWW

Variables	df	Mean square and level of significance		
		TLB	TLW	TWW
Overall mean		5.23 (n)	4.05 (n)	92.55 (kg)
Ewe type of birth	1	23.914***	13.549***	
Ewe birth year	23	2.863***	7.816***	2763.597***
Ewe two-tooth liveweight	1	54.024***	23.251***	43686.485***
Error degrees of freedom		737	737	738
Error mean square		1.03	1.31	725.59
R^2 (%)		14.43	17.48	13.91
C.V. (%)		19.41	28.24	29.11

*** $p < 0.001$

Birth year of ewes affected ($p < 0.001$) all reproduction traits considered. Nevertheless, its effect on reproduction traits did not have any pattern. The regression of ewe lifetime reproduction on two-tooth ewe liveweight was also significant ($p < 0.001$) in all cases.

Table 4.2. Overall means and analysis of variance for TWW1

Variables	df	Mean square and level of significance
Overall mean (kg)		24.23
Group of animals	1	1321.381***
Ewe birth year	23	260.526***
Ewe two-tooth liveweight	1	670.340***
Type of lambing	1	1937.003***
Error	576	
Error mean square		30.18
R ² (%)		40.55
C.V. (%)		22.67

*** $p < 0.001$

Table 4.3. Least square means (\pm SE) for TLB, TLW and TWW1

Fixed effects	TLB	TLW	TWW1
Ewe type of birth			
Single	5.1 \pm 0.05	4.0 \pm 0.06	
Multiple	5.5 \pm 0.07	4.3 \pm 0.07	
Group			
Selection group			27.9 \pm 1.37
Control group			26.4 \pm 1.36
Type of lambing			
Single			23.6 \pm 0.27
Multiple			29.0 \pm 0.56

4.3.2 Genetic parameters

Estimates of direct heritabilities and variance components are presented in Table 4.4 and estimated genetic correlations among the different traits are presented in Table 4.5. Published

heritability estimates for total number of lambs born, lambs weaned and total weight of lambs weaned per ewe lifetime production are summarised in Table 4.6. Standard errors of heritability estimates ranged from 0.06 to 0.07.

The estimated heritabilities for lifetime ewe reproduction traits were moderate and ranged from 0.17 to 0.23. Nevertheless, the estimated heritability for TWW1 was very low (0.02; Table 4.4). The estimated genetic correlations ranged from small negative to unity. The highest genetic correlation was obtained between TWW1 and TWW while the smallest and negative correlation was computed between TWW1 and TLB.

Table 4.4. Variance components and heritability estimates for TLB, TLW, TWW and TWW1

Trait	σ^2_a	σ^2_e	σ^2_p	h^2
TLB	0.24	0.80	1.04	0.23
TLW	0.22	1.09	1.31	0.17
TWW	141.89	571.86	713.75	0.20
TWW1	0.43	29.30	29.73	0.02

σ^2_a , direct additive variance; σ^2_e , residual variance; σ^2_p , phenotypic variance; h^2 , direct heritability.

Table 4.5. Genetic correlations among the different traits

	TLB	TLW	TWW
TWW1	-0.10 ± 0.24	0.57 ± 0.23	1.00 ¹
TLB		0.62 ± 0.16	0.61 ± 0.17
TLW			0.92 ± 0.04

¹ standard error is not available

Table 4.6. Published heritability estimates obtained with an animal model for total lamb born (TLB), total lamb weaned (TLW) and total weight of lambs weaned (TWW)

TLB	TLW	TWW	Breed	Reference
0.11			Rambouillet	Burfening <i>et al.</i> (1993)
0.08	0.04		Dorset	Brash <i>et al.</i> (1994a)
0.03			Border Leicester	Brash <i>et al.</i> (1994b)
0.06	0.04		Corriedale	Brash <i>et al.</i> (1994c)
0.09		0.06	Hyfer	Fogarty <i>et al.</i> (1994)
		0.22	Merino	Snyman <i>et al.</i> (1997)
		0.13	Merino	Snyman <i>et al.</i> (1997)
		0.10	Merino	Snyman <i>et al.</i> (1997)
0.23	0.17	0.19	Merino	Olivier <i>et al.</i> (2001)
0.19	0.16	0.21	Merino	Olivier <i>et al.</i> (2001)

4.4 Discussion

4.4.1 Fixed effects

Coefficients of variation obtained for TWW was less than those reported in another South African study (Snyman *et al.*, 1997). This could be due to the fact that the present study only included data from ewes lambing (ewes not lambing were deleted from the analysis). However, coefficients of variation of TLB and TLW reported by these authors accorded well with the present results. The TWW obtained in the current study was similar to those reported for the Grootfontein Merino flock over three lambing opportunities by Herselman *et al.* (1998) and Snyman *et al.* (1997). Snyman *et al.* (1998c) reported 52.4 kg of weight of lambs weaned per ewe joined over three lambing opportunities for the flock used in the current study. The TWW per ewe joined over four lambing opportunities reported for the Grootfontein Merino flock (Snyman *et al.*, 1997) was higher than that obtained in the current study. It has been reported that Merino ewes weaned only 37.8 to 91.1 kg of lambs over three lambing opportunities compared to 116.8 kg for Afrino ewes (Herselman *et al.*, 1998; Snyman *et al.*, 1998c). Herselman *et al.* (1998) indicated that a lower reproduction rate in high fibre-producing genotypes is to be expected. Moreover, Snyman *et al.* (1998a) estimated negative genetic correlations ranging for -0.32 to -0.52 between clean fleece weight and the reproduction traits. This suggested that increasing litter weight puts an added burden on the

ewe's metabolic system and results in phenotypic decreases in fleece weight (Ercanbrack & Knight, 1998).

The effect of poor environmental conditions is also reported as a major factor influencing ewe productivity (Snyman *et al.*, 1996). Reproduction, which is the key to developing, maintaining and exploiting flocks, is very susceptible to environmental influences (Moule, 1971). Snyman *et al.* (1998c), who used part of the data set of the current study, largely from the control group, reported lower TWW as compared to that of the Grootfontein flock. They attributed the lower TWW in the Tygerhoek Merino flock to the fact that this flock has not been selected for reproduction as compared to the Grootfontein flock where some emphasis has been placed on selection for reproduction in addition to the effect of environmental conditions the flocks were in. Half of the data set used in the current study was also from the genetic control group, which were randomly bred since the establishment of the farm in 1969. Some selection for increased clean fleece mass occurred almost on half of the flock, mainly through the use of sires selected for higher clean fleece weight *per se*.

Multiple born ewes were superior than single born ewes for both the TLB and TLW. The superiority of multiple born ewes as compared to those of singles obtained in the present study was in agreement with results reported by Cloete & Heydenrych (1986) who used part of the same data set. It was also in accordance with Kritzinger *et al.* (1984a). In the current study, ewe type of birth, however, did not significantly affect TWW1 and TWW.

The regression of reproduction traits on two-tooth ewe liveweight was also significant ($p < 0.01$) in all reproduction traits investigated. This confirmed an earlier suggestion by Cloete & Heydenrych (1987b), who suggested that selection for an increased two-tooth liveweight (at about 1.5 yrs of age) may probably be associated with an increase in reproduction rate.

The TLB and TLW obtained in the current study were higher than those reported for the Carnarvon Merino flock (Snyman *et al.*, 1997). They reported 2.22 and 1.88 total number of lambs born and weaned per ewe joined over three lambing opportunities, respectively. The TLB and TLW reported in the present study accorded with results reported by Basuthakur *et al.* (1973). The TLB obtained in this study also agreed with results reported by Hall *et al.* (1994).

The average number of lambs born and weaned per ewe lambing obtained were within the range (1.10 to 1.37 and 0.89 to 1.11, respectively) reported by Heydenrych (1975) but slightly higher than those reported by Basuthakur *et al.* (1973). The average number of lambs born was also slightly higher than the 1.14 reported for the Carnarvon Merino flock, but lower than

the 1.53 and 1.56 reported for Carnarvon Afrino and Grootfontein Merino sheep, respectively (Snyman *et al.*, 1997).

4.4.2 Genetic parameters

Heritabilities obtained were in the range reported in most of the literature cited (Table 4.5) but lower than those of the heritability estimates for individual lamb weaning weight (Chapter 3). The heritability of TWW per ewe joined over three and four lambing opportunities was 0.10 to 0.26 (Snyman *et al.*, 1997). The heritability values of 0.22 and 0.26 for TWW (for total weight weaned over three and four lambing opportunities, respectively) reported by Snyman *et al.* (1997) were higher than those of this study. The heritability estimate of TWW1 obtained in the present study was in agreement with those reported by Snyman *et al.* (1997). They indicated that heritability estimates for TWW increased as more information become available with an increase in number of lambing opportunities. For instance, in the Grootfontein Merino flock, heritability estimates were 0.08, 0.05, 0.13 and 0.10 in the first, second, third and fourth lambing opportunities, respectively. Corresponding estimates were 0.09, 0.17, 0.22 and 0.26 for the Carnarvon Merino flock (Snyman *et al.*, 1997).

Heritability values for TLB and TLW obtained in the current study were higher than those reported in the literature (Table 4.6). Estimates of half-sib heritability values obtained for the components of reproduction rate averaged over a number of lambing opportunities (over 2 to 5 lambing opportunities) were 0.10 to 0.30 for lambs born and 0.10 to 0.20 for lambs weaned per ewe joined (Cloete & Heydenrych, 1987a). They reported heritability estimates of 0.36 and 0.29 for total number of lambs born and weaned per ewe conceived over four lambing opportunities, respectively. These estimates are higher than those reported in this study. Fogarty (1995) indicated that REML estimates of heritability from an animal model were lower, but might be regarded as more reliable than earlier estimates for these traits. The use of an animal model to obtain genetic parameters combines information from paternal half-sib, maternal half-sib and dam-offspring effects (Visscher & Thompson, 1992). In his review, Fogarty (1995) reported an average lifetime heritability estimate of 0.14 for total number of lambs born per lambing opportunities using REML procedures and fitting an animal model. In general, the heritability estimates obtained in the present study indicate that there is scope for genetic improvement if selection is based on either of the traits considered.

The unity genetic correlation between TWW1 and TWW was in accordance with that reported for the Carnarvon Merino flock but slightly higher than those reported for the Grootfontien Merino and Carnarvon Afrino flocks (Snyman *et al.*, 1997). The high genetic correlation between TWW1 and TWW may be expected due to the fact that TWW1 forms part in the

calculation of TWW. Snyman *et al.* (1997), who obtained similar high genetic correlations between TWW1 and TWW over different lambing opportunities, concluded that the latter trait which is very important, but sex limited as well as a laborious and time consuming measurement, can be improved by indirect selection for body weight at any age. The estimated genetic correlation between TLW and TWW was very high and positive. This estimate was slightly lower than those estimates ranging from 0.97 to 0.98 reported between the same traits by Olivier *et al.* (2001) for the Grootfontein and the Carnarvon Merino flocks but slightly higher than the estimate of 0.84 reported by Snyman *et al.* (1998a) for Afrinos. The genetic correlations obtained between TLB and TLW, TLB and TWW were lower than those reported for Afrinos (Snyman *et al.*, 1998a). No comparable estimates between TWW1 and TLB could be found in the literature. The nearly zero genetic correlation between these traits (-0.10 ± 0.24) means that selection for one of them would not affect the other. In general, the high genetic correlations obtained between ewe lifetime reproduction traits indicate that significant improvement from selection can be achieved in this flock. The high genetic correlations between TWW1 and TLW, TWW1 and TWW could also indicate that TWW1 could be used to indirectly improve both TLW and TWW if selection is based on it.

4.5 Conclusions

The results of this study indicated that several non-genetic fixed factors have a significant influence on ewe reproduction traits. The regression of reproduction on two-tooth liveweight and year of birth of ewe were significant in all reproduction traits investigated. Multiple born ewes were superior, both in TLB and TLW than single born ewes. The high genetic correlations obtained between ewe lifetime reproduction traits and the moderate heritability estimates indicate that significant improvement from selection can be achieved in this flock. The high genetic correlations between TWW1 and TLW and between TWW1 and TWW could also indicate that TWW1 could be used to indirectly improve both TLW and TWW if selection is based on it.

