

Genetic evaluation of the South African Dorper sheep breed

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DECLARATION

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ABSTRACT

The Dorper sheep breeders developed their own linear type scoring system based on a 5-point scale which assesses Conformation, Size, Type, Fat distribution and Colour. For many decades Dorper sheep breeders have been so consistent with adherence to these breed standards without paying much attention to performance testing of their stud animals. However, there is a paucity of information pertaining to the genetic relationships between visually assessed traits and objectively measured growth, reproduction and fitness traits in the breed. Slow genetic gains in Dorper production traits are assumed to be caused by over-accentuation of type traits but those assumptions needed to be scientifically validated. It was therefore vital to derive these relationships as they could have a negative impact on genetic progress in the event that some antagonisms existed. Against this background, the major objectives of this study were to estimate genetic parameters and trends for production, reproduction, fitness and subjective traits using data extracted from National Small Stock Improvement Scheme (NSIS). Furthermore, the study correlated performance data with subjectively assessed traits to derive genetic relationships between them to establish the effect of selecting Dorper sheep on breed standards has on objective traits of economic importance.

Genetic parameters and relationships were estimated for subjectively assessed and objectively measured traits using linear and threshold methods. Linear methods were applied via the implementation of Residual Maximum Likelihood (REML) procedures and Bayesian methods were implemented through Gibbs sampling. It was established through the implementation of single-trait and multi-trait analyses that live weight and growth traits were moderately to highly heritable. Maternal effects were also significant for such traits. Subjectively assessed traits were demonstrated to be lowly to moderately heritable using both linear and threshold methods. There were positive genetic and environmental correlations between live weight, growth and subjectively assessed traits with the exception of Colour. There was favourable selection response to live weight and growth traits in a Dorper flock, with the exception of average daily gain during the post weaning phase where there was a slight negative trend. Subjectively assessed traits with the exception of Size responded favourably to selection. It was concluded that breeders should consider removing Colour from their breeding objectives, and focus more on selecting animals based on BLUP breeding values of objectively measured traits. The across flock genetic evaluation of all Dorper records demonstrated through the implementation of both linear and threshold methods that reproduction and fitness traits were lowly to moderately heritable and exhibited favourable genetic correlations amongst themselves. It was further established that ewe rearing ability, ewe stayability and ewe productive life are lowly heritable and have some favourable correlations with component traits of reproduction. There was little genetic change in reproduction and fitness traits, but traits generally deteriorated where significant trends were found. It was concluded that breeders should select their animals on objectively measured production and reproduction traits and not put as much emphasis on breeding standards.

OPSOMMING

Die Dorper skaaptelers het hul eie liniêre puntestelsel ontwikkel wat op 'n 5-punt skaal bouvorm, grootte, tipe, vetverspreiding en kleur beoordeel. Dorper skaaptelers se fokus was vir baie dekades om hierdie rasstandaarde na te kom, sonder om aandag te gee aan die prestasietoetsing van hul stoetdiere. Rasverbetering in die Dorperskaapas is gebaseer op subjektiewe beoordeling van eienskappe soos dit in die skouring bepaal word. Daar is egter 'n gebrek aan inligting aangaande genetiese verwantskappe tussen visueel beoordeelde eienskappe en objektiewe eienskappe soos groei, reproduksie en fiksheid. Dit word aangeneem dat stadige genetiese vordering in produksie-eienskappe van Dorpers deur 'n oorbeklemtoning van tipe eienskappe veroorsaak word, maar hierdie aannames moet wetenskaplik bewys word. Daarom is dit uiters belangrik om die verwantskappe tussen subjektiewe en objektiewe eienskappe te bepaal, aangesien hulle 'n moontlike negatiewe effek op genetiese vordering mag uitoefen as daar wel antagonismes bestaan. Teen hierdie agtergrond is die hoofdoelwitte van hierdie studie om prestasiedata vanuit die Nasionale Kleinveeverbeteringskema (NSIS) te onttrek en die beraming van genetiese parameters en tendense vir produksie, reproduksie, fiksheid en subjektiewe eienskappe. Verder het hierdie studie prestasiedata met subjektiewe beoordeelde eienskappe gekorreleer om genetiese verwantskappe tussen subjektiewe en objektiewe eienskappe te bepaal.

Genetiese parameters en -verhoudings was beraam vir subjektief beoordeelde en objektiewe gemete eienskappe met die gebruik van lineêre- en drumpelwaardemetodes. Lineêre metodes is toegepas d.m.v. die implementering van Residuele Maksimum Waarskynlikheid (REML) prosedures en die Bayesiaanse metodes deur Gibbs steekproefneming. Dit is bevestig dat dat liggaamsgewig en groei-eienskappe matig tot hoog oorerflik is. Maternale-effekte het ook 'n beduidende invloed op hierdie eienskappe gehad. Subjektiewe eienskappe is laag tot matig oorerflik, volgens beide lineêre en drempelwaarde metodes. Daar was positiewe genetiese- en omgewingskorrelasies tussen liggaamsgewig, groei en subjektiewe eienskappe, met die uitsondering van kleur. Daar was 'n gunstige seleksie respons vir liggaamsgewig en groei-eienskappe met die uitsondering van gemiddelde daaglikse toename gedurende die na-speense fase wat 'n afname in die gemiddelde voorspelde teelwaardes getoon het. Subjektiewe eienskappe, met die uitsondering van grootte, het in die studietydperk geneties verbeter. Die gevolgtrekking is dat telers dit moet oorweeg om kleur (subjektiewe eienskap) van hul teeldeelwitte te verwyder en om diere op BLUP teelwaardes van objektiewe eienskappe moet selekteer. Die genetiese evaluasie van die nasionale kudde het getoon dat reproduksie- en fiksheidseienskappe laag tot matig oorerflik is en gunstige korrelasies onderlings toon. Dit is verder bevestig dat grootmaakvermoë, terughouvermoë en produktiewe leeftyd laag oorerflik is, en sekere gunstige korrelasies met die komponente van reproduksie toon. Daar was geen genetiese verandering in reproduksie en fiksheid eienskappe in die nasionale kudde nie, moontlik omdat geen seleksie toegepas is nie, a.g.v. 'n oorbeklemtoning van rasstandaarde. Die gevolgtrekking is

dat telers diere moet selekteer gebaseer op produksie en reproduksie eienskappe, en minder klem lê op rasstandaarde.

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CHAPTER 1

GENERAL INTRODUCTION

In September 2000, building upon a decade of major United Nations conferences and summits, world leaders came together to the United Nations Headquarters in New York to adopt the United Nations Millennium Declaration, committing their nations to a new global partnership to reduce extreme poverty and setting out a series of time bound targets that have become known as the Millennium Development Goals (MDGs). The eight Millennium Development Goals form a blueprint agreed to by all nations and leading development institutes. The goals range from halving extreme poverty to halting the spread of HIV/AIDS and providing universal primary education, all by the target date of 2015 (UN, 2011). Goal 1 relates directly to hunger, which is the primary global issue of concern to the Food and Agriculture Organization (FAO). Some developing countries have made impressive gains in achieving hunger-related targets but many are falling behind (FAO, 2011). The number of hungry people in the world is currently at a historic high. FAO estimated that a total of 925 million people were undernourished in 2010, representing almost 16 percent of the population of developing countries (FAO, 2011). The 2005 South Africa's Millennium Development Goals Country Report indicated that South Africa had already met some of its MDGs targets and for those that had not been achieved the country was well on course to achieve them. The pinnacle of accomplishing the first goal lies in having a sound and robust agricultural production system. Livestock production plays an essential role in South Africa's agriculture system (Schoeman *et al.*, 2010). It accounted for approximately 48 % of total agricultural output in the 2005- 2006 season (Abstract of Agricultural Statistics, 2008). The small stock industry is of crucial significance to the South African livestock industry because approximately 80 % of South Africa's agricultural land is not suitable for crop production (Schoeman *et al.*, 2010). Sheep enterprises around the world are generally characterized by their extensive systems, making use of the natural resources available, often in marginal land areas, to produce both meat and wool. As the world population rises and climate change influences shifts in the balance of global food production, production of food from marginal lands will become increasingly important and the global sheep industries are likely to have a key role to play in this (FAO, 2011).

To achieve sound small stock production that meets South Africa's food demands in an economic way, one of the prerequisites is to have sound animal breeding programs. The South African Studbook Association was established in 1904, creating a framework for animal recording and selection (Erasmus & Hofmeyr, 1984). Breeding objectives are developed to provide a clear statement of direction in animal improvement programs. The purpose of a breeding objective is to identify the traits that affect some

production goal and to allow selection of animals that will increase the frequency of alleles with favorable effects on these traits. In livestock, animal productivity is commonly measured by income generated from the enterprise. For this reason, goals of selection usually include genetic change in traits that are more beneficial (profitable) for the livestock program. By identifying traits of economic importance, a breeding objective clarifies the role of genetics in defining profitability and facilitates development of selection strategies (Borg, 2004). In the 20th century, the South African small stock industry has undergone remarkable metamorphosis necessitated by changes in demand, adoption of new production technologies and advances in computer software and hardware which enable re-evaluation of genetic parameters to better define selection strategies for the modern market (Van Wyk *et al.*, 2003).

Small Stock Improvement in the Republic of South Africa is mainly the mandate of the South African National Small Stock Improvement Scheme (NSIS). The NSIS is housed under the Animal Production Institute of the Agricultural Research Council (ARC). It consists of an integrated pedigree and data recording system namely INTERGIS (Schoeman *et al.*, 2010). The NSIS is so designed to generate maximum information with a minimum of inputs. It further incorporates different levels of record keeping. The scheme incorporates data on reproduction, growth, survival, quality and type of animal in a holistic way enabling the use of the information as a whole. One of the aims of the scheme is to identify better producing animals to be used for breeding. The accumulation of animal production datasets from NSIS provides a unique opportunity to evaluate small stock performance records.

The NSIS currently provides breeding values for the economically important traits to all participating members of all small stock species. The species include composite sheep and goat breeds that were developed over several decades as was necessitated by the prevailing needs as at that time. Examples of such sheep breeds include the Dorper (meat), Dormer (dual-purpose), Afrino (dual-purpose), South African Mutton Merino (dual-purpose), Dohne Merino (dual-purpose) and the Boer goat (meat). Each prudent investment that was made in the novel research that culminated in the development of these composite breeds had a titanic impact on the South African small stock industry as exhibited by their prominence which has emanated in the flowing over of germplasm to other countries worldwide (Schoeman *et al.*, 2010). However, despite massive amounts of human and capital resources that have been channeled towards breed development in South Africa, there is still a dearth of genetic parameters for many traits of economic importance which include lamb growth, ewe reproduction, lamb survival, longevity, stayability, disease resistance, fitness, meat and carcass characteristics in the diverse sheep genotypes. The first step is to develop a suitable statistical model for the estimation of (co)variance components. These components are then used to estimate genetic parameters, such as heritability of traits, genetic correlations among traits and to predict breeding values for all animals.

Diverse livestock industries have achieved sustainable improvements in production efficiency through the implementation of genetic improvement programs. Breeding objectives have been developed for multiple-trait selection in various sheep breeds emphasizing a combination of prolificacy, growth, and wool characteristics worldwide (Kosgey, 2004). The South African sheep industry has struggled, compared to the beef and dairy industries in developing genetic improvement programs, however, participation in national genetic evaluation programs through the NSIS has created potential for such improvement programs to further develop and proliferate.

It was reported by Dickerson (1970) that the efficiency of lamb production depends primarily upon female production, reproduction, and growth of lambs. Furthermore, other workers which include Al-Shorepy & Notter (1996) highlighted that reproductive rate may be improved by increasing lambing frequency, which requires that ewes have the ability to lamb throughout the year, and by maintaining high prolificacy in all seasons. It has also been established that simultaneous improvement in growth rate also requires that there be no major genetic antagonisms between growth and reproduction (Al-Shorepy & Notter, 1996). Reproductive performance is of utmost importance in the efficiency of sheep production in meat, wool and dual-purpose breeds. The best single measure of productivity is the total weight of lamb weaned per year (Snyman *et al.*, 1996). Despite numerous studies involving the component traits of reproduction such as fertility, litter size, lamb survival rate and number of lambs born and weaned per ewe having been conducted in an effort to derive heritability estimates for many sheep breeds worldwide, more studies with particular emphasis on meat production need to be conducted for the South African production systems. Furthermore, fitness characteristics are difficult to measure in practice because they encompass all phenotypic expressions that influence an individual's ability to contribute offspring to the next generation. Some studies have been conducted on reproduction and fitness traits in sheep (Snyman *et al.*, 1997; Snyman *et al.*, 1997b; Cloete & Scholtz, 1998; Olivier *et al.*, 2001; Cloete *et al.*, 2002; Cloete *et al.*, 2009). However, South Africa still lags behind other countries such as Australia and New Zealand with regards to recording and genetically evaluating fitness traits in its various small stock breeds. Falconer & MacKay (1996) discussed the component traits that may influence the overall fitness of an individual with the primary characteristics including survival, reproduction, and maternal ability of the breeding female. Differences in fitness that are associated with genetic variation in the component traits of fitness are influenced by selection.

Borg *et al.* (2009) reported that the importance of fitness in commercial sheep production systems relates to the attrition of both lambs and breeding ewes. The same workers also noted that components of fitness that may be recorded include mortality rate and reproductive traits such as fertility, litter size, and number of lambs weaned, or maternal traits like milk production or body size, as they relate to lamb and breeding ewe performance. Phenotypic expressions of fitness component traits are influenced by both mortality and producer selection decisions. Lamb mortality can be attributed to factors that contribute to losses

associated with diseases, predation, or competition for postnatal nutrition. Differences in breeding ewe fitness are expressed by early removal from the flock for reasons such as illness, injury, or death, or for producer imposed reasons that include reproductive failure, poor milking ability, or unthrifty bodyweight characteristics that may lead to culling prior to the next lamb crop (Borg, 2007).

The introduction of performance recording for Merino sheep in the 1950s in South Africa resulted in performance recording for meat and dual-purpose breeds such as the Dorper, Dormer and Dohne Merino. Recording of pedigree information linked to production and utilizing the available animal breeding technology make performance recording valuable in for South African sheep farmers. Sheep improvement schemes are often hampered by relatively low use of performance recording, relatively small size of recorded flocks and frequent lack of genetic ties to facilitate across-flock genetic evaluations (Simm *et al.*, 2001). Atkins *et al.* (1998) exuberated that the sheep industry in Australia was slow to adopt across-flock genetic evaluations, while the other major livestock industries (dairy cattle, beef cattle and pigs) had already developed evaluation schemes. These schemes primarily depend upon farm data collection and centralized processing for across-flock predictions of the breeding values of seed-stock animals.

For most livestock breeds in South Africa, selection pressure on visual assessment is normally so high that few animals remain for selection based on measured productive and reproductive performance. This is probably the single most important factor limiting the effective application of performance testing (Erasmus *et al.*, 2001). Sheep breeders in South Africa have for many decades focused on subjective traits that are assessed in the show ring with much less attention being paid to objective traits that are assessed through performance recording. Subsequent to the advent of a linear type scoring system for South African Merino sheep (Olivier *et al.*, 1987), South African researchers have also included some wool quality and conformation traits in their studies (Cloete *et al.*, 1992; Groenewald *et al.*, 1999; Snyman & Olivier, 2002a). In the recent comprehensive review of genetic parameters in sheep, Safari *et al.* (2005b) included wool, growth, meat and reproduction traits. The only subjectively assessed trait included in the review was crimp frequency which can also be measured objectively (Matebesi *et al.*, 2009).

The inclusion of subjectively assessed wool traits into the Merino selection programmes using the Tygerhoek Merino flock and the Cradock fine wool Merino stud data sets have been investigated (Naidoo *et al.*, 2006; Olivier *et al.*, 2006a; Matebesi *et al.*, 2009). Apart from the work of Snyman & Olivier (2002a), genetic and phenotypic correlations between subjectively assessed wool and conformation traits with objective wool and live weight traits were derived by Matebesi *et al.*, (2009). However, despite these few studies having been conducted in Merino sheep (wool sheep), there is a paucity of information on genetic parameters for subjectively assessed traits and their genetic and phenotypic correlations with several objectively measured traits for meat sheep breeds. Against this background, the current study obtained

pedigree information, and recorded data for live weight production, subjectively assessed traits (scores), reproduction, stayability, longevity and lamb survival from the NSIS for the Dorper breed. This breed is considered as one of the most important meat sheep breeds used in South Africa. Breed improvement is based mainly on subjective assessment in the show ring. However, income from Dorper sheep in South Africa is generated mainly from reproduction (expressed as total weight weaned per ewe), growth rate to slaughter age and the quality of the carcass produced under natural environmental conditions (Olivier & Cloete, 2006).

Against this background, the objectives of this study were to:

1. Determine the most suitable models for the estimation of variances and prediction of breeding values for subjectively assessed and objectively measured traits using both linear and threshold models in the Dorper sheep breed.
2. Determine variance components and heritability estimates of both subjectively assessed and objectively measured traits using both linear and threshold models.
3. Estimate covariance components and correlations amongst subjectively assessed and objectively measured live weight, average daily weight gain, and fitness traits using both linear and threshold models.
4. Determine across flock variance components, posterior density distributions and heritability estimates for live weight, reproduction and fitness traits in the Dorper sheep breed utilizing linear and threshold models.
5. Estimate relationships (genetic, maternal, phenotypic and environmental correlations) between stayability, live weight, average daily weight gain, reproduction (Number of Lambs Born per Ewe Lifetime, Number of Lambs Weaned per Ewe Lifetime, Times Lambed per Ewe Lifetime, Lambing Chances per Ewe Lifetime, Total Weaning Weight per Ewe Lambing), fertility, longevity, lamb survival to weaning and interlambing period using both linear and threshold model.
6. Estimate breeding values for live weight, reproduction and fitness traits and construct genetic trends over the years to assess genetic change in the Dorper sheep breed.

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CHAPTER 2

LITERATURE REVIEW

2.1 Introduction

The literature review explores the productive performance of the Dorper sheep breed under South African conditions. Breed standards as well as type scoring in the Dorper is visited. Methods of deriving genetic parameter estimates are discussed. Case studies of genetic parameter estimates for growth, reproduction and fitness traits in sheep are also considered. Finally a number of relevant issues pertaining to the planning of this study are also reviewed with the aim of exposing the gaps in the current knowledge.

2.2 Productive performance of the Dorper sheep breed

The Dorper breed was developed in the 1930's as a culmination of the need for a sheep breed suitable for the production of slaughter lambs under adverse arid environments in South African (Cloete *et al.* 2000). The initial need was to develop a sheep breed adapted to the harsh low rainfall areas of the Northern Cape Province. A relatively easy care sheep breed with an acceptable meat carcass from a slaughter lamb had to be bred for this adverse environment. The sheep breed had to have significant reproductive fitness with the capability to lamb in autumn and withstand extreme heat, radiation, cold and wind. With these objectives in mind, farmers in the Karoo began co-operative experiments. A number of different crosses were carried out initially until it was established that the cross between the Black Headed Persian and Dorset Horn outperformed the rest. The Black Head Persian was selected as the dam breed because of its outstanding adaptability to harsh environmental conditions. The Dorset Horn was selected as the sire breed because of its longer breeding season in comparison to other British sheep breeds and high mutton production (Cloete, 2000; Milne, 2000). The breed proved itself as a hardy mutton sheep with a top quality carcass at a relative early age. These characteristics resulted in the Dorper today being exported to other African countries, the Middle East, North America and Australia (Milne, 2000).

2.2.1 Reproductive performance of the Dorper sheep breed

There is a paucity of estimates for reproduction and fitness traits in meat sheep under South African production systems despite numerous comparable parameters from other parts of the world such as Australia and New Zealand. This is even more pronounced in the Dorper where no genetic parameter

estimates for these traits have been estimated. The only issues that have been tackled so far with regards to reproduction and fitness are least square means and repeatability estimates for reproduction (Cloete & De Villiers, 1987). The Dorper is considered to be an early-maturing sheep breed which achieves oestrous at younger ages of 213 days at a weight of 39 kg in comparison with Romanov ewes which attain puberty at 228 days and 28 kg respectively (Greeff *et al.*, 1988). During the foundation period Dorset Horn X Persian ewes attained puberty at 399.7 days with a range between 195 and 872 days (Joubert, 1962). Later work reported substantially younger ages at first oestrous. Subsequent figures by Schoeman *et al.* (1993b) were an age of 240 days, thus later than the figure reported by Greeff *et al.* (1988) and a live weight of 50.8 kg. Under an 8-monthly breeding cycle, Dorper ewes born in the autumn were reported to conceive for the first time at their first mating at an average age of 328 days and a live weight of 45.9 kg (Basson *et al.*, 1970). It was also concluded that Dorper ewes lambed for the first time at an average age of 19.6 months under an accelerated lambing system (Schoeman & Burger, 1992). Snyman (unpublished) also deduced that ewe fertility of 208 Dorper ewes mated to fertile rams at an age of 7 months was 0.58 with an average litter size of 1.16. Lamb survival (number of lambs weaned per ewe mated) averaged 0.79 and overall reproduction 0.53 in these ewes. It was also proven that Dorper rams are capable of fertilizing ewes from quite an early age because their sperm concentration increases significantly from 140 days of age (Skinner, 1971).