Chapter 5

Testicular measurements in rams and its influence on ewe fertility

5.1 Introduction

Fertility of males and females and successful reproduction are important to efficient livestock production (Meyer *et al.*, 1991). However, most female reproductive traits are lowly heritable and selection intensities for them usually are low; thus, little improvement through selection is expected (Smith *et al.*, 1989a).

In contrast to low heritabilities for female reproductive traits, moderate heritabilities have been summarised for testicular traits in sheep (Fogarty, 1995). Particularly, since Land (1973) suggested a likely genetic correlation between reproductive characters of males and females, considerable research has been directed at studying testicular traits. Among the variety of alternatives involving physiological traits, testis size in the male may be the most suitable trait in rams to indirectly improve the reproductive performance of females (Walkley & Smith, 1980). Further, several authors indicated that males with larger testes have either greater sperm production or higher daily sperm output (Cameron *et al.*, 1984; Purvis *et al.*, 1984).

Testicular size is best described in terms of testis weight (Matos *et al.*, 1992). Nevertheless, in the live animals, scrotal size is more easily measured and is a reliable indicator of testis weight (Coulter & Keller, 1982). Purvis *et al.* (1984), Shrestha *et al.* (1983) and Schoeman & Combrink (1987) recommended either testis diameter or scrotal circumference as important practical measurements of testicular size. Testicular size is more closely associated with body weight than with chronological age (Matos & Thomas, 1992) and has continuous variation (Kritzinger *et al.*, 1984b). In order to increase flock fertility, improve the genetic merit of a flock and to reduce the number of breeding males, rams with superior reproductive traits are required (Mukasa-Mugerwa & Ezaz, 1992).

According to Venter *et al.* (1984), the major causes for variation in fertility are lack of libido, small scrotal circumference and poor quality semen. Testicular traits provide a good indication of quantitative sperm production (Rege *et al.*, 2000) in that rams with larger size testes produce semen with greater volume and more sperm cells at puberty than rams with smaller testes (Mukasa-Mugerwa & Ezaz, 1992). Venter *et al.* (1984) proposed that minimum scrotal circumference standards at a certain age should be established for individual breeds. In addition, the value of testicular size as an indirect selection criterion for the

improvement of female reproduction is dependent on the heritability of testicular size and the genetic correlation between testicular size and female reproductive traits (Matos *et al.*, 1992). Thus, it is important to establish the phenotypic and genetic relationships between testis measurements and liveweight at measurement in the Tygerhoek Merino flock where such work has never been done before. Therefore, the objectives of this study were to investigate genetic and non-genetic factors affecting testis measurements and to examine the effect of testis size on fertility in the flock of Merinos maintained at the Tygerhoek Experimental Farm.

5.2 Materials and Methods

Records of testis measurements of rams at the Tygerhoek Experimental Farm covering the period 1986 through 1998 were used in this study. After editing, 1380 records on two-tooth rams were available where scrotal circumference (SC), testis diameter (TD) as well as liveweight (LW) were recorded. After running a preliminary analysis, those records deviating more than three standard deviations from the respective means were excluded from the model of analyses. Measurements were taken at about 16 months of age (when $\pm 80\%$ of mature liveweight for this flock is attained) before allowing selected male rams for mating. In this flock, it was approximately 2 months before age at first breeding (18 mo).

SC was measured as described in literature (Schoeman & Combrink, 1987; Mukasa-Mugerwa & Ezaz, 1992; Gojjam *et al.*, 1995; Gizaw & Thwaites, 1997). The testes were brought firmly and evenly to the bottom of the scrotum until ventral skin folds were eliminated. The testes were then held firmly in place by grasping the neck of the scrotum with one hand above the heads of the epididymides. The opposite hand then guided a flexible tape upward from the bottom of the scrotum. The area of the scrotum with the greatest circumference was then identified for measurement. Manual pressure on the tape was exerted to the extent of slight skin indentation. TD measurements were taken with a caliper at the anterior-posterior position on each testis at its maximum width as described by Schoeman & Combrink (1987). The mean of both right and left testis diameter was taken as the testis diameter for individual animals.

The General Linear Models of the Statistical Analysis System (SAS, 1996) were used in the analyses of the data to determine the importance of each fixed effect on testis measurements and LW. The model of analysis for SC and TD included birth year of lambs (1986 to 1998) and group (the group of animals selected for increased clean fleece weight and an unselected control) as fixed effects and LW as linear covariable for testis traits. In case of LW, birth year and group were fitted as fixed effects. Preliminary models for testis measurements and LW

also included age of dam, birth type and all possible two-factor interactions among fixed effects. None of these were found to be significant sources of variation and they were not included in the final models.

In case of ewe fertility, a total of 3717 ewe records (from 1988 to 1999) were used. In this analysis, ewes that lambed were recorded as '1' and those that did not were recorded as '0'. Ewe fertility was analysed using the CATMOD procedure of SAS (1996). Subclass proportions were computed using the procedure of Rege & Sherington (1996) as implemented by Rege (1997).

Fixed effects fitted for ewe fertility were ewe age at lambing (2- to 6-yr-old) and SC of service sires which was grouped in to three categories (1 = 24.0 to 30.0 cm; 2 = 31.0 to 35.0 cm; 3 = 36.0 to 40.0 cm). Initially, SC, TD and LW were included simultaneously in the model. Owing to the high genetic correlations between testis traits and LW (Fogarty, 1995; Toe *et al.*, 2000), it seemed appropriate to include either of the testis traits than LW in the analysis of ewe fertility as it is the trait more likely influenced by testis traits than by service sires' LW. The high positive genetic correlation between SC and TD, the relatively larger h^2 estimates for SC than for TD (Toe *et al.*, 2000) and ease of measurement for SC as compared to TD resulted in the use of models that contained only SC for the analysis of these data being favoured.

Variance components for testis measurements were estimated with Restricted Maximum Likelihood procedures (REML) using the VCE 4.2.5 package developed by Groeneveld (1998). An animal model was fitted which included a random additive direct animal effect and the fixed effects used in GLM analyses. The genetic correlations between traits were estimated using two-trait pairwise analyses.

The model fitted for unitrait analyses was as follows:

$$Y = X\mathbf{b} + Z\mathbf{a} + e$$

where:

y = vector of records

\mathbf{b} = vector of fixed effects which include year of birth of rams and selection groups

\mathbf{a} = vector of random animal effects (direct animal genetic)

X = incidence matrix for fixed effects

Z = incidence matrix for random effects, and

e = vector of random residual effects

It was assumed that all effects in the models are independent and normally distributed.

5.3 Results

5.3.1 Non-genetic factors

5.3.1.1 Testis measurements

Table 5.1 summarises overall means and least squares analyses of variance for SC, TD and LW. LW was significant ($p < 0.001$) for both SC and TD. Heavier animals tended to have larger SC and TD measurements. A linear increase in testis measurements with an increase in liveweight was evident (Figures 5.1 and 5.2). A one kg increase in LW was associated with increases of 0.21 cm and 0.81 mm in SC and TD, respectively. Testis size also differed between the selection groups. The selected line for clean fleece mass had larger SC and TD measurements than animals from the control group. The mean difference in SC between the two groups was not large (0.44 cm or 1.4 %), though significant ($p < 0.001$). The mean difference in TD between the two groups was 6.8 mm. Year was also a significant ($p < 0.001$) effect influencing both SC and TD, with no distinct trend over years.

LW was affected ($p < 0.001$) by the selection group, with animals born from the control group being 5.0 kg lighter than those born from the selected group. Year had also a significant ($p < 0.001$) influence on LW, with no distinct trend.

Table 5.1. Analysis of variance of SC, TD and LW

	Df	SC	TD	LW
Overall mean		32.1 cm	112 mm	53.8 kg
LW	1	2843.34***	35315.61***	
Year of birth	12	174.11***	4653.51***	1721.28***
Selection group	1	55.97***	267.15*	8395.97***
Error degrees of freedom		1365	1365	1366
Error mean square		5.38	108.11	40.62
R ² (%)		46.86	43.11	34.14
C.V. (%)		7.22	8.90	11.85

* = $p < 0.05$; *** = $p < 0.001$

5.3.1.2 Ewe fertility

Maximum-likelihood analyses of ewe fertility are presented in Table 5.2. Ewe fertility was significantly ($p < 0.05$) influenced by ewe age. Ewe fertility increased with an increase in ewe age from two to six years (Figure 5.3). Average ewe fertility was 0.93, and varied from 0.90 to 0.95.

Ewe fertility was also influenced ($p < 0.001$) by the SC of service sires. Mean ewe fertility increased from 0.88 in SC size category 1 to 0.96 and 0.95 in SC size categories 2 and 3, respectively (Table 5.3).