Fertility in the Dorper ewes compares fairly well with the Australian Merino of approximately 0.90 ewes lambed per lambing opportunity (Manyuchi *et al.*, 1991; Schoeman & Burger, 1992; Ackermann, 1993). The average length of the oestrous cycle in Dorper ewes is 17.3 days (Boshoff *et al.*, 1975). The duration of oestrus ranged from 28.0 to 35.1 hours in Dorper ewes depending on the interval between oestrus recordings (Joubert & Louw, 1964). The corresponding range in Dohne Merino ewes was 20.5 to 26.6 hours. In subsequent work, the average duration of oestrus was recorded at 36 h for mature Dorper ewes and at 28 h for primiparous ewes (Elias *et al.*, 1985). Dorper ewes give birth to an average litter size in the range of 1.45 to 1.60 (Buitendag, 1985; Cloete & De Villiers, 1987; Greeff *et al.*, 1990; Badenhorst *et al.*, 1991). However, it is crucial to take note that litter size of Dorper ewes was affected by ewe age, multiple birth rate increasing to an age of 4 to 6 years, followed by a tendency towards a decline (Cloete & De Villiers, 1987; Schoeman & Burger, 1992). Ewes born as multiples had a higher litter size than single contemporaries (Cloete & De Villiers, 1987; Schoeman & Burger, 1992). Gestation length in Dorper ewes ranges from 142 to 150 days and was shorter than woolled sheep when maintained together (Van Niekerk & Mulder, 1965). Dorper ewes have the capacity of weaning 0.99 to 1.40 lambs per ewe mated (Buitendag, 1985; Elias *et al.*, 1985; Cloete & De Villiers, 1987; Manyuchi *et al.*, 1991; Ackermann, 1993). The breed is capable of acceptable reproduction, even under harsh environmental conditions typical of the Karoo region in South Africa. There have not been any genetic evaluations for reproduction and fitness traits in the Dorper breed. Against this background, this study was conducted to derive genetic parameter estimates for reproduction, growth and fitness traits in the Dorper.

2.2.2 Live weight and growth performance of the Dorper

Selection objectives for South African meat sheep have centred on weaning weight (at around 100 days) and growth (Cloete *et al.*, 2000). There have not been numerous studies on genetic parameter estimates in the South African Dorper sheep breed except for those of Nesper *et al.* (2001) and Olivier & Cloete (2006). Further afield, Dorper, genetic and phenotypic parameters were estimated for lamb growth traits in semi arid Kenya using an animal model (Kariuki *et al.*, 2010). Data on lamb growth performance were extracted from available performance records at the Sheep and Goats Station in Naivasha, Kenya. However, Campbell (1989) demonstrated that there had been a significant increment in 100 day adjusted weaning weights in Dorper sheep during the period 1964 to 1988. This significant increment was not attributed to sound genetic improvements but rather to improvements in environmental conditions. Nesper *et al.* (1995) estimated genetic parameters for birth weight, 42-day weight and weaning weight for the Dorper flock at Glen Agricultural Institute.

Direct genetic responses to the selection for lamb weaning weight of Dorpers on natural pastures were comparatively slow in the only long-term selection experiment reported by Nesper *et al.* (1995), amounting to 0.087 kg per year (0.29 % of the phenotypic mean per year). Furthermore, a smaller gain (0.05 % of the phenotypic mean per year) was observed as far as maternal breeding values were concerned (0.016 kg per year). A regime of selection where ewe lambs were selected on weaning weight under pasture conditions and the 20 best ram lambs on weaning weight and post-weaning feedlot performance was far less effective for the genetic improvement of weaning weight than direct selection in both sexes (Nesper *et al.*, 1995). Direct genetic gains amounted to 0.030 kg per year (0.10 % per annum), with no change in maternal breeding values. Olivier & Cloete (2006) reported that the direct additive heritability (h^2) of weaning weight was 0.19. They also estimated for variance ratios of respectively 0.10 and 0.07 for maternal genetic effects (m^2) and dam permanent environmental effects (c^2). Growth traits considered by Kariuki *et al.* (2010) were body weights at birth, at 1 month, at 2 months, at weaning, at 6 months, at 9 months and at yearling, average daily gain from birth to 6 months and from 6 months to 1 year. Estimates of h^2 were, respectively, 0.18, 0.36, 0.32, 0.28, 0.21, 0.14, 0.29, 0.12 and 0.30. The corresponding (m^2) estimates for body weights up to 9 months were 0.16, 0.10, 0.10, 0.19, 0.21 and 0.18 respectively. Direct-maternal genetic correlations were negative and high ranging between -0.47 to -0.94. There is a need therefore, to estimate across-flock genetic parameters for live weight and growth traits in the Dorper sheep breed as well as constructing across-flock genetic trends to assess genetic change.

2.3 Dorper breed standards

Selective breeding goes back at least to Jacob during the biblical days around 1800 BC who selected the speckled fitter rams for his own flock. Traditional sheep breeding has largely relied on visual assessment

with many people involved in subjective assessment (referred to as classers) having considerable skill in recognizing genetic potential with respect to their objective, whether breeding war horses, dogs or pigeons (Gilmour, 2009). The South African Dorper Sheep Breeders Society adheres to specific breed standards that are used to indicate the degree of excellence of the sheep. The society assesses their sheep by means of a description and a score points relative to visual appearance which they claim to be correlated with actual animal performance. It has been reported that the society certifies and approves inspectors on a regular basis to judge sheep and capture the classing details on the registration record of the inspected sheep (DorperSA, 2011). For descriptive and comparative purposes Dorper sheep may be compared with each other according to a score card, and the following points are allotted, corresponding to the respective terms of the main sections of the standard of excellence (DorperSA, 2011), as depicted in Table 2.3.

Table 2.3 Dorper score card (DorperSA, 2011)

Very good	5 points
Above average	4 points
Average	3 points
Poor or below average	2 points
Very poor with cull points	1 point

2.3.1 Subjectively assessed traits in the Dorper

Traditionally, the breed development of the Dorper has been based on subjective assessment in the show ring with much less emphasis on objectively measured traits (Olivier & Cloete, 2006). The Dorper Breeders' Society is very strict to the adherence of mainly six standards of excellence namely: conformation, size or growth rate, distribution of fat, type, colour pattern and fleece cover (DorperSA, 2011). Despite a preliminary study having been undertaken by Olivier & Cloete (2006) in which they validated the need for further investigations, there is a paucity of information on the genetic basis of subjectively assessed traits and their correlations with objectively measured traits in the Dorper breed. Against this background, one of the objectives of this study was to extract live weight and average daily gain performance as well as subjectively assessed score data from the NSIS data base and estimate genetic parameters for all the recorded traits as well as computing genetic correlations between subjectively assessed and objectively measured traits. To shed more light into the Dorper breed subjective assessment, it is crucial at this point in time to give a brief description of the breed standards of excellence regardless of the possibility that many informed scientists might debunk their validity because

the only other source of their partial endorsement apart from the preliminary study by Olivier & Cloete (2006) comes from the Dorper Breeders' Society.

2.3.1.1 Conformation

According to the Dorper Breeders' Society (2011), I quote, "the head should be strong and long, with large eyes, widely spaced and protectively placed. The nose must be strong; the mouth must be strong and well-shaped with well-fitted deep jaws. The forehead must not be dished. The size of the ears must be in relation to the head. A developed horn base or small horns are the ideal. Heavy horns are undesirable but permissible. The head must be covered with short, dullish black hair in the Dorper and dull, white hair in the White Dorper. The head must be dry i.e. without indications of fat localisation. The neck should be of medium length, well-fleshed as well as broad and well-coupled to the forequarters. Shoulders should be firm, broad and strong. A moderate protrusion of the brisket beyond the shoulders, moderate width and good depth are the ideal. Forelegs must be strong, straight and well-placed with strong pasterns and hoofs not too widely split. Weak pasterns and X legs must be discriminated against according to degree. Shoulders which appear loose, a brisket which slants up too sharply with no projection beyond the shoulders, crooked legs and weak walking ability, are faulty. The ideal barrel is a long, deep, wide body, ribs well sprung, with the loin broad and full. The sheep must have a long straight back without a "devil's grip". A slight dip behind the shoulders is permissible. A long and wide rump is the ideal. The inner and outer twist has to be well fleshed and deep in adult animals. The hind legs must be strong and well-placed, with sturdy feet and strong pasterns. Faulty pasterns must be discriminated against according to degree. The hocks must be strong without a tendency to turn in or out. Sickie, bandy or perpendicular hocks are culling faults. A well-developed udder and sex organs are essential in the ewe. The scrotum of the ram should not be too long and the testicles should be of equal size and not too small. A split scrotum is undesirable. The sheep should be symmetrical and well-proportioned. A calm temperament with a vigorous appearance is the ideal."

2.3.1.2 Size or growth

The Dorper Breeders Society (2011) adheres to specific breed standards pertaining to size which can be quoted as, "a sheep with a good weight for its age is ideal. Discrimination against extremely small or extremely big animals must be exercised. It is recognized that the production capacity of larger animals during extreme conditions is compromised due to the burden of maintaining their body weight."

2.3.1.3 Distribution of fat

“Too much localisation of fat on any part of the body is undesirable. An even distribution of a thin layer of fat over the carcass as well as between the muscle-fibres is the ideal. The sheep must be firm and muscular when handled” (DorperSA, 2011).

2.3.1.4 Colour pattern

“Black-headed Dorpers are white sheep with black confined to the head and neck is the ideal. Black spots, to a limited extent on the body and legs are permissible, but an entirely white sheep or a predominantly black sheep is undesirable. Brown hair around the eyes, white teats, white under the tail and white hoofs are undesirable. White Dorpers are white sheep, with full pigmentation around the eyes, under the tail, on the udder and on the teats are the ideal types. A limited number of other coloured spots are permissible on the ears and underline” (DorperSA, 2011).

2.3.1.5 Cover or Fleece

“The ideal is a short, loose, light covering of hair and wool with wool predominating on fore quarter and with a natural clean kemp underline. Too much wool or hair is undesirable. Exclusively wool or hair is a fault” (DorperSA, 2011).

2.3.1.6 Type

“Type is judged according to the degree to which the sheep conforms to the general requirements of the breed. Emphasis is placed on conformation, size and fat distribution when determining type, while colour and covering are of secondary importance” (DorperSA, 2011).

2.4 Methods of deriving (co)variance components and ratios in animal breeding

Accurate genetic parameter and breeding value estimation for traits of economic importance is helpful to affect changes to quantitative traits to meet the ever-changing needs of consumers and breed societies. Improved statistical methods such as Restricted or Residual Maximum Likelihood (REML), advances in computer technology, hardware and software give animal breeders the capacity to re-evaluate genetic parameters to better define selection strategies for the modern market (Van Wyk *et al.*, 2003). The development of sophisticated computer software (Meyer, 1993; Groeneveld & Garcia-Cortes, 1998; Gilmour, 2002; Misztal *et al.*, 2002; Misztal *et al.*, 2008) has enabled estimation of additional variance

components and/ or the partitioning of animal variance into direct and maternal effects, animal and dam permanent environmental effects, litter effects as well as the correlation between direct and maternal genetic effects. Partitioning of the (co)variances enables the estimation of the contribution of each individual effect to the overall performance of the animal. This study aimed to estimate genetic parameters for live weight, growth, reproduction and fitness traits as well as their relationships with subjectively assessed traits in the Dorper sheep breed using both REML and Bayesian methods. Both Bayesian and Frequentist schools of thought are well established and software from both schools is available for scientists to obtain (co)variance components and ratios. Both schools have been thoroughly reviewed and further explained by Blasco (2001). It is therefore essential to briefly discuss and summarise both Frequentist and Bayesian methods as reviewed by Blasco (2001) because the output from them formed the backbone of this study.