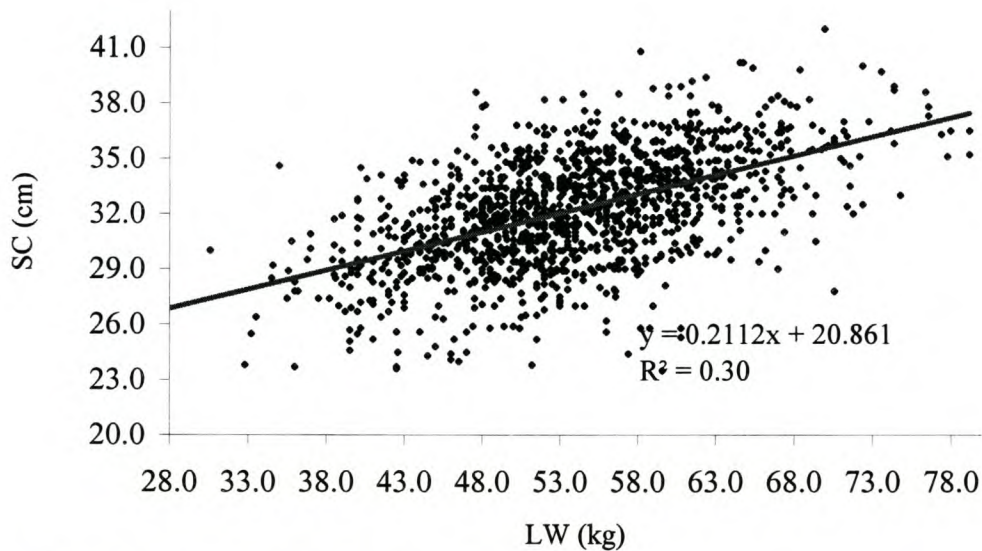


Figure 5.1. The regression of SC on LW

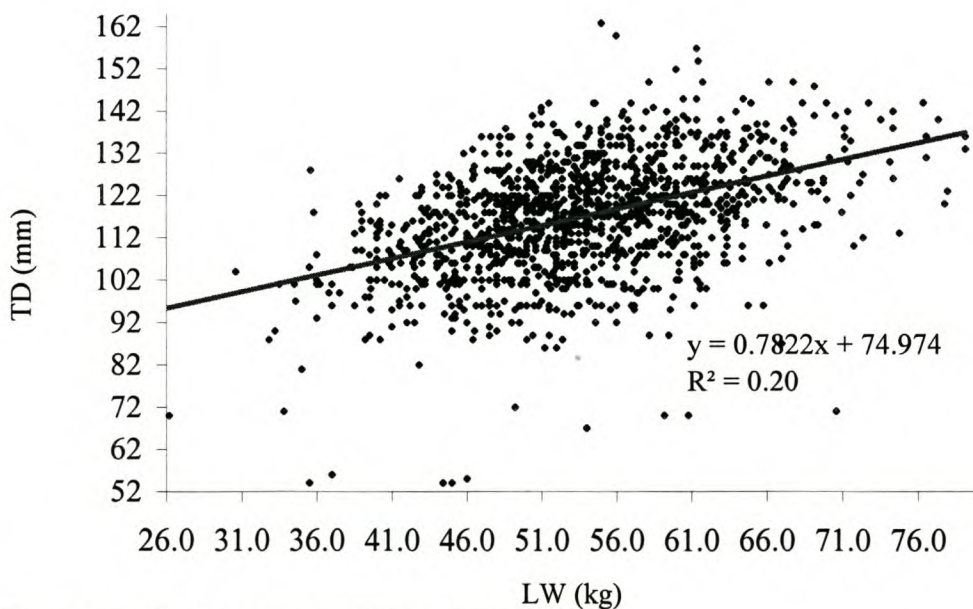


Figure 5.2. The regression of TD on LW

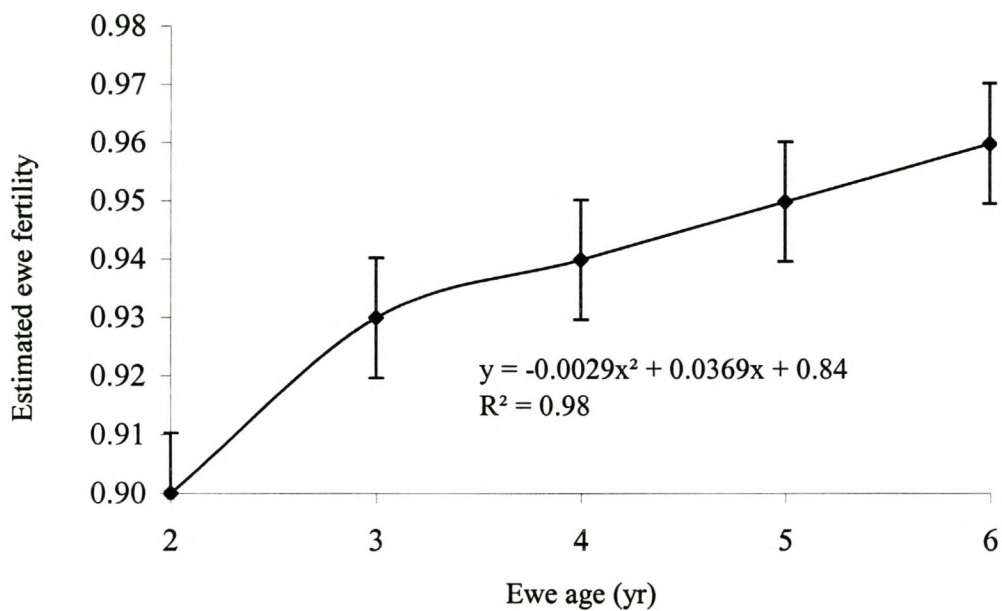
Table 5.2. Maximum-likelihood analysis of variance of ewe fertility

Source	df	Chi-square
Intercept	1	1325.93***
Ewe age	4	20.78***
SC	2	61.80***
Likelihood ratio	8	21.95***

*** p < 0.001

Table 5.3. Predicted estimates (\pm SE) of ewe fertility for SC

Effect	Category	Predicted estimates (\pm SE)
Overall		0.93 \pm 0.004
SC		
	1	0.88 \pm 0.010
	2	0.96 \pm 0.004
	3	0.95 \pm 0.008

**Figure 5.3. The regression of estimated ewe fertility on ewe age**

5.3.2 Genetic parameters

5.3.2.1 Testis measurements

Estimates of heritability (h^2) for SC, TD and LW from unitrait analyses are presented in Table 5.4, while those of two-trait pairwise analyses are presented in Table 5.5. Heritability estimates for testicular measurements (both from unitrait and two-trait analyses) were ranged from medium to high. Estimates of h^2 increased in two-trait pairwise analyses for testis measurements (Table 5.5). Adjustments for LW reduced h^2 estimates for both testis traits. Estimates of h^2 for SC were relatively more affected than those of TD (Table 5.5). Estimates of genetic correlations between SC and TD investigated were unity, indicating that they are in fact the same trait. Adjustment for LW differences did not affect the genetic correlation between them.

Table 5.4. Estimated variance components and genetic parameters from unitrait analyses of SC, TD and LW

Variance components	SC	TD	LW
σ^2_a	1.586	108.885	21.536
σ^2_e	3.838	164.299	20.208
σ^2_p	5.424	273.184	41.744
h^2	0.29 ± 0.04	0.25 ± 0.05	0.52 ± 0.05

Table 5.5. Heritability estimates on diagonal and genetic correlations between SC and TD, SC and LW and TD and LW either adjusted or unadjusted for LW differences

Trait	Unadjusted for LW			Adjusted for LW		
	SC	TD	LW	SC	TD	LW
SC	0.40 ± 0.05	1.00 ± 0.06	0.70 ± 0.05	0.29 ± 0.05	1.00 ± 0.08	0.09 ± 0.05
TD		0.38 ± 0.03	0.68 ± 0.06		0.30 ± 0.03	0.38 ± 0.06
LW			0.52 ± 0.05			

5.4 Discussion

5.4.1 Non genetic factors

5.4.1.1 Testis measurements

The coefficients of variation (CV) for SC, TD and LW were in agreement with results reported in the literature. Fogarty (1995) summarised values ranging from 6 to 24 % for SC, 9 to 13 % for TD and 6 to 18 % for hogget liveweight (for wool breeds). The influence of LW on testis measurements was also in general agreement with those reported in the literature (Bourdon & Brinks, 1986; Schoeman & Combrink, 1987; Mukassa-Mugerwa & Ezaz, 1992; Gojjam *et al.*, 1995; Mandiki *et al.*, 1998). Animals from the control group had smaller SC and TD than those from the selected group. The testis size differences between the selected and control groups may reflect the LW differences between the two groups. Heydenrych *et al.* (1984) indicated that selection for clean fleece weight in this flock has resulted in a correlated increase in LW. Comparable results were also reported in the studies by Cloete *et al.* (1992; 1998b), which was possibly closer to the period over which data for the present study was derived.

The effect of year on SC, TD and LW may be a reflection of differences in feed availability between years, caused by differences in rainfall. The Southern Cape area is subjected to dry years with limited feed availability. Purvis (1985) reported that environmental influences had a significant influence on variation in gonadal size at all ages up to 19 months. Testicular size was drastically reduced in grazing rams (Master & Fels, 1984) and rams gain and lose testicular size at a greater rate than LW (Oldham *et al.*, 1978; Master & Fels, 1984). The changes in testicular size are also accompanied by changes in the sperm-producing activity of the testis (Oldham *et al.*, 1978).

5.4.1.2 Ewe fertility

In the present study, ewe fertility was increased with an increase in ewe age from two to six years of age. This was in close agreement with reports of Moule (1971), Heydenrych (1975) and Fourie & Heydenrych (1983), who observed similar increasing trends of ewe fertility with an increase in ewe age up to 6-yr of age. The former two references reported results derived from Merino flocks. The age trend observed was also accorded with results reported by Cloete & Heydenrych (1986) for the same flock used in the current study and by Schoeman (1990) for Döhne Merino's. The 0.93 ewe fertility obtained in the present study agreed well with those reported by Cloete & Durand (1994), Fourie & Heydenrych (1983) and Brash *et al.* (1994a), but in the upper range of those reported (0.76 to 0.90) by Heydenrych (1975) for the

same flock and 0.80 for Döhne Merino's (Schoeman, 1990). A previous study by Cloete & Heydenrych (1986) on the same flock reported that conception rate improved from 0.73 in the 2-yr-old ewes to approximately 0.86 in the older ewes ($p \leq 0.01$).

The significant effect of SC on ewe fertility found was in contrast to results reported by Gizaw & Thwaites (1997). In their study, though rams with larger SC tended to have higher fertility (0.85 vs. 0.77), they reported that there was not any significant benefit to be gained in fertility by increasing SC from 27.0 to 31.0 cm for Horro sheep of western Oromia. The small number of observation in the data set used may attributed to the non-significant effect of SC. Moreover, the absence of significant influences in their study was due to the low ewe: ram ratio used in which even rams with a smaller SC were presumably able to cope with the mating load. This was because after the first oestrus cycle there was not sufficient ewes to allow the high SC ram to continue serving until the end of the 6-week mating period in that sheep flock. Schoeman *et al.* (1987) concluded that serving capacity is the only criterion that offers some advantage as a selection aid to improve efficiency of reproductive performance in pen-tested rams. According to Schoeman & Combrink (1987), testicular size serves as an indicator of ram fertility and increases the probability of impregnating more females under heavy breeding pressure. In rams, the larger the male's testicles, the greater is the sperm producing capacity (Blockey, 1980). Sperm production and testicular size in rams have been influenced by plane of nutrition (Cameron *et al.*, 1988). In view of the established relationship between testicular measurements and semen characteristics (Knight, 1984; Al-Nakib *et al.*, 1986; Rege *et al.*, 2000), advantages from the use of male animals with a larger testis size is likely to be greater when the ewe: ram ratio is high, and when ewes are exposed to only a single ram. In the Merino flock of Tygerhoek, the proportion of the rams per breeding ewe particularly in the control flock was higher than in the selection group (Heydenrych *et al.*, 1984). However, a wider spectrum of rams, which may incidentally have included rams with a lower fertilizing ability, was used in this group (Cloete & Heydenrych, 1986). According to Mukasa-Mugerwa & Lahlou-Kassi (1995), good fertility rates are important since, aside from reduced flock productivity, low fertility involves the nutritionally expensive maintenance of unproductive ewes and lessens the effectiveness of any selection.

5.4.2 Genetic parameters

5.4.2.1 Testis measurements

The h^2 estimates for the testis traits were all medium to high and are in general agreement with most of the literature estimates (Fogarty, 1995; Burfening & Davis, 1998). In his review,

Fogarty (1995) summarised h^2 estimates for SC, which varied from 0.08 to 0.50 with a mean value of 0.23. The corresponding estimates for TD ranged between 0.10 and 0.69 with a mean value of 0.37. The present h^2 estimates were lower than those reported by Fossceco & Notter (1995) and Toe *et al.* (2000), but larger than estimates reported by Al-Shorepy & Notter (1996).

The estimated h^2 for testis measurements varied between the unitrait and two-trait pairwise analyses. Lin & Lee (1986) indicated that parameter estimates from a data set vary depending upon the type of analysis (single- or multitrait model) and upon the other traits included in the multitrait analysis.

Adjustments for LW differences reduced h^2 estimates of SC by 11.0 % and that of TD by 8.0 %. These are in agreement with results reported by Fogarty *et al.* (1980) and Toe *et al.* (2000). Fogarty *et al.* (1980) reported that after correcting for LW, the h^2 estimates of SC and TD were reduced by 41 and 24 %, respectively. On the other hand, apparent increases in h^2 estimates of testicular measurements following adjustment for LW were also reported (Matos & Thomas, 1992; Nowakowski & Cwikla, 1994). Matos & Thomas (1992) reported that h^2 for SC in Rambouillet rams was nearly constant between 90 and 180 days, but the linear adjustment for LW over this age range increased h^2 estimates of SC by 42 %. According to Matos *et al.* (1992), adjusting testis traits for LW may result in less genetic progress in female reproductive traits than when selection is based on SC unadjusted for LW.

Genetic correlation estimates between SC and TD were high and in accordance with those reported by Toe *et al.* (2000) for yearling Horro and Menz sheep of Western and Central Ethiopia, respectively. The genetic correlations between both testis traits and LW found in the current study agreed with a 0.62 weighted average genetic correlation between LW and testis measurements summarised by Fogarty (1995). The reduced genetic correlation between SC and LW after adjusting for LW was also in agreement with those of Fogarty *et al.* (1980). Bourdon & Brinks (1986) suggested that adjustment for weight is likely to remove differences in SC associated with genetic differences in weight. Literature results (Haley *et al.*, 1990; Lee *et al.*, 1991; Burfening & Davis, 1998) indicated that selection of rams based on testis size adjusted for LW would result in an increase in number of lambs born but a decrease in mature liveweight. In this flock, estimates of heritability ranging from 0.32 to 0.55 were reported for two-tooth liveweight (Cloete *et al.*, 1998b; Snyman *et al.*, 1998c). Thus, their offspring would have a lighter LW if selections could be based on testis size adjusted for LW. This decrease in LW might not be desirable in Merino sheep where approximately about 50 to 60 % of their income is generated through mutton production (Snyman *et al.*, 1998c). Moreover, it is well

documented that LW and wool production are positively genetically correlated (Heydenrych, 1975; Heydenrych *et al.*, 1984; Cloete *et al.*, 1998b).

5.5 Conclusions

Estimates of h^2 for SC and TD, both from the unitrait and two-trait pairwise analyses, were moderate, indicating an opportunity of improving male fertility by selecting for these traits. Moreover, the high and positive genetic correlations between testis traits and LW could indicate that selection for larger testis size will also improve ram fertility via the increased LW. In this study, rams with larger SC had a significant effect on ewe fertility. Thus, the use of rams with larger testis will allow a reduction in the number of breeding rams required each year and increase the overall reproductive efficiency of the flock.

Chapter 6

The effect of non-genetic factors on preweaning lamb survival rate

6.1 Introduction

Lamb mortality results in serious financial losses in sheep production (Petersson & Danell, 1985). It is a major factor affecting the number of lambs weaned per ewe (Fogarty *et al.*, 1985; Haughey *et al.*, 1985). Efficiency of lamb production can thus in many situations be improved more readily by increasing the preweaning survival rate than by improved growth and body composition (Dickerson, 1978). In terms of reproductive wastage, lamb losses represent a serious problem because all investments made for ewes to conceive and maintain pregnancy are wasted (Mukasa-Mugerwa & Lahlou-Kassi, 1995). Land *et al.* (1983) indicated that no discussion of increasing lambing rates would be complete without the mentioning of lamb survival after birth.

Preweaning lamb survival is a complex trait influenced by the lamb's ability to survive and by its dam's rearing ability (Burfening, 1993). Various studies have reported that birth weight, age of dam, year of birth, sex of lamb and type of birth are some of the likely factors affecting preweaning lamb survival (Meyer & Clarke, 1978; Dalton *et al.*, 1980; Schoeman, 1990; Yapi *et al.*, 1992a; Burfening, 1993; Mukasa-Mugerwa & Lahlou-Kassi, 1995). Birth weight plays an important role in lamb survival. An intermediate optimum has been shown to exist for birth weight (Al-Shorepy, 2001), with very large lambs which are more likely subjected to dystocia losses while very small lambs are at risk of death from hypothermia, starvation, respiratory diseases and other causes (Meyer & Clarke, 1978; Petersson & Danell, 1985; Al-Shorepy, 2001).

Environmental conditions and management practices are expected to make a considerable impact on lamb survival. Nevertheless, unless it is practiced along with some selection against high death losses, improved management alone may not resolve the problem of high lamb mortality rates (Yapi *et al.*, 1992b). Except for the work of Heydenrych (1975), there is no information on the non-genetic factors affecting preweaning lamb survival rate in Merinos maintained at the Tygerhoek Experimental Farm. The purpose of the present study was to investigate the effects of various non-genetic factors influencing preweaning lamb survival rate of this flock.

6.2 Materials and methods

Data of 8823 Merino lambs born from 1970 through 1994 at the Tygerhoek Experimental Farm were used in this study. These lambs were the progeny of 2422 dams and 629 sires. Details of the animals, the farm environment and management procedure are described in Chapter 2. Lamb survival is defined in this study as the number of lambs weaned per 100 lambs born alive ($LW/LB \times 100$). Data on dead lambs were obtained from lambs that were born alive and died subsequently. Lamb survival rate from birth to weaning was coded as '1' if the lamb survived to weaning and as '0' if the lamb died prior to weaning. Information on cause of death was not available.

Significant fixed effects were identified using the CATMOD procedure of the SAS Statistical Package (SAS, 1996). Parameters measured to determine their effect on preweaning death losses included dam age (2- to 6-yr of age), type of birth (single, multiple), sex (male, female), group (selection and control group), year of birth (1970 to 1995) and birth weight. Birth weight was categorised as follows: 1 = ≤ 2.0 kg; 2 = 2.1 – 2.9 kg; 3 = 3.0 – 3.9 kg; 4 = 4.0 – 4.9 kg; 5 = ≥ 5.0 kg. Birth weight was categorised into discrete classes as CATMOD is not modelled optimally for continuous variables (SAS, 1996). Simple t-test statistics indicated significant ($p < 0.05$) differences between the birth weight categories in mean preweaning survival rates.

6.3 Results

Sources of variation considered and the associated probability levels are presented in Table 6.1. Maximum-likelihood analysis of variance for preweaning survival showed significant ($p < 0.001$) effects of all fixed effects considered. Standard error was not available in this analysis. The average survival rate from birth to 100 days was 0.79.

Survival rate was significantly ($p < 0.001$) affected by birth weight of lambs. The lightest lambs generally had the highest mortality rate. Losses were particularly high in lambs of ≤ 2.0 kg at birth (0.63). Increased birth weight showed an increased survival of lambs' up to 4.0 to 4.9 kg of liveweight at birth (Figure 6.1) where the maximum survival rate of 0.87 was obtained. The mean birth weight of this flock (3.7 kg; Chapter 2) was at the bottom of this weight range.

Table 6.1. Maximum-likelihood analysis of variance of preweaning survival rate

Source	df	Chi-square
Intercept	1	138.27***
Birth weight	4	315.72***
Year of birth	24	549.90***
Type of birth	1	223.55***
Age of dam	4	53.55***
Sex of lamb	1	34.76***
Likelihood ratio	2000	3031.93***

***= $p < 0.001$

Age of dam had a significant ($p < 0.001$) influence on preweaning lamb survival. Survival of lambs from 2-yr-old ewes was the lowest, whilst it was highest in lambs from 4-year old ewes. The general trend was for preweaning survival to increase as ewes increased in age from 2- to 4-yr, whereafter it decreased (Figure 6.2).

Type of birth had a significant ($p < 0.001$) influence on preweaning survival rate of lambs. Single born lambs had a higher survival rate than multiples (0.85 and 0.70, respectively).

Preweaning survival rate was also significantly ($p < 0.001$) influenced by year of birth of lambs. The general trend was for preweaning survival rate to improve from 1972 to 1983, and then dropped until 1988. An improvement was observed from 1989 to 1992, whereafter it declined again (Figure 6.3). In general, differences in year means for survival rate were very large ranging from 0.62 in 1988 to 0.96 in 1983. Survival rate was better in earlier years than in later years of the study period.

Survival rate was also significantly ($p < 0.001$) influenced by sex of lambs. Male lambs showed a higher mortality incidence than female lambs (0.23 and 0.20, respectively). The sex ratio ($\text{♂}/\text{♀}$) for surviving lambs was about 0.48:0.52.

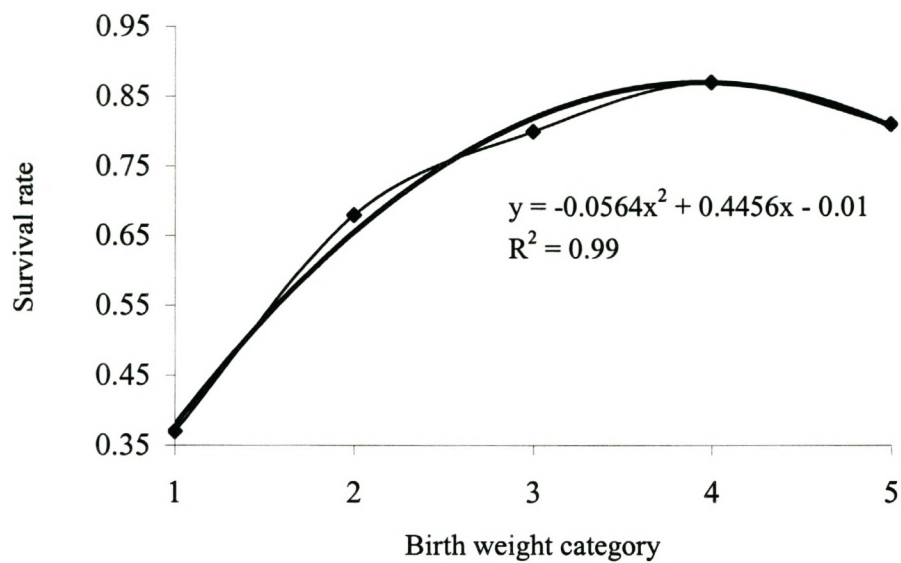


Figure 6.1. The regression of lamb survival on birth weight category

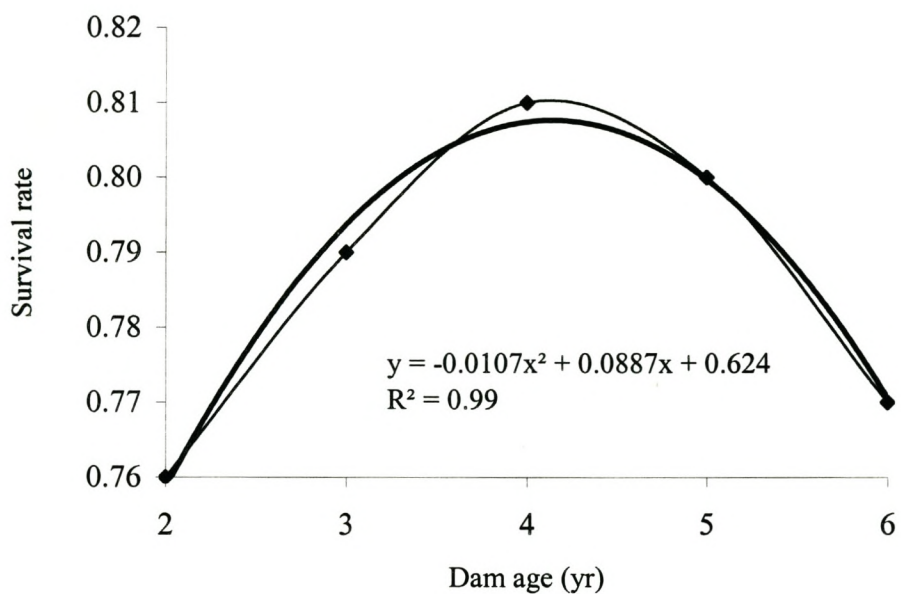


Figure 6.2. The regression of lamb survival rate on dam age

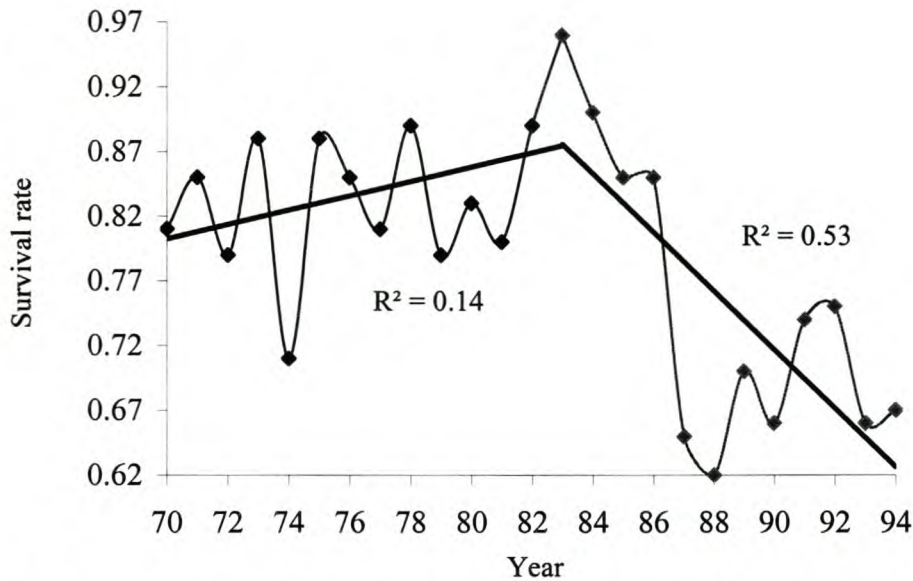


Figure 6.3 . The regression of lamb survival rates on year of birth

6.4 Discussion

Average survival rate from birth to 100 days obtained in the present study was within the range of 0.74 to 0.85 reported in the literature for other sheep breeds (Dalton *et al.*, 1980; Wiener *et al.*, 1983; Schoeman, 1990; Mukasa-Mugerwa & Lahlou-Kassi, 1995; Cloete & Scholtz, 1998; Abegaz & Duguma, 2000). Low birth weight, poor mothering ability, environmental stress on the newborn, starvation and exposure were reported as the major causes of death of lambs (Heydenrych, 1975; Dalton *et al.*, 1980; McCutcheon *et al.*, 1981; Mukasa-Mugerwa & Lahlou-Kassi, 1995; Abegaz & Duguma, 2000). According to McCutcheon *et al.* (1981), about one-third of preweaning lamb mortality is considered to be due to starvation and exposure losses.