2.4.1 Mixed models in animal breeding

Modern animal breeding is characterized by taking objective measurements on animals and adjusting for environmental effects (Gilmour, 2009). Henderson (1949) developed the renowned method of Best Linear Unbiased Prediction (BLUP) by which fixed effects and breeding values can be estimated simultaneously. BLUP has found widespread usage in genetic evaluation of domestic animals because of its desirable statistical properties. This has been enhanced by the steady increase in computing power and has evolved in terms of its application to simple models, such as the sire model, in its early years, and to more complex models, such as the animal, maternal, multivariate and random regression models, in recent years (Mrode, 2005). Advances in the digital age have been characterized by an increase in the number of traits included in the breeding objective, as well as the usage of data on relatives to improve the partitioning of random genetic effects from fixed environmental effects.

It has been highlighted by Schaeffer (1984) amongst other researchers that one of the main advantages of multivariate BLUP (MBLUP) is that it increases the accuracy of genetic evaluations. The gain in accuracy is dependent on the absolute difference between the genetic and residual correlations between the traits. The larger the differences in these correlations, the greater the gain in accuracy of evaluations (Schaeffer, 1984; Thompson & Meyer, 1986). When, for instance, the heritability, genetic and environmental correlations for two traits are equal, multivariate predictions are equivalent essentially to those from univariate analysis for each trait. Moreover, traits with lower heritabilities benefit more when analysed together with traits with higher heritabilities in a multivariate analysis. Also, there is an additional increase in accuracy with multivariate analysis resulting from better connections in the data due to residual covariance between traits (Thompson & Meyer, 1986). One of the disadvantages of a multiple trait analysis is the high computing cost. The cost of multiple analyses of n traits is more than the cost of n

single analyses. Secondly, a multiple trait analysis requires reliable estimates of genetic and phenotypic correlations among traits and these may not be readily available (Mrode, 2005).

Henderson *et al.* (1959) published the Best Linear Unbiased Prediction (BLUP) mixed model equations used to estimate genetic parameters and to derive resultant breeding values. Their development of these equations included implementation of the additive genetic relationship matrix, demonstrating how it accommodates selection as well as their primary role of adjusting for fixed effects, which as sometimes referred to as nuisance environmental effects. However, the mixed model equations assume knowledge of variance parameters. Henderson (1953) defined the main methods used to estimate these until Robin Thompson (Patterson & Thompson, 1971) introduced the Residual Maximum Likelihood (REML) method. Software to implement REML methods in animal breeding were subsequently developed and distributed by Karin Meyer and Dorothy Robinson (Gilmour, 2009). However, due to extensive iterative processes, analysis needed extensive computation power until the development of the Average Information method (underpinning the ASREML software program) which became generally available in 1997 (Gilmour, 2009). The application of mixed models through the implementation of REML procedures using software such as ASREML have spearheaded a revolution in quantitative genetic in the past couple of decades.

2.4.1.1 The Frequentist School

It has been reported in a review paper by Blasco (2001) that the frequentist school was pioneered in the 1930s and 1940s and was based on the foundation work of Karl Pearson and Ronald Fisher. The author also noted that the concept of likelihood and the method of Maximum Likelihood (ML) were developed by Fisher between 1912 and 1922 (Fisher, 1912; 1922), although there is historical evidence of inputs attributed to Bernoulli (1782, as translated by Kendall, 1961). In modern animal genetic evaluation exercises, the Frequentist school is mainly applied by solving numerous Mixed Model Equations (MMEs) using the concept of ML to estimate variance components and ratios. The ML procedure is characterized by complex equations that should be solved approximately by using iterative algorithms (Mrode, 2005). Different methods of solving MMEs which include direct inversion of the coefficient matrix, iteration of MMEs until convergence is achieved at a predetermined criterion were described by Mrode (2005). In recent years, REML has been the preferred method of animal breeders for variance component estimation.

2.4.2 The Bayesian methods in animal breeding

Bayesian methods in animal breeding were first introduced by Gianola & Foulley (1982) for the analysis of threshold traits. Gianola & Fernando (1986) highlighted additional possibilities associated with Bayesian

techniques in subsequent years. It has been reported by Mrode (2005) that Bayesian inference is more appropriate for the estimation of variance components and ratios for ordered categorical traits. However, it is possible to analyse categorical traits using linear methods with more advanced software such as ASREML (Gilmour *et al.*, 2002). During such analyses in ASREML, the multinomial ordinal function is invoked whereby the number of categories that are ordered on a gradient as well as the number of thresholds are declared. Furthermore, for binary traits, data are transformed on a logit or probit scale and the residual variance is fixed at an arbitrary value of 3.29 for the logit scale and 1.00 for the probit scale. It has however been reported by Gianola & Foulley (1982) that some principles BLUP do not hold when categorical traits are analysed using linear methods, hence the need to use alternative procedures such as Bayesian inference.

Amongst other workers such as Gianola & Foulley (1982) as well as Gianola & Fernando (1986), Pretorius & van der Merwe (2000) evaluated the application of Bayesian inference in animal breeding using the Elsenburg Dorper sheep data. They reported that this type of inference operates under a platform in which parameters are regarded as random variables possessing prior distributions reflecting the accumulated state of knowledge. This type of inference utilizes methods of inverse probability as described by Gianola & Foulley (1982). Pretorius & van der Merwe (2000) reported that in typical animal breeding problems, it is usually assumed that the data assumes a mixed linear model. When the values of the variance components are unknown, the routine approach to the challenge of predicting linear combinations of fixed and random effects has been to estimate the variance components using restricted maximum likelihood (REML), and to proceed thereafter as if these estimates were the true values. The same authors further stated that the Bayesian approach has several practical advantages over the classical (REML) approach. However, the purpose of this review is not to discuss the statistical theory related to these methods but to acknowledge their existence and highlight their possible application in solving animal breeding problems. Against this background, some of the objectives of this study were to demonstrate their use in solving animal breeding problems by utilizing both Bayesian and linear methods to estimate genetic parameters for subjectively assessed and objectively measured traits in the Dorper sheep breed. It was also intended to compare and contrast estimates obtained using REML and Gibbs sampling for growth, reproduction, fitness and subjectively assessed traits in the Dorper breed.

2.4.2.1 The Bayesian School

Blasco (2001) in a review of the Bayesian controversy in animal breeding reported that Stigler (1986) mentioned that Count Laplace was the founder of the Bayesian School. The author reported that in a Bayesian context, the objective is to use the principles of conditional probability and numerical intergration to draw inferences about the true value of some parameter basing on the given data. In simple terms the author described Bayesian inference as being driven by assumptions of conditional

probability. Bayes' theorem estimates population parameters by using the methods of inverse probability (Gianola & Fernando, 1986). For example Blasco (2001) demonstrated that if the parameter of interest is the heritability of a trait. Bayesian inference computes the probability density of the heritability on condition of the given the data, $f(h^2|\mathbf{y})$, where \mathbf{y} is the vector of observations (Figure 2.4.1). When this distribution is obtained, conclusions can be drawn in several ways: for example, one can calculate the probability of h^2 to be between 0.1 and 0.3, by integrating the function between these values. The shortest interval in which the probability of finding h^2 is more than 95% can be ascertained using the Highest Posterior Density (HPD) distributions. If we are interested in a point estimate, we can give several values of h^2 calculated from the distribution $f(h^2|\mathbf{y})$. The mode is the value that maximizes $f(h^2|\mathbf{y})$.

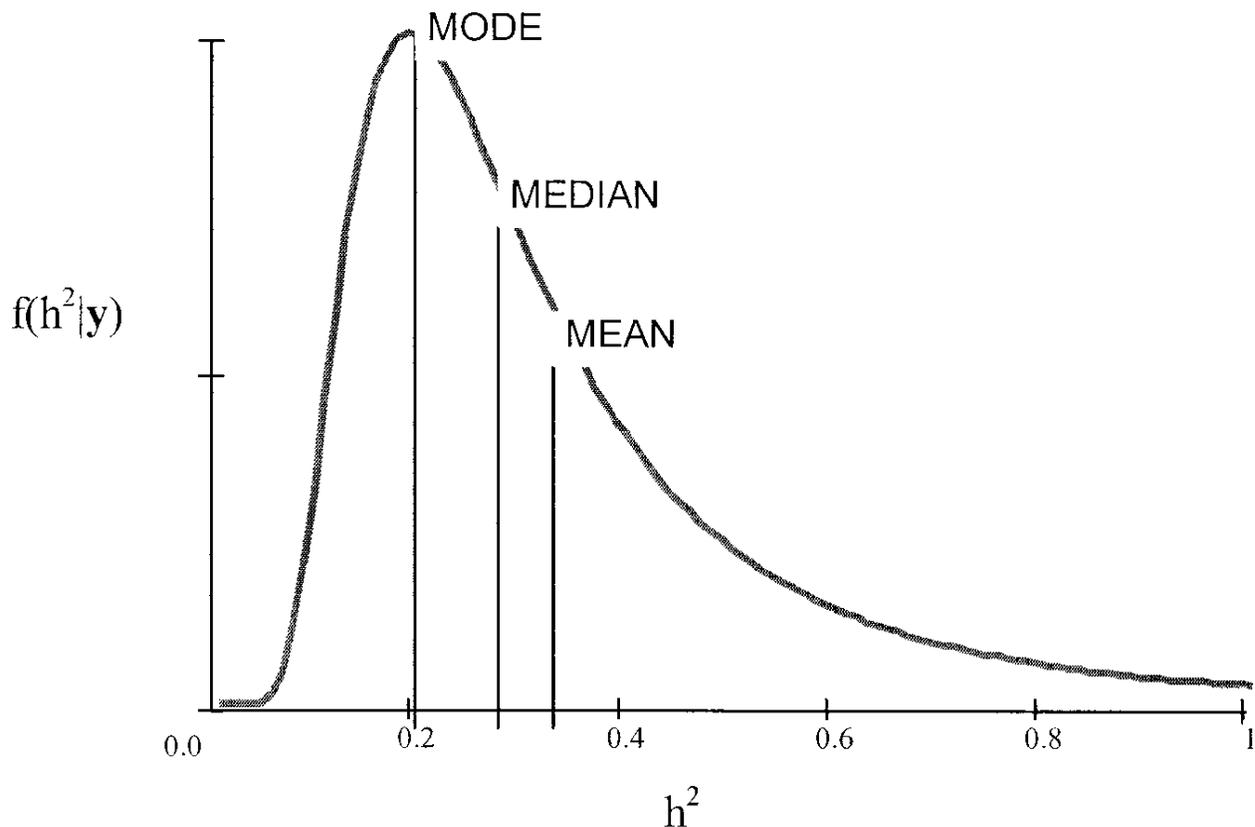


Figure 2.4.1 Example of a probability density for heritability (h^2) given the data (\mathbf{y}) and estimates from posterior distribution (Blasco, 2001)

In his review Blasco (2001), further highlighted the fact that the main difference between the two schools of inference lay in the use of prior information. The frequentist school produces inferences based on the data and prior knowledge of the distribution of estimators in the sampling space. Against this background, this study aimed to estimate genetic parameters for live weight, growth, reproduction and fitness traits as well as their relationships with subjectively assessed traits in the Dorper sheep breed using both REML and Bayesian methods.