Birth weight was one of the most important factors affecting preweaning lamb survival in this study. Heydenrych (1975) who used part of the same data set indicated that low body weight at birth and a concomitant rapid exhaustion of energy reserves appeared to be the most significant cause of perinatal deaths in twin lambs while excessive body mass and consequent dystocia seemed to cause most deaths amongst single born lambs. In the present study losses were also particularly high in lambs of ≤ 2.0 kg at birth. These results accord with those of Abegaz & Duguma (2000) and Mukasa-Mugerwa *et al.* (2000). These authors indicated that those lambs that were born with less than 2.0 kg birth weight had a greater risk of dying before weaning in two indigenous Ethiopian sheep breeds. The mean birth weights of the two breeds were ranging from 2.1 to 2.7 kg (Abegaz & Duguma, 2000; Mukasa-Mugerwa *et al.*, 2000). The maximum survival rate obtained from lambs with medium liveweight at birth was

in accordance with results reported by Heydenrych (1975). In his study lambs with a body weight at birth between 3.8 and 5.2 kg showed the highest survival rate. Dalton *et al.* (1980) also reported that lamb birth weights deviating from optimum are associated with lower survival. According to Peterson & Danell (1985), optimal birth weight seems to be higher than the mean birth weight.

In this study, lambs that survived to weaning weighed 0.5 kg more at birth than lambs that died prior to weaning (3.7 and 3.2 kg, respectively). This is in general agreement with results reported in the literature (Meyer & Clarke, 1978; Dalton *et al.*, 1980; Wiener *et al.*, 1983; Schwulst & Martin, 1993; Woolliams *et al.*, 1983; Mukasa-Mugerwa & Lahlou-Kassi, 1995; Abegaz *et al.*, 2000). Dalton *et al.* (1980) indicated that considerable importance has been attached to the role of birth weight as a factor in lamb mortality. This agreed with the results of the present study. For instance, 1983 was the year at which the maximum survival rate of 0.96 was obtained in this flock. The mean birth weight of lambs born in this particular year was 1.0 kg higher than the mean birth weight of the flock (Chapter 2). Factors, which lower birth weight, might also contribute to lowered survival via other pathways, such as poorer maternal care and lower milk production (Bradford, 1972). Thus, since the relationship between birth weight and preweaning lamb survival is causative, it would be advisable to introduce farm management routines, which can help to increase birth weight. One option is to supplement ewes in the last trimester (Scales *et al.*, 1986; Gojjam *et al.*, 1998), especially animals in poor condition carrying twins since both the foetus and the udder undergo rapid development during this period (Mukasa-Mugerwa *et al.*, 2000). According to these latter authors, cross-foster of weak or orphan or abandoned lambs shortly after parturition is also an option. They also indicated that the rotation of twins during nursing could also help to ensure that each twin mates gets enough milk. Cloete *et al.* (2000) also indicated that shearing of ewes prior to lambing might be advantageous under certain conditions, particularly when lamb survival is likely to be low. Nevertheless, in their study, lambs born to ewes that were shorn prior to lambing tended to be lighter than those from ewes shorn prior to joining.

The dam age effect found in the present study was in contrast to results reported by Schoeman (1990) and Cloete & Scholtz (1998). They reported that there were no significant differences in survival rate between lambs born to ewes of different ages. The difference might be due to management practices. It was, however, in general agreement with most results reported in the literature (Wiener *et al.*, 1983; Petersson & Danell, 1985; Atkins, 1986; Gama *et al.*, 1991; Abegaz & Duguma, 2000; Morris *et al.*, 2000; Mukasa-Mugerwa *et al.*, 2000) where preweaning lamb survival increased with ewe age, reached its peak and then decreased. This

was partly accounted for by birth weight that was significantly lower for lambs born to 2-yr-old ewes. It might also be attributed to poorer rearing ability for older ewes, possibly resulting from udder damage, poor body condition and other factors. Lambs born to 6-yr-old ewes were lighter at weaning than those lambs born to 3- to 5-yr-old ewes (Chapter 2). In general, maiden ewes require better management than the other age groups of ewes to enhance survival rate in this age group.

Single born lambs had a higher survival rate than multiples. This is in contrast to results reported by Yapi *et al.* (1992a) and Malik *et al.* (1998). It was, nevertheless, in general agreement with most other results reported in the literature (Petersson & Danell, 1985; Wiener *et al.*, 1983; Schoeman, 1990; Gama *et al.*, 1991; Cloete & Scholtz, 1998; Mukasa-Mugerwa *et al.*, 2000; Abegaz & Duguma, 2000). Schoeman (1990) reported that survival rate was significantly ($p < 0.001$) affected by type of birth, with a higher survival rate in singles (0.88) as compared to twins (0.78). Notter & Copenhaver, (1980), Wiener *et al.* (1983), Schoeman (1990), Abegaz *et al.* (2000) and Mukasa-Mugerwa *et al.* (2000) suggested that the differences in mortality rates between singles and twins were primarily determined by differences in birth weight *per se*.

In results reported by Meyer & Clarke (1978), surviving twins averaged 0.3 kg heavier than dead twins. In general, in both sexes the mean birth weight of lambs surviving was higher than for lambs dying. Schwulst & Martin (1993) also indicated, within the range of weights observed in the data, that each kilogram increase in birth weight was associated with a 10.4 % decrease in preweaning death rate.

The occurrence of year effects in preweaning survival may be attributed to weather conditions and the general management of the flock. According to Ducker & Fraser (1973), a “low level of husbandry” at the time of lambing may increase lamb mortality. Nevertheless, in a South African study, Cloete & Scholtz (1998), referring to the work of Brand *et al.* (1985), pointed out that very intensive management failed to reduce lamb mortality to levels of below 15 %. Differences between years may also be a reflection of differences in feed availability between years, caused by differences in rainfall. Severe weather conditions that were occasionally experienced at lambing can contribute to high environmental variance for lamb survival (Brash *et al.*, 1994a). The Southern Cape area is subjected to dry years with limited feed availability. For other South African studies, Schoeman (1990) and Cloete & Scholtz (1998) reported that survival rate was significantly influenced by year and season of birth. In general, to improve lamb survival the constraints imposed by genetics, nutrition, husbandry, disease and weather should be addressed (Haughey, 1991).

In the present study, male lambs showed a higher incidence of death losses than female lambs. This finding was in contrast to results reported by Schoeman (1990), Cloete & Scholtz (1998), Malik *et al.* (1998) and Abegaz *et al.* (2000). They reported that survival rate was not influenced by sex of lambs. Generally, the current results were in agreement with several results reported in the literature (Meyer & Clarke, 1978; Gama *et al.*, 1991; Schwulst & Martin, 1993; Peterson & Danell, 1985).

6.5 Conclusions

The results of this study indicated that several non-genetic fixed factors have a significant influence on preweaning lamb survival. Of these, birth weight was one of the most important factors affecting preweaning lamb survival. Thus, improving birth weight of lambs by using different management practices such as improving prepartum feeding of breeding ewes may partially solve the problem. Preferential treatments of maiden ewes as a separate management group and providing preferential treatment to ewes lambing multiples are also suggested.

Chapter 7

General conclusions

This study revealed important effects of some environmental factors on early growth traits, which should be accounted for during genetic evaluations. Sex, selection group, type of birth, year of birth and ewe age significantly affected both birth and weaning weights and preweaning growth rate. In comparing different age groups of ewes with respect to preweaning growth performance of their lambs, adjustments should be made for the effects of important environmental factors identified in this study. During the current study, 6-yr-old ewes had lambs that were significantly ($p < 0.001$) heavier at birth than all other age groups. However, their lambs were lighter at weaning than those from 3- to 5-yr-old ewes. This could be due to a better pre-natal environment, while not providing as much milk to support preweaning growth at the same level. Practically, production characteristics that peak at different ages could have an important impact on the optimum age structure for maximum production. In this flock, WW of lambs increased up to about 4-yr of age and declined thereafter. Thus, it becomes more profitable to keep a larger number of the middle-aged ewes (between about 3-to 5-yr-old ewes) to improve productivity of this flock.

The present results show that estimates of genetic parameters for the Tygerhoek Merino flock were generally comparable to literature values obtained using REML animal model procedures. With these data, ignoring maternal effects lead to an overestimation of the h^2 estimates. Likewise, exclusion of permanent environmental effects of the dam results in overestimation of the m^2 estimates, particularly for BW. Regarding BW, maternal effects (the sum of maternal additive genetic and maternal permanent environmental effects) were higher than direct additive effects. Hence, they need to be considered in any selection programme. For WW, direct additive genetic effects were higher than maternal effects. The contribution of maternal effects declined with the increasing age of lambs from birth to weaning. The genetic antagonisms between direct and maternal additive genetic effects observed in early growth traits in the current study were not large enough to prevent genetic improvement, if selection is based on individual weight performance. The direct genetic correlation between BW and WW was small. Thus, selecting for heavier WW may possibly not result in substantial increases in BW. In general, the genetic trend estimates, direct and maternal heritability estimates, the genetic correlations between animal effects and the genetic correlations between traits have indicated that selection progress in the preweaning growth traits is possible.

The regression of reproduction on two-tooth liveweight and year of birth of ewe were significant ($p < 0.001$) in all reproduction traits investigated. Multiple born ewes were also superior, both in total number of lambs born and weaned than singles. Heritability estimates of 0.23, 0.17 and 0.20 were obtained for TLB, TLW and TWW, respectively. High and positive genetic correlations, ranging from 0.61 to 0.92 were obtained among the different ewe lifetime reproduction traits. The genetic correlations between TWW1 and TLW and TWW1 and TWW ranged from 0.57 to 1.00, but that of TWW1 and TLB was nearly zero. The high positive genetic correlations together with the moderate heritability estimates obtained indicate that genetic improvement could be expected from selection of either of these traits.

The medium range h^2 estimates found for SC and TD in the present study demonstrated an opportunity of improving male fertility by selecting for these traits. The high genetic correlations between LW and both testis traits also confirmed earlier results and indicated that selection for increased LW of ram lambs will also improve ram fertility via the increased testis size. However, adjustment for LW decreased the value of the genetic correlations between LW and SC, LW and TD and the h^2 estimates of both testis traits. Literature results indicated that selection based on LW adjusted testis measurements could decrease mature LW and increase ewe productivity in terms of number of lambs born. In the present study, rams with larger SC had a significant effect on ewe fertility. So it was concluded that the use of such rams could increase flock fertility. This will allow a reduction in the number of breeding rams required each year and increase the overall reproductive efficiency of the flock.

The overall level of preweaning survival of lambs (0.79) falls within literature ranges. Of all non-genetic factors considered, birth weight tended to be the most important factor affecting preweaning lamb survival. Lighter lambs at birth had the highest mortality rate. Thus, improving birth weight of lambs either by selection for correlated traits or by improving prepartum feeding of breeding ewes might solve the problem. Strategies to improve survival rate and preweaning growth rate in this flock could include treating the maiden ewes as a separate management group, and also providing preferential treatment to ewes lambing multiples.