2.5 Genetic parameters for subjectively assessed traits in South African sheep breeds

Development of effective genetic evaluation and improvement programs requires knowledge of genetic parameters from well-recorded populations for production traits of economic importance (Safari *et al.*, 2007). The recent compilation of genetic parameters in sheep (Safari & Fogarty, 2003), subsequently reviewed by Safari *et al.* (2005b) demonstrated that there was a dearth in literature estimates for subjective traits and their correlations with growth, reproduction and fitness traits. Commercial Merino breeders in South Africa frequently use subjectively assessed wool traits in selecting breeding sires and dams (Naidoo *et al.*, 2004). Linear type scoring was developed as a potential indicator of genetic and phenotypic indicators of production (Olivier *et al.*, 1987).

Subsequently it has been used to obtain data to determine phenotypic correlations between some subjectively assessed fleece traits and objective wool traits (Cloete *et al.*, 1992). There are only a few studies on genetic parameters of subjectively assessed traits and their correlations with production traits in South Africa (Snyman & Olivier 2002; Naidoo *et al.*, 2004; Olivier & Cloete, 2006; Matebesi *et al.*, 2009). The usage of subjective traits as breeding objectives without knowledge of their relationships with other economically important traits could be counter productive if correlations prove to be antagonistic. Knowledge of the genetic variation of visually assessed traits and their relationships with measured production traits will assist in the prediction of outcomes from breeding programs and is required for more accurate genetic evaluation of animals (Mortimer *et al.*, 2009). At the least, selection based on subjective traits could be ineffectual if genetic correlations are favourable but low. It is crucial at this juncture to state that apart from the work of Snyman & Olivier (2002) in the dual purpose Afrino sheep as well as the preliminary study by Olivier & Cloete (2006) which investigated the relationships between subjectively assessed and objectively measured traits in the South African Dorper sheep breed there is no other information for meat sheep. This paucity of information motivated the present study.

2.5.1 The relationship between subjectively assessed and objectively measured traits in the South African Dorper sheep breed

A preliminary study was conducted by Olivier & Cloete (2006) to compute the relationships between subjectively assessed and objectively measured traits in the Dorper sheep breed. The outcomes of this study are presented in Table 2.5.1. The genetic correlations between weaning weight (WW) and type traits varied from moderate for conformation (CONF) to very high and approaching unity (size). The very high genetic correlation between WW and size that they derived was expected due to the fact that the

animals were assessed shortly after weaning. Genetic correlations of type traits and post-weaning weight (PWW) were low for CONF and type and high for size. Both CONF and type were unfavourably correlated with total weight of lamb weaned (TWW). Olivier & Cloete (2006) highlighted their concern over the high standard errors of these estimates. On the other hand, size was positively correlated to TWW on the genetic level. Phenotypic correlations between traits were generally lower in magnitude than corresponding genetic correlations, but similar in sign. Oliver & Cloete (2006) attributed the slow genetic gains in Dorper production traits to over-accentuation of type traits and recommended the need for further investigations. Their conclusions motivated the current study.

Table 2.5.1.1 The relationships between subjectively assessed and objectively measured traits in a preliminary study by Olivier & Cloete (2006)

Trait	Correlation	Conformation	Size	Type
Weaning weight	Genetic	0.43±0.09	0.98±0.01	0.60±0.07
	Phenotypic	0.30±0.01	0.77±0.01	0.41±0.01
Post weaning weight	Genetic	0.12±0.16	0.71±0.09	0.19±0.16
	Phenotypic	0.12±0.01	0.42±0.01	0.19±0.01
Total Weaning Weight	Genetic	-0.51±0.28	0.30±0.24	-0.21±0.27
	Phenotypic	-0.04±0.02	0.08±0.02	-0.02±0.02

2.5.2 Correlations of subjective conformation traits with production and reproduction in Afrino sheep

It was important to review the correlations between subjectively assessed and objectively measured traits in the dual purpose Afrino sheep that were derived by Snyman & Olivier (2002). In their study they used data collected from the Carnarvon Afrino flock from 1986 to 1998, and included records of several subjectively assessed traits, body weight and fleece traits of 3291 animals, the progeny of 127 sires and 772 dams. The subjective conformation trait definitions as well as the scale definitions are depicted in Table 2.5.2.1. Reproduction data of 686 ewes born from 1986 to 1997 were also included. The heritabilities of and genetic and phenotypic correlations among the subjectively assessed traits were estimated, as well as genetic and phenotypic correlations of these traits with body weight, objective fleece traits and reproduction. Heritability estimates for the various subjectively assessed conformation traits ranged from 0.06±0.02 for straightness of the topline to 0.36±0.04 for hocks (Table 2.5.2.2).

Table 2.5.2.1 Linear scale for subjective assessment of conformation traits in Afrino sheep (Snyman & Olivier, 2002)

Subjective trait	Scale of Assessment		
	1	25	50
Conformation	Poor	Average	Ideal
General Head Conformation (HEAD)	Poor	Average	Ideal
Front Quarters (FRONT)	Poor	Average	Ideal
Top line (TOPL)	Poor	Average	Ideal
Hocks (HOCK)	Poor	Average	Ideal
Front Pasterns (FPAS)	Poor	Average	Ideal
Hind Pasterns (HPAS)	Poor	Average	Ideal

Table 2.5.2.2 Heritability estimates (diagonal, bold face) (s.e.) of, genetic (above diagonal) and phenotypic (below diagonal) correlations (s.e) among various subjectively assessed conformation traits (Snyman & Olivier, 2002)

	HEAD	FRONT	TOPL	HOCK	FPAS	HPAS
HEAD	0.32±0.04	0.80±0.06	0.33±0.18	0.42±0.09	0.15±0.12	0.14±0.16
FRONT	0.45±0.02	0.22±0.03	0.53±0.19	0.65±0.09	-0.04±0.13	-0.18±0.16
TOPL	0.11±0.02	0.11±0.02	0.06±0.02	0.64±0.16	0.18±0.20	0.10±0.25
HOCK	0.15±0.02	0.14±0.02	0.19±0.02	0.36±0.04	0.02±0.10	0.00±0.14
FPAS	0.04±0.02	0.04±0.02	0.04±0.02	0.01±0.02	0.21±0.04	-
HPAS	0.05±0.02	0.01±0.02	0.00±0.02	0.03±0.02	-	0.08±0.03

Positive genetic correlations, ranging from 0.33±0.18 to 0.80±0.06 were estimated amongst the conformation traits head, front quarters, top line and hocks (Table 2.5.3.2). The conformation traits had moderate to high phenotypic correlations with body weight at all ages. These were similar in sign, but smaller in magnitude than the corresponding genetic correlations. It was evident from the results that general conformation of the head, forequarters, hocks and pastern joints will not deteriorate in a selection program which has increased TWW and increased body weight as its aim. It was concluded that, with the exception of two or three traits, the subjectively assessed traits would not be negatively influenced when selection is based on the economically important production traits (Table 2.5.2.3). It was, however stressed that important selection priorities be based on economic values of the traits.

Table 2.5.2.3 Genetic correlations (s.e.) of reproduction (Total Weaning Weight (TWW), Number of Lambs Born (NLB) and Number of Lambs Weaned (NLW), body weight (weaning weight (WW), weight at 9 months (W9) and weight at 15 months (W15) and various subjectively assessed conformation traits (Snyman & Olivier, 2002)

	TWW	NLB	NLW	WW	W9	W15
HEAD	0.79±0.24	0.45±0.21	0.57±0.21	0.85±0.05	0.85±0.04	0.82±0.05
FRONT	0.88±0.35	0.47±0.31	0.27±0.35	0.70±0.08	0.81±0.05	0.87±0.04
TOPL	-0.42±0.36	-0.14±0.30	-0.34±0.30	0.30±0.21	0.37±0.18	0.49±0.18
HOCK	0.14±0.27	0.10±0.22	0.07±0.23	0.50±0.10	0.41±0.08	0.41±0.08
FPAS	0.20±0.32	0.12±0.27	0.11±0.27	0.25±0.14	0.17±0.11	0.09±0.09
HPAS	0.01±0.34	0.28±0.29	0.20±0.30	0.32±0.16	0.30±0.13	0.30±0.13

2.5.3 Relationships of subjectively conformation traits with objectively measured live weight traits in the Tygerhoek Merino flock

It has been previously reported by other workers that traditionally Merino sheep have been selected using a classing system that relied on visual differences, with a common belief that subjective traits were either an essential part of production or are correlated to qualitative or quantitative traits of economic importance (Cloete *et al.*, 1992; Lewer *et al.*, 1995). In reality, these traits are often regarded as important for the economic viability of sheep enterprises (Olivier *et al.*, 2006a) and were in some instances used exclusively for the selection and culling of breeding stock (Lewer *et al.*, 1995; Snyman & Olivier, 2002).

To investigate this further, Matebesi *et al.* (2009) utilized records of the Tygerhoek Merino resource flock to estimate genetic, phenotypic and environmental parameters between subjective wool and conformation traits with objective wool and live weight traits. However, only results for correlations between subjectively assessed conformation traits with live weight traits are reviewed due to their relevance to the current study. The database contained records of 4 495 animals, the progeny of 449 sires and 1 831 dams, being born from 1989 to 2004. Based on genetic correlations (r_g) live weight was favourably related to general head conformation (GEN) (0.67), conformation of the hind legs (HOCKS) (0.36), conformation of the front legs (FQ) (0.42), topline (TOPL) (0.25) and total fold score (TOT) (Table 2.5.3.1). The genetic correlations between subjective conformation traits and live weight were moderate to high and variable in sign. It was evident from the results that heavier Merino sheep at Tygerhoek were generally plainer and had better scores for GEN, HOCKS and FQ as well as for TOPL, as suggested by significant genetic correlations between these traits.

Table 2.5.3.1 Genetic, phenotypic and environmental correlations between live weight and subjectively assessed traits in the Tygerhoek Merino flock (Matebesi *et al.*, 2009)

Live weight			
	Genetic	Phenotypic	Environmental
Pastern Score	0.18±0.10	0.04±0.02	-0.01±0.03
Head general	0.67±0.05	0.55±0.01	0.45±0.03
Hocks	0.36±0.07	0.28±0.02	0.25±0.03
Front Quarters	0.42±0.09	0.29±0.02	0.28±0.03
Topline	0.25±0.10	0.21±0.02	0.21±0.03
Total Fold Score	-0.23±0.07	0.00±0.02	0.14±0.03

The genetic correlation between live weight and Pastern Score (PS) was also favourable but not significant. Previous studies on South African Merino sheep reported comparable genetic correlations of -0.24 and -0.26 between LW and TOT (Cloete *et al.*, 1998; 2005). These correlations are regarded as favourable in view of plainer genotypes being preferred in South Africa at present, as well as the well-known favourable genetic relationship of between wrinkle score and reproduction (Atkins, 1980). A corresponding favourable correlation (0.67) of LW with FQ was also reported for Cradock fine wool Merino sheep (Olivier *et al.*, 2006b). Phenotypic correlations for live weight and conformation traits were low to high and variable in sign. Comparable estimates of phenotypic correlations were found in the literature for specific traits in Merino (Lewer *et al.*, 1995; Cloete *et al.*, 1998; Olivier *et al.*, 2006a; b) and Afrino sheep (Snyman & Olivier, 2002). Corresponding environmental correlations were also low to high and comparable in sign. In general, the phenotypic and environmental correlations of LW and objective wool traits with conformation traits were similar in sign but lower in magnitude.