References

- ABEGAZ, S. & DUGUMA, G., 2000. Genetic and phenotypic parameters of growth, reproductive and survival performance of Horro sheep at Bako Agricultural Research Center. *Research fellowship report*. International Livestock Research Institute (ILRI), Addis Ababa, Ethiopia.
- ABEGAZ, S., DUGUMA, G., REGE, J. E. O., VAN WYK, J. B., NESER, F. W. C. & ERASMUS, G. J., 2000. Early growth, survival and litter size in Ethiopian Horro sheep. *S. Afr. J. Anim. Sci.* 30: (Suppl. 1) 1 - 3.
- ALBUQUERQUE, L. G. & MEYER, K., 2001. Estimates of direct and maternal genetic effects for weights from birth to 600 days of age in Nelore cattle. *J. Anim. Breed. Genet.* 118: 83- 92.
- AL-SHOREPY, S. A., 2001. Estimates of genetic parameters for direct and maternal effects on birth weight of local sheep in United Arab Emirates. *Small Rumin. Res.* 39: 219 – 224.
- AL-NAKIB, F. M. S., LODGE, G. A. & OWEN, J. B., 1986. A study of sexual development of ram lambs. *Anim. Prod.* 43: 459 – 486.
- AL-SHOREPY, S. A. & NOTTER, D. R., 1996. Genetic variation and covariation for ewe reproduction, lamb growth and lamb scrotal circumference in a fall-lambing sheep flock. *J. Anim. Sci.* 74: 1490 – 1498.
- ATKINS, K. D., 1986. A genetic analysis of the components of lifetime productivity in Scottish Blackface sheep. *Anim. Prod.* 43: 405 – 419.
- AZZAM, S. M. & NIELSEN, M. K., 1987. Expected responses to index selection for direct and maternal additive genetic effects of gestation length or birth date in beef cattle. *J. Anim. Sci.* 64: 357 – 365.
- BASUTHAKUR, A. K., BURFENING, P. J., VAN HORN, J. L. & BLACKWELL, R. L., 1973. A study of some aspects of lifetime production in Targhee and Columbia sheep. *J. Anim. Sci.* 36: 813 – 820.
- BLACKBURN, H. D. & CARTWRIGHT, T. C., 1987. Description and validation of the Texas A & M sheep simulation model. *J. Anim. Sci.* 65: 373 – 386.
- BLOCKEY, M. A. de B., 1980. Correlation of male and female fertility traits. *Proc. Aust. Soc. Anim. Prod.* 13: 57 – 59.

- BOUJENANE, I. & KERFAL, M., 1990. Estimates of genetic and phenotypic parameters for growth traits of D'man lambs. *Anim. Prod.* 51: 173 – 178.
- BOUJENANE, I., BRADFORD, G. E., BERGER, Y. M. & CHIKHI, A., 1991. Genetic and environmental effects on growth to one year and viability of lambs from crossbreeding study of D'man and Sardi breeds. *J. Anim. Sci.* 69: 3989 – 3998.
- BOURDON, R. M., 2000. Understanding animal breeding. 2nd ed. Upper Saddle River, New Jersey 07458, USA.
- BOURDON, R. M. & BRINKS, J. S., 1986. Scrotal circumference in yearling Hereford bulls: Adjustment factors, heritabilities and genetic, environmental and phenotypic relationships with growth traits. *J. Anim. Sci.* 62: 958 – 967.
- BRADFORD, G. E., 1972. The role of maternal effects in animal breeding. VII. Maternal effects in sheep. *J. Anim. Sci.* 35: 1324 – 1334.
- BRADFORD, G. E., 1985. Selection for litter size. In: Land, R. B. & Robinson, D. W. (Eds). *Genetics of reproduction in sheep*. pp. 3 – 18. Butterworths, London.
- BRASH, L. D., FOGARTY, N. M. & GILMOUR, A. R., 1994a. Reproductive performance and genetic parameters for Australian Dorset sheep. *Aust. J. Agric. Res.* 45: 427 – 441.
- BRASH, L. D., FOGARTY, N. M., BARWICK, S. A. & GILMOUR, A. R., 1994b. Genetic parameters for Australian maternal and dual-purpose meat sheep breeds. I. Liveweight, wool production and reproduction in Border Leicester and related types. *Aust. J. Agric. Res.* 45: 459 – 468.
- BRASH, L. D., FOGARTY, N. M. & GILMOUR, A. R., 1994c. Genetic parameters for Australian maternal and dual-purpose meat sheep breeds. II. Liveweight, wool and reproduction in Corriedale sheep. *Aust. J. Agric. Res.* 45: 469 – 480.
- BUNGE, R., THOMAS, D. L. & STOOKEY, J. M., 1990. Factors affecting productivity of Rambouillet ewes mated to ram lambs. *J. Anim. Sci.* 68: 2253 – 2262.
- BURFENING, P. J., 1993. Direct and maternal genetic effects on lamb survival. *Small Rumin. Res.* 11: 267 – 274.
- BURFENING, P. J. & DAVIS, K. C., 1998. Genetic parameter estimates for scrotal circumference in ram lambs and estimated co-variances with ewe body weight, fleece traits and reproductive rate. *Sheep and Goat Res. J.* 14: 121 – 126.
- BURFENING, P. J. & KRESS, D. D., 1993. Direct and maternal effects on birth and weaning weight in sheep. *Small Rumin. Res.* 10: 153 – 163.

- BURFENING, P. J., KACHMAN, S. D., HANFORD, K. J. & ROSSI, D., 1993. Selection for reproductive rate in Rambouillet sheep: Estimated genetic change in reproductive rate. *Small Rumin. Res.* 10: 317 – 330.
- CAMERON, A. W. N., FAIRNIE, I. J., CURNOW, D. H., KEOGH, E. J. & LINDSAY, D. R., 1984. The relationship between testicular size and daily sperm output of rams. *Proc. Aust. Soc. Anim. Prod.* 15: 658.
- CAMERON, A. W. N., MURPHY, P. M. & OLDHAM, C. M., 1988. Nutrition of rams and output of spermatozoa. *Proc. Aust. Soc. Anim. Prod.* 17: 162 – 165.
- CLOETE, S. W. P. & DURAND, A., 1994. Reproduction of Merino sheep subjected to divergent selection on maternal values for lambs weaned per ewe joined. *S. Afr. J. Anim. Sci.* 24: 27 – 29.
- CLOETE, S. W. P. & HYDENRYCH, H. J., 1986. Factors affecting reproduction in Merino ewes of the Tygerhoek. *S. Afr. J. Anim. Sci.* 16: 36 – 42.
- CLOETE, S. W. P. & HEYDENRYCH, H. J., 1987a. Genetic parameters for reproduction rate in the Tygerhoek Merino flock. 1. Heritability. *S. Afr. J. Anim. Sci.* 17: 1 – 7.
- CLOETE, S. W. P. & HEYDENRYCH, H. J., 1987b. Genetic parameters for reproduction rate in the Tygerhoek Merino flock. 2. Genetic correlations with wool and live mass traits. *S. Afr. J. Anim. Sci.* 17: 8 – 14.
- CLOETE, S. W. P. & SCHOLTZ, A. J., 1998. Lamb survival in relation to lambing and neonatal behaviour in medium wool Merino lines divergently selected for multiple rearing ability. *Aust. J. Exp. Agric.* 38: 801 – 811.
- CLOETE, S. W. P., DELPORT, G. J., ERASMUS, G. J., OLIVIER, J. J., HEYDENRYCH, H. J. & DU TOIT, E., 1992. Environmental and genetic trends in clean fleece mass, live mass and fibre diameter in selection and control flocks involving a selection experiment for increased clean fleece mass in South African Merino sheep. *S. Afr. J. Anim. Sci.* 22: 50 – 57.
- CLOETE, S. W. P., SCHOLTZ, A. J. & AUCAMP, B. B., 1998a. Environmental effects, heritability estimates and genetic trends in a Western Cape Döhne Merino nucleus flock. *S. Afr. J. Anim. Sci.* 28: 185 – 195.
- CLOETE, S. W. P., OLIVIER, J. J., SNYMAN, M. A. & TOIT, E. D., 1998b. Genetic parameters and trends in a selection experiment for increased clean fleece weight involving South African Merinos. *Aust. J. Exp. Agric.* 38: 427 – 432.

- CLOETE, S. W. P., GREEFF, G. C. & LEWER, R. P., 2001. Environmental and genetic aspects of survival and early liveweight in Western Australian Merino sheep. *S. Afr. J. Anim. Sci.* 31: 123 – 130.
- CLOETE, S. W. P., MULLER, C. J. C. & DURAND, A., 2000. The effects of shade and shearing date on the production of Merino sheep in the Swartland region of South Africa. *S. Afr. J. Anim. Sci.* 30: 164 – 171.
- COULTER, G. H. & KELLER, D. G., 1982. Scrotal circumference of young beef bulls: Relationship to paired testes weight, effect of breed and predictability. *Can. J. Anim. Sci.* 32: 133 – 139.
- DALTON, D. C., KNIGHT, T. W. & JOHNSON, D. L., 1980. Lamb survival in sheep breeds on New Zealand hill country. *N. Z. J. Agric. Res.* 23: 167 – 173.
- DICKERSON, G. D., 1978. Animal size and efficiency basic concepts. *Anim. Prod.* 27: 367 – 379.
- DUCKER, M. J. & FRASER, J., 1973. A note on the effect of level of husbandry at lambing on lamb viability and subsequent performance. *Anim. Prod.* 16: 91 – 94.
- ERCANBRACK, S. K. & KNIGHT, A. D., 1998. Responses to various selection protocols for lamb production in Rambouillet, Targhee, Columbia and Polypay sheep. *J. Anim. Sci.* 76 : 1311 – 1325.
- ELTAWIL, E., HAZEL, L. N., SIDWELL, G. M. & TERRILL, C. E., 1970. Evaluation of environmental factors affecting birth, weaning and yearling traits in Navajo sheep. *J. Anim. Sci.* 31: 823 – 827.
- FADILI, M. El., MICHAUX, C., DETILLEUX, J. & LEROY, P. L., 2000. Genetic parameters for growth traits of the Moroccan Timahdit breed of sheep. *Small Rumin. Res.* 37: 203 – 208.
- FAHMY, M. H., 1989. Reproductive performance, growth and wool production of Romanov sheep in Canada. *Small Rumin. Res.* 2: 253 – 264.
- FOGARTY, N. M., 1995. Genetic parameters for live weight, fat and muscle measurements, wool production and reproduction in sheep: a review. *Anim. Breed. Abstr.* 63: 101 – 143.
- FOGARTY, N. M., LUNSTRA, D. D., YOUNG, L. D. & DICKERSON, G. E., 1980. Breed effects and heritability of testis measurements in sheep. *J. Anim. Sci.* 51 (Suppl. 1): 117 (Abstr.).

- FOGARTY, N. M., BRASH, L. D. & GILMOUR, A. R., 1994. Genetic parameters for reproduction and lamb production and their components and liveweight, fat depth and wool production in Hyfer sheep. *Aust. J. Agric. Res.* 45: 443 – 457.
- FOGARTY, N. M., DICKERSON, G. E. & YOUNG, L. D., 1985. Lamb production and its components in pure breeds and composite lines. III. Genetic parameters. *J. Anim. Sci.* 60: 40 – 57.
- FOSSCECO, S. L. & NOTTER, D. R., 1995. Heritabilities and genetic correlations of body weight, testis growth and ewe lamb reproduction traits in crossbred sheep. *Anim. Sci.* 60: 185 – 195.
- FOURIE, A. J. & HEYDENRYCH, H. J., 1982. Phenotypic and genetic aspects of production in the Döhne Merino I. The influence of non-genetic factors on production traits. *S. Afr. J. Anim. Sci.* 12: 57 – 60.
- FOURIE, A. J. & HEYDENRYCH, H. J., 1983. Phenotypic and genetic aspects of production in the Döhne Merino. III. The influence of age of the ewe on reproductive performance. *S. Afr. J. Anim. Sci.* 13: 164 – 166.
- GALAL, E. S. E. & AWGICHEW, K., 1981. Ethiopian Adal sheep: Genetic and environmental factors affecting body weight and postweaning gain. *Int. Goat Sheep Res.* 1: 1310.
- GAMA, L. T., DICKERSON, G. E., YOUNG, L. D. & LEYMASTER, K. A., 1991. Effects of breed, heterosis, age of dam, litter size, and birth weight on lamb mortality. *J. Anim. Sci.* 69: 2727 – 2743.
- GARRICK, D. J., POLLAK, E. J., QUAAS, R. L. & VAN VLECK, L. D., 1989. Variance heterogeneity in direct and maternal weight traits by sex and percent purebred for Simmental-sired calves. *J. Anim. Sci.* 67: 2515 – 2528.
- GERSTMAYR, S., 1992. Impact of data structure on the reliability of the estimated genetic parameters in an animal model with maternal effects. *J. Anim. Breed. Genet.* 109: 321 – 336.
- GIZAW, S. & THWAITES, C. J., 1997. Changes in liveweight, body condition and scrotal circumference and their relationships with sexual activity and flock fertility in Ethiopian Horro rams over a 3-cycle joining period. *J. Agric. Sci., Camb.* 128: 117 – 121.
- GOJJAM, Y., ABEGAZ, S. & DUGUMA, G., 1998. Late pregnancy ewe feeding and its effect on lamb growth and survival to weaning and body weight changes of ewes in

Horro sheep. In: the *Fifth National Conference of Ethiopian Society of Anim. Prod.* 15 - 17 May 1997, Addis Ababa, Ethiopia.