2.6 Genetic parameters for objectively measured growth traits in meat sheep

Fogarty *et al.* (1994) suggested that biological and economic efficiency can be increased more through genetic selection for improved reproductive rate than by improving growth rate or body composition. Profitability of sheep production for meat depends to a great extent on lamb weight, so selection objectives concentrate on this trait. Genetic parameters are needed to estimate breeding values and compare responses from different selection programs (Tosh & Kemp, 1994). Early lamb growth not only results in the production of good quality carcasses, but also in a shorter production cycle and the ability to maintain a larger ewe flock (Olivier, 1999). One way to increase meat output or achieve rapid growth and heavy market weight is by using terminal sire breeds (Mousa *et al.*, 1999). Precise genetic parameters

are needed to estimate breeding values and to compare responses from different selection programs. Breeding objectives for South African sheep enterprises are becoming increasingly complex partly due to fluctuations in meat and wool prices. The increasing economic value of meat relative to wool means that more traits are contributing to the overall objective and profit of the diverse sheep enterprises. The increased value of meat also enhances the importance of reproduction traits both in Merino and maternal meat breeds (Safari & Fogarty, 2003). In order to achieve greater meat production, other traits such as live weights, growth, reproduction and survival among many will also determine the quantity of meat that is produced. Therefore, breeding objectives need to be changed when the major focus shifts from wool to meat. Furthermore, the dynamics of the sheep industry across the globe have impacted greatly by increasing the demand for dual purpose breeds.

Safari & Fogarty (2003) demonstrated that there is a plethora of literature estimates for variance ratios for production traits and correlations among traits in different sheep breeds. These estimates are a consequence of the rapid evolution of sheep improvement schemes as well as advances in statistical techniques, computer software and hardware which has enabled large data sets to be manipulated and analyzed in a fast, logical and effective way. This study aims to estimate genetic parameters for live weight and average daily weight gain from weaning to yearling age, as well their correlations with subjectively assessed traits as well as reproduction and fitness traits in the Dorper sheep. It is thus relevant to give an overview of literature values for genetic parameter estimates of live weight and growth traits in meat sheep breeds so as to establish benchmarks for the current study.

Literature estimates reported by Safari & Fogarty (2003), and subsequently summarized by Safari *et al.* (2005b). Several workers across the globe have estimated genetic parameters for growth traits in meat sheep. Tosh & Kemp (1994) partitioned genetic variation of the Hampshire and Polled Dorset sheep breeds into additive direct and maternal effects as well as their correlation. The workers derived direct heritability estimates for weaning weight that ranged from 0.16 to 0.39 between 50 and 100 days. The direct maternal effects that they derived were in the range of 0.08 to 0.19. In both breeds dam permanent environmental effects ranged from 0.18 to 0.27. The correlation between additive direct and maternal effects was negative moderate to high in both cases. Other workers partitioned genetic variation of weaning weight in the Suffolk breed reasonably (Rao & Notter, 2000; Maniatis & Pollot, 2002a, b; Simm *et al.*, 2002). It has also been established in various meat breeds that the heritability of post weaning weight from an age range between 146 days up to 12 months varies from low to high (Atkins *et al.*, 1991; Brash *et al.*, 1992; Gilmour *et al.*, 1994; Janssens *et al.*, 2002; Maniatis & Pollot, 2002a, b; Simm *et al.*, 2002). Some of the previously cited workers also reported significant maternal and dam permanent environmental effects during the post weaning period. Moderate to high direct heritability estimates of hogget weight from an age range between 14 and 31 months in meat sheep were derived by Mousa *et al.* (1999) as well as some of the previously cited workers. Moderate to high direct heritability estimates for

growth assessed as average daily weight gains between various ages have been derived in various meat sheep breeds (Maria *et al.*, 1993; Notter & Hough, 1997; Yazdi *et al.*, 1997; Mousa *et al.*, 1999; Rao & Notter, 2000; Matika *et al.*, 2003). However, low heritability estimates for average daily gains at various stages have also been derived (Van Wyk *et al.*, 1993b; Hall *et al.*, 1995; Bromley *et al.*, 2002). It has also been established in the previously cited literature that there are positive genetic, phenotypic and environmental correlations between live weights and growth trait in various meat sheep breeds. It should be stressed that the variance components and ratios that have been derived depended on the models that were fitted.

In their review of genetic parameter estimates, Safari *et al.* (2005b) concluded that the weighted means of heritability for growth traits were moderate to high in magnitude and ranged from 0.15 to 0.41 with very low standard errors (range 0.01–0.04) of the means. They also noted that heritability increased with age to post weaning and adult weights. There was a tendency for the mean heritabilities to be higher for the wool breeds than for dual-purpose and meat breeds at all ages. The mean coefficient of variation was greater among meat breeds than dual-purpose and wool breeds for birth and weaning weight, but this trend was reversed for post weaning and adult weights.

The correlations among growth traits in meat sheep breeds have been reported by Safari & Fogarty (2003). Genetic correlations among weights were inversely proportional to the interval between weight records, with very high correlations (approaching unity) often reported for adjacent weights. Phenotypic correlations were generally slightly lower than the corresponding genetic correlations. The genetic correlations among weaning, post-weaning and adult weights were very high and ranged from 0.75 to 0.93 (Safari & Fogarty, 2005b). Growth rate was highly correlated with weaning weight on the genetic level. The weighted mean genetic and phenotypic correlations reported in the review by Safari *et al.* (2005) were remarkably similar to those previously reported by Fogarty (1995).

Safari & Fogarty (2005) further articulated that the wide confidence intervals generally found for the genetic correlations reflect the variation between different studies. There is a need for more estimates of these genetic correlations from larger data sets and for models that included maternal components. In view of the literature estimates that have been given for growth traits so far, it is crucial to mention that selection for growth is important to enable the shortening of the production cycle. Growth under natural production environments can also be accepted as an indication of adaptability, particularly in the adverse South African environment (Olivier, 1999). In conclusion, it is worth mentioning that the development of efficient breeding programs, that consider the hierarchical structure of breeds and the flow of genetic improvement through the industry, requires knowledge of genetic variability in, and genetic correlations among, the important traits (Brash *et al.*, 1994).

2.7 Genetic parameters for reproduction in sheep

Reproduction is a complex composite trait influenced by many components including puberty, ovulation, estrus, fertilization, embryo implantation, pregnancy, parturition, lactation, and mothering ability (Snowder, 2007). The genetic effect on each component of reproduction varies (Safari *et al.*, 2005b). Although component traits of reproduction are under the influence of many genes, a limited number of major genes associated with separate components of reproduction have been reported in sheep (Piper & Bindon, 1982; Bradford *et al.*, 1986; Davis *et al.*, 1991). Reproduction and survival rate are the most important factors determining the efficiency of lamb production (Snyman *et al.*, 1997). Falconer & Mackay (1996) demonstrated that several components influence ewe productivity and that each of these components can potentially be used as a selection criterion, as each has a direct impact on total ewe productivity. One of the main objectives in the South African sheep industry is improved ewe productivity. This could be accomplished in part by increasing the number of lambs weaned and weight of lambs weaned per ewe per year (Cloete *et al.*, 2002). Until recently, emphasis has mostly been placed on the individual component traits of reproduction such as fertility, litter size, lamb survival rate and the number of lambs born and weaned per ewe joined (which are composite traits in themselves). Ewe productivity, defined as the number or total weight of lamb weaned per ewe joined, which comprises of several component traits has received much less attention (Fogarty, 1995) and only a few genetic parameter estimates are available.

The 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. There is relatively large phenotypic variation in total weight of lamb weaned regardless of the reproductive rate of the flock (Snyman *et al.*, 1997). Selection for total weight of lamb weaned would result in a correlated genetic increase in weaning weight of individual lambs (Olivier *et al.*, 2001). 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 the growth potential of the lamb (Snyman *et al.*, 1997). Genetic improvement of reproductive performance could be achieved either by direct selection for a composite trait (total weight of lamb weaned) or by indirect selection for one of the component traits. It is important to determine whether direct selection for total weight of lamb weaned per ewe joined is more efficient than selection for number of lambs born, number of lambs weaned or weaning weight (Olivier *et al.*, 2002). Against this background this study aimed to estimate genetic parameters for reproduction traits in the Dorper sheep breed as well as their correlations with some fitness traits such as lamb survival to weaning, fertility and stayability. It is therefore essential to review genetic parameters for reproduction traits in sheep

Safari *et al.* (2005b) thoroughly explored and reviewed a substantial amount of reproduction literature and came to the conclusion that mean weighted heritabilities of reproduction traits are generally low. Prior to the former workers review several workers had established low heritability estimates for Number of Lambs Weaned per Ewe Joined (NLW/EJ) in various sheep breeds (Brash *et al.*, 1994d; Hanford *et al.*, 2002; Rosati *et al.*, 2002; Matika *et al.*, 2003). Similarly, low heritability estimates had been derived for Number of Lambs Born per Ewe Joined (NLB/EJ) (Brash *et al.*, 1994d; Fogarty *et al.*, 1994; Hansen & Shrestha, 1997; Hanford *et al.*, 2002; Hansen & Shrestha, 2002; Rosati *et al.*, 2002; Matika *et al.*, 2003; Van Vleck *et al.*, 2003). The Number of lambs weaned per ewe lambing has been confirmed to be low (Van Haandel & Visscher, 1995; Bromley *et al.*, 2000; Rosati *et al.*, 2002; Matika *et al.*, 2003). Other traits of reproduction that were confirmed to have low heritability by these and other workers were litter size; ewe rearing ability fertility and lamb survival. It should be stressed that despite significant amounts of work having been conducted on reproduction of meat sheep, not much work has been done for the Dorper sheep breed. These and other factors motivated this study.

In the review by Safari *et al.* (2005b), the means for number of lambs born (0.10 ± 0.01), number of lambs weaned (0.07 ± 0.01) and weight of lamb weaned (0.13 ± 0.03), all per ewe joined and for the same traits per ewe lambing (0.13 ± 0.01 , 0.05 ± 0.01 and 0.11 ± 0.02 , respectively) as well as ewe fertility (0.08 ± 0.01), ewe rearing ability (0.06 ± 0.02) and lamb survival (0.03 ± 0.01) were very close to the means reported by Fogarty (1995). The coefficients of variation for the heritability estimates were generally high. They further on reported that very few reproduction traits reported estimates for maternal effects. Generally, the animal permanent environmental effects for reproduction traits were lower than direct heritability with the exception of embryo survival and ewe rearing ability. The preferred model for the analysis of reproduction traits included both direct genetic and animal permanent environmental effects (this refers to repeatability models). Multivariate analysis is preferred to the repeatability model due to an increase in variance components (genetic and environmental) from first to third litters (Safari *et al.*, 2005b), if sufficient data is available.

Safari *et al.* (2005b) subsequently elaborated in their review that there was a very high weighted mean genetic correlation (0.84) between the number of lambs weaned and the number of lambs born on a per ewe joined basis. The genetic correlations for weight of lamb weaned (per ewe joined) with number of lambs weaned (0.80) was higher than with the number of lambs born (0.60), suggesting that the number of lambs weaned and weight weaned are genetically similar traits in meat sheep. The phenotypic correlations between these traits were also very high (0.59–0.93). The number of lambs born per ewe joined was highly correlated with both its components, lambs born per ewe lambing or litter size (genetic 0.89, phenotypic 0.80) and fertility (genetic 0.79, phenotypic 0.72). These correlations were higher than those for number of lambs weaned per ewe joined with litter size (genetic 0.62, phenotypic 0.46) and fertility (genetic 0.73, phenotypic 0.54). There were moderately high correlations between number of

lambs weaned per ewe joined and its other component ewe rearing ability (genetic 0.63, phenotypic 0.76). Ewe fertility was moderately genetically correlated with both ewe rearing ability (0.44) and litter size (0.44), although the phenotypic correlations were close to zero. On the other hand litter size had a small negative genetic correlation with ewe rearing ability (-0.14). Fertility in ewes and scrotal circumference in rams have been reported to have a genetic correlation of 0.20 (Fossceco & Notter, 1995).

The genetic correlations between reproduction traits were generally highly variable because the traits having generally low genetic variation ratios, and they were generally higher than the phenotypic correlations which were more uniform (Safari *et al.*, 2005b). This may be due to breed differences, modeling and data structure used to estimate the parameters. Accurate estimation of genetic correlations requires very large numbers of individuals of known parentage with data on both traits. These weighted mean genetic and phenotypic correlations among reproduction traits were similar to those reported by Fogarty (1995). Safari & Fogarty (2005b) also reported that reproductive traits were moderately positively correlated with reproductive traits

2.8 Genetic parameters for lamb survival in sheep

Haughey (1991) noted that decreased and variable lamb survival is generally considered a major constraint to efficient sheep production. The Australian Merino industry has reported that 90-95% of the pre-weaning deaths occur between birth and weaning whilst ante-natal and parturient deaths account for 5-10%, depending on the breed (Kilgour, 1992; Kleemann & Walker, 2005). Given the complexity of lamb survival and the extensive Merino production systems in Australia, selecting sheep with a genetic propensity for lamb survival is a very beneficial and desirable option. Including lamb survival in the breeding objective offers a permanent low-cost solution provided there is genetic variation and effective selection criteria are developed with favourable correlations with survival (Hatcher *et al.*, 2010).

It has been demonstrated that genetic improvement of reproduction has typically focused on selection for the ability of ewes to rear multiples (Atkins, 1980; Cloete & Scholtz, 1998; Cloete *et al.*, 2004). Be that as it may, improvements in lamb survival are unlikely if litter size is increased through selection with disregard to whether the additional lambs can be successfully reared (Lindsay, 1982) as multiple born lambs are more likely to die than singles (Hatcher *et al.*, 2009). When determining the contribution of genetic variation to lamb survival, it is of paramount importance to consider the direct genetic effect due to the genes of the lamb and the maternal effect of the dam, which has genetic and environmental components (Bradford, 1972).

Direct heritability of survival in Merino sheep, or lamb viability, has been reported to be very low (Piper & Bindon, 1977) with low estimates reported in other breeds (Barwick *et al.*, 1990; Gama *et al.*, 1991;

Lopez-Villalobos and Garrick, 1999; Morris *et al.*, 2000; Safari *et al.*, 2005a; Riggio *et al.*, 2008). Most reports on the maternal component of survival, or ewe rearing ability, suggest that it may be greater than the direct genetic effect (Lopez-Villalobos & Garrick, 1999; Morris *et al.*, 2000; Riggio *et al.*, 2008), but not all concur (Barwick *et al.*, 1990; Burfening, 1993) due to differences in analytical techniques and models. More recently it has been suggested that genetic variation in lamb viability is influenced by lamb age with estimates declining with time after birth (Southey *et al.*, 2001; Sawalha *et al.*, 2007; Riggio *et al.*, 2008).

Cloete *et al.* (2009) reported that studies on the potential genetic improvement of lamb survival have found limited genetic variation (Snyman *et al.*, 1998b; Lopez-Villalobos & Garrick, 1999). The lack of genetic variation has led to recommendations that the improvement of lamb survival should rather be based on modification of the environment to create conditions suitable for survival of lambs (Morris *et al.*, 2000; Everett-Hincks *et al.*, 2005). However, contrary to that, Cloete *et al.* (2009) noted that some previous studies suggested differences between lines within breeds that were brought about by selective breeding (Haughey, 1983; Knight *et al.*, 1988). Gudex *et al.* (2005) more recently reported significant variation in survival of the progeny of respective sires. Other scholars have also postulated that it would be fruitless to study lamb mortality without considering lamb birth weight (Morris *et al.*, 2000; Gudex *et al.*, 2005).

In view of all the things that have been said and done pertaining to lamb survival, it was judicious to review some specific case studies amongst the available few that have investigated genetic parameters for lamb survival to provide background for the current study.

2.8.1 Genetics of lamb survival in Australian Merino sheep

Direct and maternal components of variance for lamb survival to birth, 7 days, and weaning (110 days) were estimated by REML procedures in a flock of Australian Merino sheep (Hatcher *et al.*, 2010). A total of 14,142 lambs descendent from 421 sires and 3,666 dams, between 1975 and 1983 were available for analysis. The study derived some of the most precise and fascinating estimates of genetic parameters for lamb survival in the Australian Merino. Very low heritabilities for lamb viability (0.03) and the performance of the dam or ewe rearing ability (0.07) suggested that genetic improvement in lamb survival were unlikely to be significant (Table 2.8.1.1). However, despite the low heritabilities, the researchers reported that there was still potential for improvement through selective breeding.

This study evaluated lamb survival to weaning in the Dorper breed as defined by the ability of ewes to rear progeny up to weaning (ewe rearing ability). Likewise, it has been demonstrated in Merino sheep that maternal genetic effects (ewe rearing ability) were more important than direct genetic effects (lamb viability) for cumulative lamb survival at birth, 7 d of age, marking and weaning, and for survival between

1 and 7 d of age of those lambs that survived birth. Whereas that result was consistent with earlier work using other breeds of sheep (Burfening, 1993; Lopez-Villalobos & Garrick, 1999; Sawalha *et al.*, 2007; Maxa *et al.*, 2009). However, few previous studies have further partitioned the maternal effects to separate the permanent environment component (Morris *et al.*, 2000; Southey *et al.*, 2001; Cloete *et al.*, 2009). The estimated repeatability of at least 0.10 demonstrated that multiple records on the rearing ability of a ewe over its lifetime can increase selection accuracy. More essentially, such repeatability estimates indicated that current generation improvement can be achieved by culling ewes from the breeding flock with poor rearing ability. A summary of their findings are presented in Table 2.8.1.1.

Table 2.8.1.1 Estimates of direct and maternal heritability and dam repeatability for lamb survival reported by Hatcher *et al.* (2010)

Trait	Direct heritability	Maternal heritability	Dam repeatability
Survival within time periods			
1 to 7 d	0.022±0.010	0.045±0.017	0.120±0.011
7 to 110 d	0.053±0.014	0.029±0.016	0.060±0.013
Cumulative survival from birth to			
1 d	0.035±0.011	0.066±0.018	0.140±0.012
7d	0.028±0.010	0.040±0.017	0.147±0.011
30d	0.020±0.010	0.048±0.017	0.129±0.011
110d	0.027±0.010	0.034±0.015	0.110±0.011

2.8.2 Genetic parameters for lamb survival in a Merino flock divergently selected for multiple rearing ability using the Gibbs sampler

Cloete *et al.* (2009) analyzed data from about 7 generations of 5,390 Merino lambs born from 1986 to 2007 to estimate genetic parameters for age-specific and overall lamb survival on the underlying scale using Gibbs sampling through the THRGIBBSF90 and POSTGIBBSF90 software (Misztal *et al.*, 2002). Analyses included the covariance between direct and maternal genetic effects, except where it was not estimable owing to small direct additive variance components, a high incidence of lambs surviving, or both. Direct heritability estimates were 0.02 for lamb survival at birth, 0.12 for lamb survival from birth to tail docking, 0.39 for lamb survival from docking to weaning, and 0.28 for overall lamb survival. Corresponding estimates for the maternal genetic effect were 0.26, 0.14, 0.16, and 0.14. Dam permanent environmental variance ratios were, respectively, 0.14, 0.09, 0.05, and 0.07. Estimates of the direct-maternal genetic correlation were -0.60 for lamb survival from docking to weaning, -0.61 for overall lamb survival, and -0.15 to -0.23 for birth weight. Table 2.8.2.1 depicts a summary of their findings.

Elaboration of the results further indicates that the estimate of h^2 for survival at birth on the underlying scale was small and not significant at 0.02 ± 0.05 ($P > 0.10$; Table 2.8.2.1). In contrast, both maternal components were significant at 0.26 for m^2 and 0.14 for c^2 . The direct additive variance component for survival from birth to tail docking (Table 2.8.2.1) on the underlying scale approached significance ($P < 0.10$), with 90% HPD confidence intervals of 0.025 and 0.350. Estimates of m^2 and c^2 were greater than double the corresponding SE at 0.14 and 0.09, respectively. Derived 95% HPD confidence intervals for variance ratios for lamb survival from tail docking to weaning included zero in all instances (Table 2.8.2.1). However, 90% HPD confidence intervals excluded zero in all cases, being 0.007 and 1.415 for additive effects, 0.007 and 0.565 for maternal genetic effects, and 0.002 and 0.169 for dam permanent environmental effects. The absolute value of the estimate of h^2 was fairly high, at 0.39. Comparatively smaller maternal variance ratios were found, namely 0.16 for m^2 and 0.05 for c^2 . The direct-maternal correlation was high at -0.60 for survival from docking to weaning, but the 90% HPD confidence intervals for the direct-maternal covariance component included zero and were -0.574 and 0.024 , respectively. Point estimates (\pm SE) for overall lamb survival were 0.28 ± 0.12 for h^2 , 0.14 ± 0.06 for m^2 , 0.07 ± 0.03 for c^2 and -0.61 ± 0.35 for the direct-maternal correlation (Cloete *et al.*, 2009). These estimates on the underlying scale are considerably greater than the bulk of comparable literature values. Sixteen literature estimates for h^2 of overall lamb survival averaged 0.03 (Safari *et al.*, 2005b). The estimates obtained by in this study were higher than literature estimates because a threshold model was utilized whereas in most literature estimates linear methods using link functions such as logit and probit were used to link binomially distributed lamb survival to the normal distribution (Cloete *et al.*, 2009).