- GOJJAM, Y., GIZAW, S., ABEGAZ, S. & THWAITES, C. J., 1995. Relationships between body weight, and scrotal characteristics and between environmental effects and fertility in Ethiopian Horro rams. *J. Agric. Sci., Camb.* 124: 297 – 299.
- GOULD, M. B. & WHITEMAN, J. V., 1975. Relationship between preweaning growth rate of female lambs and the growth of their offspring. *J. Anim. Sci.* 40: 585 – 589.
- GROENEVELD, E., 1998. A multivariate multimodel REML (co)variance component estimation package. User's Guide, Version 4.2.5, D-31535, Neustadt, Germany.
- HALEY, C. S., LEE, G. J., RITCHIE, M. & LAND, R. B., 1990. Direct responses in males and correlated responses for reproduction in females to selection for testicular size adjusted for body weight in young male lambs. *J. Reprod. Fert.* 89: 383 – 396.
- HALL, D. G., GILMOUR, A. R. & FOGARTY, N. M., 1994. Variation in reproduction and production of Poll Dorset ewes. *Aust. J. Agric. Res.* 45: 415 – 426.
- HANRAHAN, J. P., 1976. Maternal effects and selection response with an application to sheep data. *Anim. Prod.* 22: 359 – 369.
- HAUGHEY, K. G., 1991. Perinatal lamb mortality-its investigation, causes and control. *J. S. Afr. Vet. Ass.* 62: 78 – 91.
- HAUGHEY, K. G., GEORGE, J. M. & MCGUIRK, B. J., 1985. The repeatability of rearing performance of Merino and Dorset Horn ewes and its relationship with mature pelvic size. *Aust. J. Exp. Agric.* 25: 241- 249.
- HERSELMAN, M. J., OLIVIER, J. J. & SNYMAN, M. A., 1998. Studies on small ruminant breeds with inherent differences in fibre production and ewe productivity 1. Relationship between ewe productivity and wool production potential. *S. Afr. J. Anim. Sci.* 28: 1 – 8.
- HEYDENRYCH, H. J., 1975. 'n Studie van kuddestatistieke, nie-genetiese faktore, genetiese parameters en seleksievordering met betrekking tot die Tygerhoek Merinokudde. *Ph.D. (Agric) treatise*. University of Stellenbosch. (English summary in Agricultural Research. 1976. Pretoria, South Africa; Dept. Agric. Tech. Services. 1977, 125 – 127).
- HEYDENRYCH, H. J., DU PLESSIS, J. J. & CLOETE, S. W. P., 1984. Increasing the wool production of Merino sheep in the South Western Districts of South Africa by direct and

indirect selection. *Proc. 2nd Wrlld Congr. Sheep and Beef Cattle Breeding*. In: Hofmeyr, J. H. & Meyer, E. H. H. (eds). Pretoria, South Africa, p. 399 – 407.

- KNIGHT, T. W., 1984. Testicular growth and size in rams from flocks of different reproductive potential. *N. Z. J. Agric. Res.* 27: 179 – 187.
- KOMINAKIS, A., ROGDAKIS, E. & KOUTSOTOLIS, K., 1998. Genetic parameters for milk yield and litter size in Boutsico dairy sheep. *Can. J. Anim. Sci.* 78: 525 – 532.
- KOOTS, K. R., GIBSON, J. P. & WILTON, J. W., 1994. Analyses of published genetic parameter estimates for beef production traits. 2. Phenotypic and genetic correlations. *Anim. Breed. Abstr.* 62: 825 – 853.
- KRITZINGER, N. M., STINDT, H. W. & VAN DER WESTHUYSEN, J. M., 1984a. Assessment of different selection criteria for reproduction rate in Dormer and S. A. Mutton Merino sheep. 1. Birth type and early reproductive performance of the ewe. *S. Afr. J. Anim. Sci.* 14: 79 – 83.
- KRITZINGER, N. M., STINDT, H. W. & VAN DER WESTHUYSEN, J. M., 1984b. Assessment of different selection criteria for reproduction rate in Dormer and S. A. Mutton Merino sheep. 3. Pre-pubertal testis size of ram lambs. *S. Afr. J. Anim. Sci.* 14: 88 – 90.
- LAND, R. B., 1973. Expression of female sex-limited characters in the male. *Nature.* 241: 208 – 209.
- LAND, R. B., ATKINS, K. D. & ROBERTS, R. C., 1983. Genetic improvement of reproductive performance. In: *Sheep Production*. (Ed.) Haresign, W., Butterworths, London. p. 515 – 531.
- LEE, G. J., HALEY, C. S. & LAND, R. B., 1991. Correlated changes in growth patterns and overall production efficiency following selection for testis size adjusted for body weight in young male lambs. *Anim. Prod.* 52: 477 – 488.
- LEE, J. W., CHOI, S. B., JUNG, Y. H., KEOWN, J. F. & VAN VLECK, L. D., 2000. Parameter estimates for direct and maternal genetic effects on yearling, eighteen-month, and slaughter weights of Korean native cattle. *J. Anim. Sci.* 78: 1414 – 1421.
- LEWER, R. P., WOOLASTON, R. R. & HOWE, R. R., 1994. Studies on Western Australian Merino sheep. II. Genetic and phenotypic parameter estimates for objectively measured traits on ram and ewe hoggets using different model types. *Aust. J. Agric. Res.* 45: 829 – 840.

- LEWIS, R. M. & BEATSON, P. R., 1999. Choosing maternal effect models to estimate (co)variances for live and fleece weight in New Zealand Coopworth sheep. *Livest. Prod. Sci.* 58: 137 – 150.
- LIGDA, Ch., GABRIILIDIS, G., PAPADOPOULOS, Th. & GEORGOUDIS, A., 2000. Investigation of direct and maternal genetic effects on birth and weaning weight of Chios lambs. *Livest. Prod. Sci.* 67: 75 – 80.
- LIN, C. Y. & LEE, A. J., 1986. Sequential estimation of genetic and phenotypic parameters in multitrait mixed model analysis. *J. Dairy Sci.* 69: 2696 – 2703.
- MALIK, R. C., RAZZAQUE, M. A., AALI, M. A. T., AL-KHOZAM, N. M., AL-MUTAWA, T. A. & ABBAS, S., 1998. Factors affecting preweaning lamb survival in continuously housed sheep. *Aust. J. Exp. Agric.* 38: 795 – 799.
- MANDIKI, S. N. M., DERYCKE, G., BISTER, J. L. & PAQUAY, R., 1998. Influence of season and age on sexual maturation parameters of Texel, Suffolk and Ile-de-France rams. 1. Testicular size, semen quality and reproductive capacity. *Small Rumin. Res.* 28: 67 – 79.
- MARIA, G. A., BOLDMAN, K. G. & VAN VLECK, L. D., 1993. Estimates of variances due to direct and maternal effects for growth traits of Romanov sheep. *J. Anim. Sci.* 71: 845 – 849.
- MASTER, D. G. & FELS, H. E., 1984. Seasonal changes in the testicular size of grazing rams. *Proc. Aust. Soc. Anim. Prod.* 15: 444 – 447.
- MATOS, C. A. P. & THOMAS, D. L., 1992. Physiology and genetics of testicular size in sheep: a review. *Livest. Prod. Sci.* 32: 1 – 30.
- MATOS, C. A. P., THOMAS, D. L., NASH, T. C., WALDRON, D. F. & STOOKEY, J. M., 1992. Genetic analyses of scrotal circumference, size and growth in Rambouillet lambs. *J. Anim. Sci.* 70: 43 – 50.
- MAVROGENIS, A. P., 1996. Environmental and genetic parameters influencing milk and growth traits of Awassi sheep in Cyprus. *Small Rumin. Res.* 20: 141 – 146.
- McCUTCHEON, S. N., HOLMES, C. W. & McDONALD, M. F., 1981. The starvation exposure syndrome and neonatal lamb mortality: a review. *Proc. N. Z. Soc. Anim. Prod.* 41: 209 – 217.
- MEYER, H. H. & CLARKE, J. N., 1978. Genetic and environmental effects on incidence and causes of lamb mortality. *Proc. N. Z. Soc. Anim. Prod.* 38: 181 – 184.

- MEYER, H. H. & CLARKE, J. N., 1982. Effect of ewe ovulation rate and uterine efficiency on breed and strain variation in litter size. *Proc. N. Z. Soc. Anim. Prod.* 42: 33 – 35.
- MEYER, K., 1992. Variance components due to direct and maternal effects for growth traits of Australian beef cattle. *Livest. Prod. Sci.* 31: 179 – 204.
- MEYER, K., 1993. Covariance matrices for growth traits of Australian Polled Hereford cattle. *Anim. Prod.* 57: 37 - 45.
- MEYER, K., 1997. Estimates of genetic parameters for weaning weight of beef cattle accounting for direct-maternal environmental covariances. *Livest. Prod. Sci.* 52: 187 – 199.
- MEYER, K., HAMMOND, K., MACKINNON, M. J. & PARNELL, P. F., 1991. Estimates of covariances between reproduction and growth in Australian beef cattle. *J. Anim. Sci.* 69: 3533- 3543.
- MORRIS, C. A., HICKEY, S. M. & CLARKE, J. N., 2000. Genetic and environmental factors affecting lamb survival at birth through to weaning. *N. Z. J. Agric. Res.* 43: 515 – 524.
- MOULE, G. R., 1971. Vital statistics in sheep and wool production. *Anim. Breed. Abstr.* 39: 623 - 636.
- MUKASA-MUGERWA, E. & EZAZ, Z., 1992. Relationship of testicular growth and size to age, body weight and onset of puberty in Menz ram lambs. *Theriogenology.* 38: 979 – 988.
- MUKASA-MUGERWA, E. & LAHLOU-KASSI, A., 1995. Reproductive performance and productivity of Menz sheep in the Ethiopian highlands. *Small Rumin. Res.* 17: 167 – 177.
- MUKASA-MUGERWA, E., LAHLOU-KASSI, A., ANINDO, D., REGE, J. E. O., TEMBELY, S., TIBBO, M. & BAKER, R. L., 2000. Between and within breed variation in lamb survival and the risk factors associated with major causes of mortality in indigenous Horro and Menz sheep in Ethiopia. *Small Rumin. Res.* 37: 1 – 12.
- NAGY, I., SÖLKNER, J., KOMLÓSI, I. & SÁFÁR, L., 1999. Genetic parameters of reproduction and fertility traits in Hungarian Merino sheep. *J. Anim. Breed. Genet.* 116: 399 – 413.

- NAPIER, K. M. & JONES, L. P., 1982. Effect of age, maternal handicap, birth and survival type on five fleece and body characters of Corriedale rams. *Aust. J. Exp. Anim. Husb.* 22: 281 – 287.
- NÄSHOLM, A. & DANELL, Ö., 1996. Genetic relationships of lamb weight, maternal ability, and mature ewe weight in Swedish Finewool sheep. *J. Anim. Sci.* 74: 329 – 339.
- NESER, F. W. C., ERASMUS, G. J. & VAN WYK, J. B., 2000. Genetic studies on the South African Mutton Merino: growth traits. *S. Afr. J. Anim. Sci.* 30: 172 – 177.
- NESER, F. W. C., ERASMUS, G. J. & VAN WYK, J. B., 2001. Genetic parameter estimates for pre-weaning weight traits in Dorper sheep. *Small Rumin. Res.* 40: 197 – 202.
- NJWE, R. M. & MANJELI, Y., 1992. Milk Yield of Cameroon Dwarf Blackbelly Sheep. pp. 527-532. In: Rey B., Lebbie S. H. B. and Reynolds L. (Eds). 1992. Small Ruminant Research and Development in Africa. Proceedings of the First Biennial Conference of the African Small Ruminant Research Network, ILRAD, Nairobi, Kenya, 10 - 14 December 1990. ILCA (International Livestock Center for Africa), Nairobi, Kenya.
- NOTTER, D. R. & COPENHAVER, J. S., 1980. Performance of Finnish Landrace ewes under accelerated lambing. II. Lamb growth and survival. *J. Anim. Sci.* 51 : 1043 – 1050.
- NOTTER, D. R., 2000. Effects of ewe age and season of lambing on prolificacy in US Targhee, Suffolk and Polypay sheep. *Small Rumin. Res.* 38: 1 – 7.
- NOWAKOWSKI, P. & CWIKLA, A., 1994. Seasonal variation in testes size in Polish Merino rams and its relationship to reproductive performance in spring. *Theriogenology.* 42: 613 – 622.
- OLDHAM, C. M., ADAMS, N. R., GHERARDI, P. B., LINDSAY, D. R. & MACKINTOSH, J. B., 1978. The influence of level of feed intake on sperm-producing capacity of testicular tissue in the ram. *Aust. J. Agric. Res.* 29: 173 – 179.
- OLIVIER, W. J., SNYMAN, M. A., OLIVIER, J. J., VAN WYK, J. B. & ERASMUS, G. J., 2001. Direct and correlated responses to selection for total weight of lamb weaned in Merino sheep. *S. Afr. J. Anim. Sci.* 31: 115 – 121.
- PETERSSON, C. J. & DANELL, Ö., 1985. Factors influencing lamb survival in four Swedish sheep breeds. *Acta. Agric. Scand.* 35: 217 – 232.
- PURVIS, I. W., 1985. Genetic relationships between male and female reproductive traits. Ph.D. Thesis, University of New England, Armidale, NSW, Australia.

- PURVIS, I. W., KILGOUR, R. J., EDEY, T. N. & PIPER, L. R., 1984. Variation in testis diameter and serving capacity within and between 14 Merino lines. *Proc. Aust. Soc. Anim. Prod.* 15: 545 – 548.
- PURVIS, I. W., PIPER, L. R., EDEY, T. N. & KILGOUR, R. J., 1988. The genetic relationship between ovulation rate and testicular diameter in a random-breeding Merino flock. *Livest. Prod. Sci.* 18:35 – 54.
- RAJAB, M. H., CARTWRIGHT, T. C., DAHM, P. F. & FIGUEIREDO, E. A. P., 1992. Performance of three tropical Hair sheep breeds. *J. Anim. Sci.* 70: 3351 – 3359.
- REGE, J. E. O., 1997. LOGMLVAR: A computer program for estimating variances of predicted probabilities from maximum-likelihood estimates in a logit response function. International Livestock Research Institute (ILRI), Addis Ababa, Ethiopia.
- REGE, J. E. O. & SHRINGTON, J., 1996. A method for estimating sampling variances of predicted probabilities from maximum-likelihood estimates in a logit response function. *Discovery and Innovation* 8: 171.
- REGE, J. E. O., TOE, F., MUKASA-MUGERWA, E., TIMBELY, S., ANINDO, D. BAKER, R. L. & LAHLOU-KASSI, A., 2000. Reproductive characteristics of Ethiopian highland sheep. II. Genetic parameters of semen characteristics and their relationships with testicular measurements in ram lambs. *Small Rumin. Res.* 37: 173 – 187.
- ROBINSON, D. L., 1996. Estimation and interpretation of direct and maternal genetic parameters for weight of Australian Angus cattle. *Livest. Prod. Sci.* 45: 1 – 11.
- ROBISON, O. W., 1981. The influence of maternal effects on the efficiency of selection: a review. *Livest. Prod. Sci.* 8: 121 – 137.
- SAS, 1996. SAS User's Guide, Statistics. Statistical Analysis Systems Institute, Inc., Cary, North Carolina.
- SCALES, G. H., BURTON, R. N. & MOSS, R. A., 1986. Lamb mortality, birth weight and nutrition in late pregnancy. *N. Z. J. Agric. Res.* 29: 75 – 82.
- SCHENKEL, F. S. & SCHAEFFER, L. R., 2000. Effects of non-random parental selection on estimation of variance components. *J. Anim. Breed. Genet.* 117: 225 – 239.
- SCHOEMAN, S. J., 1990. Production parameters for Döhne Merino sheep under accelerated, intensive lambing system. *S. Afr. J. Anim. Sci.* 20: 174 – 179.
- SCHOEMAN, S. J., 2000. A comparative assessment of Dorper sheep in different production environments and systems. *Small Rumin. Res.* 36: 137 – 146.

- SCHOEMAN, S. J. & COMBRINK, G. C., 1987. Testicular development in Dorper, Döhne Merino and crossbred rams. *S. Afr. J. Anim. Sci.* 17: 22 – 26.
- SCHOEMAN, S. J., MAREE, C. & COMBRINK, G. C., 1987. The relationship between testis size and stimulated plasma testosterone concentrations and its influence on mating performance in Dorper rams. *S. Afr. J. Anim. Sci.* 17: 63 – 69.
- SCHWULST, F. J. & MARTIN, L. C., 1993. Factors affecting preweaning lamb death losses. *The Professional Animal Scientist.* 9: 10 – 13.
- SHRESTHA, J. N. B., FISER, P. S., LANGFORD, G. A. & HEANEY, D. P., 1983. Influence of breed, birth date, age and body weight on testicular measurements of growing rams maintained in controlled environment. *Can. J. Anim. Sci.* 63: 835 – 847.
- SINHA, N. K. & SINGH, S. K., 1997. Genetic and phenotypic parameters of body weights, average daily gains and first shearing wool yields in Muzaffarnagri sheep. *Small Rumin. Res.* 26: 21 – 29.
- SMITH, B. A., BRINKS, J. S. & RICHARDSON, G. V., 1989a. Relationships of sire scrotal circumference to offspring reproduction and growth. *J. Anim. Sci.* 67: 2881- 2885.
- SMITH, B. A., BRINKS, J. S. & RECHARDSON, G. V., 1989b. Estimation of genetic parameters among reproductive and growth traits in yearling heifers. *J. Anim. Sci.* 67: 2886 – 2891.
- SNYMAN, M. A., ERASMUS, G. J. & VAN WYK, J. B., 1998a. Genetic and phenotypic correlations among reproduction traits in Afrino sheep. *S. Afr. J. Anim. Sci.* 28: 74 – 81.
- SNYMAN, M. A., ERASMUS, G. J. & VAN WYK, J. B., 1998b. The possible genetic improvement of reproduction and survival rate in Afrino sheep using a threshold model. *S. Afr. J. Anim. Sci.* 28: 120 – 124.
- SNYMAN, M. A., CLOETE, S. W. P. & OLIVIER, J. J., 1998c. Genetic and phenotypic correlations of total weight of lamb weaned with body weight, clean fleece weight and mean fibre diameter in three South African Merino flocks. *Livest. Prod. Sci.* 55: 157 – 162.
- SNYMAN, M. A., ERASMUS, G. J., VAN WYK, J. B. & OLIVIER, J. J., 1995. Direct and maternal (co)variance components and heritability estimates for body weight at different ages and fleece traits in Afrino sheep. *Livest. Prod. Sci.* 44: 229 – 235.

- SNYMAN, M. A., OLIVIER, J. J. & OLIVIER, W. J., 1996. Variance components and genetic parameters for body weight and fleece traits of Merino sheep in an arid environment. *S. Afr. J. Anim. Sci.* 26: 11 – 14.
- SNYMAN, M. A., OLIVIER, J. J., ERASMUS, G. J. & VAN WYK, J. B., 1997. Genetic parameter estimates for total weight of lamb weaned in Afrino and Merino sheep. *Livest. Prod. Sci.* 48: 111 – 116.
- SWALVE, H. H., 1993. Estimation of direct and maternal (co)variance components for growth traits in Australian Simmental beef cattle. *J. Anim. Breed. Genet.* 110: 241 – 252.
- TOE, F., REGE, J. E. O., MUKASA-MUGERWA, E., TEMBELY, S., ANINDO, D., BAKER, R. L. & LAHLOU-KASSI, A., 2000. Reproduction characteristics of Ethiopian highland sheep. I. Genetic parameters of testicular measurements in ram lambs and relationship with age at puberty in ewe lambs. *Small Rumin. Res.* 36: 227 – 240.
- TORSHIZI, R. V., NICHOLAS, F. W. & RAADSMA, H. W., 1996. REML estimates of variance and covariance components for production traits in Australian Merino sheep, using an animal model. 1. Body weight from birth to 22 months. *Aust. J. Agric. Res.* 47: 1235 – 1249.
- TOSH, J. J. & KEMP, R. A., 1994. Estimation of variance components for lamb weights in three sheep populations. *J. Anim. Sci.* 72: 1184 – 1190.
- TOSH, J. J. & KEMP, R. A., 2000. Genetic trends for weaning weight during development of a multibreed population of beef cattle in two contrasting environments. *Can. J. Anim. Sci.* 80: 191 – 193.
- VAN WYK, J. B., ERASMUS, G. J. & KONSTANTINOV, K. V., 1993a. Non-genetic factors influencing early growth traits in the Elsenburg Dormer sheep stud. *S. Afr. J. Anim. Sci.* 23: 67 – 71.
- VAN WYK, J. B., ERASMUS, G. J. & KONSTANTINOV, K. V., 1993b. Variance component and heritability estimates of early growth traits in the Elsenburg Dormer sheep stud. *S. Afr. J. Anim. Sci.* 23: 72 – 76.
- VAN WYK, J. B., ERASMUS, G. J. & KONSTANTINOV, K. V., 1993c. Genetic and environmental trends of early growth traits in the Elsenburg Dormer sheep stud. *S. Afr. J. Anim. Sci.* 23: 85 – 87.

- VENTER, H. A. W., VAN ZYL, J. G. E. & TAMI VASCONCELLOS, O. A. D. R., 1984. Comparative testicular development in young beef bulls. *Proc. 2nd Wld Congr. Sheep and Beef cattle breeding*. (Eds) Hofmeyr, J. H. & Meyer, E. H. H. April 1984, Pretoria, South Africa.
- VISSCHER, P. M. & THOMPSON, R., 1992. Comparisons between genetic variances estimated from different types of relatives in dairy cattle. *Anim. Prod.* 55: 315 – 320.
- WALKLEY, J. R. W. & SMITH, C., 1980. The use of physiological traits in genetic selection for litter size in sheep. *J. Reprod. Fert.* 59: 83 – 88.
- WIENER, G., WOOLLIAMS, C. & MACLEOD, N. S. M., 1983. The effects of breed, breeding system and other factors on lamb mortality 1. Causes of death and effects on the incidence of losses. *J. Agric. Sci., Camb.* 100: 539 – 551.
- WILLHAM, R. L., 1972. The role of maternal effects in animal breeding: III. Biometrical aspects of maternal effects in animals. *J. Anim. Sci.* 35: 1288 – 1293.
- WILLHAM, R. L., 1980. Problems in estimating maternal effects. *Livest. Prod. Sci.* 7: 405 – 418.
- WILSON, D. E. & WILLHAM, R. L., 1986. Within-herd phenotypic, genetic and environmental trend lines for beef cattle breeders. *J. Anim. Sci.* 63: 1087 – 1094.
- WOOLLIAMS, C., WIENER, G. & MACLEOD, N. S. M., 1983. The effects of breed, breeding system and other factors on lamb mortality 3. Factors influencing the incidence of weakly lambs as a cause of death. *J. Agric. Sci.* 100: 563 - 570.
- YAPI, C. V., BOYLAN, W. J. & ROBINSON, R. A., 1992a. Effect of genetic and environmental factors on lamb mortality. *World Rev. Anim. Prod.* 27: 35 –41.
- YAPI, C. V., BOYLAN, W. J. & ROBINSON, R. A., 1992b. Heritability and repeatability estimates and the correlations of lamb mortality with birth weight and litter size. *World Rev. Anim. Prod.* 27: 55 –60.
- YAZDI, M. H., EFTEKHARI-SHAHROUDI, F., HEJAZI, M. & LILJEDAHL, L.-E., 1998. Environmental effects on growth traits and fleece weights in Baluchi sheep. *J. Anim. Breed. Genet.* 115: 455 – 465.
- YAZDI, M. H., ENGSTRÖM, G., NÄSHOLM, A., JOHANSSON, K., JORJANI, H. & LILJEDAHL, L.-E., 1997. Genetic parameters for lamb weight at different ages and wool production in Baluchi sheep. *Anim. Sci.* 65: 247 – 255.