Table 2.8.2.1 Mean (co)variance components, posterior SD (PSD), 95% highest posterior density (HPD) confidence intervals and variance ratios for lamb survival as reported by Cloete *et al.* (2009)

	(Co)variance		95 % HPD confidence interval			
Trait and item	Component	PSD	Lower	Upper	Item	Ratio \pm SE
Survival at birth on the underlying scale						
σ_A^2	0.026	0.087	-0.145	0.197	h^2	0.02 \pm 0.05
σ_M^2	0.442	0.196	0.058	0.825	m^2	0.26 \pm 0.11
σ_{AM}	NA	NA	NA	NA	r_{AM}	NA
σ_C^2	0.243	0.116	0.015	0.471	c^2	0.14 \pm 0.07
σ_E^2	1.003	0.028	0.949	1.057		
Lamb survival from birth to docking on the underlying scale						
σ_A^2	0.187	0.099	-0.007	0.382	h^2	0.12 \pm 0.06
σ_M^2	0.214	0.073	0.070	0.358	m^2	0.14 \pm 0.05

σ_{AM}	NA	NA	NA	NA	r_{AM}	NA
σ_C^2	0.131	0.061	0.012	0.251	c^2	0.09±0.04
σ_E^2	1.004	0.028	0.950	1.058		
Lamb survival from docking to weaning on an underlying scale						
σ_A^2	0.711	0.429	-0.129	1.552	h^2	0.39±0.23
σ_M^2	0.286	0.170	-0.046	0.619	m^2	0.16 ±0.09
σ_{AM}	-0.272	0.184	-0.633	0.090	r_{AM}	-0.60 ± 0.40
σ_C^2	0.086	0.051	-0.013	0.184	c^2	0.05 ±0.03
σ_E^2	1.004	0.029	0.948	1.060		

2.8.3 Threshold model analysis of lamb survivability in Romney sheep in New Zealand

Welsh *et al.* (2006) utilized flock data that were obtained from Landcorp Farming Limited and comprised two New Zealand Romney flocks with lambs born from 1997 to 2000. The Waihora flock was located on the western shore of Lake Taupo and the Lynmore flock was located in the Te Anau basin in the South Island. The objectives of the study were to estimate variance components for direct, maternal, and permanent environmental components of lamb survivability. Threshold model procedures were used to estimate variance components from 25 362 lamb survival observations representing 136 sires and 9894 dams, with four sires common to both flocks. The four sires were represented in both flocks in one year and in only one flock in another year. A three-generation pedigree was created using parental information. The final pedigree file consisted of 35 261 individuals, with 34 290 having known sires and 34 570 having known dams. Lamb survivability scores were created according to the recorded presence of the lamb at weaning. If a lamb had a weaning weight, it received a score of 1. If a lamb did not have a weaning weight, it was assumed not to have survived and received a score of 0. There were 5866 scores of 0 and 25 261 scores of 1. Lynmore had 11 516 lamb records during the study period and Waushara had 19 611. A Method \mathfrak{R} procedure was used in the context of maximum *a posteriori* (MAP) procedures appropriate to threshold models (Gianola & Foulley 1983). The MAP-Method \mathfrak{R} approach provided estimates of direct, maternal, and permanent environmental components of lamb survivability (Reverter *et al.* 1994; Snelling *et al.* 1995). Table 2.8.3.1 summarizes their findings.

Median heritabilities were 0.106 ± 0.010 for direct, 0.082 ± 0.005 for maternal, and a median proportion of phenotypic variation 0.098 ± 0.003 for permanent environmental effects. The direct-maternal correlation was -0.75 ± 0.03 . The relatively low heritability estimates for direct and maternal lamb survivability were expected and consistent with other reported estimates (Welsh *et al.*, 2006). However, they were higher than the estimates reported by Lopez-Villalobos & Garrick (1999) and the maternal estimate was higher than that reported by Everett-Hincks *et al.* (2002).

Table 2.8.3.1 Summary of genetic parameter estimates for lamb survivability in New Zealand Romney sheep obtained using a threshold model as reported by Welsh *et al.* (2006)

	h^2	m^2	r_{am}	c^2
Median	0.106	0.082	-0.754	0.098
SE	0.00986	0.00467	0.03122	0.00250
Minimum	0.011	0.003	-0.984	0.061
Maximum	0.409	0.229	0.206	0.152

2.9 Genetic analysis of ewe stayability

Stayability is defined as the probability of survival to a specific age, given the opportunity to reach that age (Hudson & Van Vleck, 1981) and reflects underlying fitness characteristics that cause removal of breeding animals from the flock. Genetic variation in stayability has been identified in dairy (Van Vleck, 1980) and beef cows (Snelling *et al.*, 1995) and swine (Lopez- Serrano *et al.*, 2000), but few studies have addressed genetic control of stayability in sheep (Brash *et al.*, 1994; Conington *et al.*, 2001). Stayability is typically measured as a binary trait and has been evaluated with linear and threshold models (Borg *et al.*, 2009). Stayability has been studied in dairy and beef cattle (Jairath *et al.*, 1998; Maiwashe, 2009). However studies on stayability in sheep are very rare in literature.

Stayability is an economically relevant trait due to its direct relationship with profitability of the production system. Increased stayability is associated with a reduction in annual cost of the replacement of ewes, increased flock production and an increase in voluntary culling. Stayability of individual ewes can only be assessed after the ewe leaves the flock, and, in extensive production systems, detailed information about time of ewe removal may be limited. Incorporation of associations between stayability and other traits in multiple-trait evaluations could improve accuracy (Borg *et al.*, 2009). Against this background one of the many objectives of this study was to estimate genetic parameters for stayability in Dorper sheep as well as its correlations with other production and reproductive traits. In order to be in a position to debate parameter estimates obtained in the current study, the groundbreaking study by Borg *et al.* (2009) is reported.

Borg *et al.* (2009) carried out a genetic evaluation of the Targhee sheep breed using data from 12 154 sheep born between 1960 and 2005 at Montana State. Stayability data were available for ewes born between 1960 and 2002 and included 2 525 ewes from 183 sires and 1 498 dams using the MTDFREML

program (Boldman *et al.*, 1995). The variance components that they derived using single trait analyses are presented in Table 2.9.1.

Table 2.9.1 Variance components for ewe stayability using single-trait analyses as reported by Borg *et al.* (2009)¹

Item	Overall stayability				Marginal stayability			PL
	STAY3/2	STAY4/2	STAY5/2	STAY6/2	STAY4/3	STAY5/4	STAY6/5	
N	2525	2450	2373	2287	1955	1500	1108	2287
Mean	0.791	0.628	0.499	0.341	0.787	0.752	0.703	4.314
σ_p^2	0.158	0.222	0.239	0.218	0.158	0.182	0.189	2.492
h^2	0.00	0.01	0.05	0.08	0.01	0.09	0.03	0.05
h_u^2	0.00	0.0164	0.0786	0.1337	0.0200	0.1675	0.0521	-

¹Overall stayability (STAY *ij*2) is the probability that a ewe lambed at *i* yr of age given that she lambed at 2 yr of age. Marginal stayability (STAY *ijj*) is the probability that a ewe lambed at *i* yr of age given that she lambed at *j* yr of age. PL = productive life.

σ_p^2 = phenotypic variance; h^2 = heritability; h_u^2 = h^2 adjusted to the assumed underlying normal distribution of stayability

Phenotypic variances that were derived by Borg *et al.* (2009) for overall stayability ranged from 0.158 to 0.239 and were greater than corresponding variances in marginal stayability traits (Table 2.9.1). The low phenotypic variances meant that stayability will respond slowly to selection even if selection pressure is applied. Heritability estimates for stayability ranged from 0.00 to 0.09 in single-trait evaluations with significant genetic variation only expressed for STAY 5|2, STAY 6|2, STAY 5|4, and STAY 6|5 ($P < 0.05$). These findings demonstrated that stayability is a heritable trait in sheep. Similar reasoning and methods can be utilized to investigate the genetic basis of stayability in the Dorper sheep breed. Additive genetic variance for PL approached significance with a heritability of 0.05 ($P < 0.10$). Hudson & Van Vleck (1981) postulated that additive variance in the proportion of surviving animals is expected to increase as the frequency of surviving females decreases with age toward 0.5, because the variance of a binomial trait equals $p(1-p)$, where p is the incidence of survival and increases with more equal proportions in each category. This expectation is valid, however, only if the additive genetic variance in survival on an assumed underlying normal scale is constant across age classes. Borg *et al.* (2009) derived measures of stayability that expressed genetic variation and had proportions of surviving females that ranged from 23 to 73%.

In the latter study, means for overall stayability ranged from 0.34 to 0.79, but heritability estimates on the binomial and underlying scales were much greater for STAY 6|2 (0.08 and 0.13, respectively). Means for marginal stayability were similar across ages. These results thus suggest that the increases in observed

heritability estimates in older ewes were not simply a result of distributional properties of the data. However, the average incidence of ewes removed from the flock for most STAY3|2 contemporary groups was less than 20%, indicating that a threshold model may have been superior to account for disproportional variance among fixed-effect classes in STAY3|2 (Borg *et al.*, 2009).

In conclusion, Borg *et al.* (2009) demonstrated that genetic variation in stayability implies that breeding objectives could incorporate selection for ewes that stay in the flock for a longer period of time. However, genetic relationships between stayability and other production traits were unclear and did not provide a good indicator for early life traits suitable for indirect selection criteria for stayability. They recommended further study with more detailed information regarding time and reason for flock removal are needed to properly address genetic and environmental effects on early growth and ewe productivity to account for their influence on ewe stayability. Their conclusions also partly motivated this study.

2.10 Conclusion

The literature review has shown that subjectively assessed traits are heritable and may have correlations with other traits of economic importance. However, knowledge of the latter traits as well as their correlations with growth, reproduction and fitness is limited in the Dorper sheep breed to the preliminary study that was conducted by Olivier & Cloete (2006). It is possible to derive genetic parameters for subjectively assessed traits as well as their relationships with objectively measured traits using either linear methods or Bayesian methods. The literature has demonstrated that lamb survival has got an effect on net reproduction rate. Knowledge of lamb survival is scanty in the Dorper breed. The literature has also highlighted the need to assess whether the longevity of sheep flocks is affected by genetics. Such studies are very essential in this volatile macro-economic environment where the costs of ewe replacement can be quite high.

2.11 References

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CHAPTER 3

DESCRIPTION OF DORPER SHEEP BREEDERS SOCIETY DATA

3.1 Introduction

The present South African National Small Stock Improvement Scheme (NSIS) consists of an integrated pedigree and data recording system namely the INTERGIS. It currently provides breeding values for economically important traits to all participating members of sheep and goat species. These also include information in composite breeds that were developed over several decades as was dictated by needs, environmental limitations and market requirements. The most important of such breeds are the Dorper (meat), Dormer (meat), Afrino (dual-purpose), Dohne Merino (dual-purpose) and Boer goat (meat). The investment in the research that led to the development of these composite breeds had a marked economic impact on the South African small stock industry as shown by their popularity, which has resulted in the flow of genetic material to other countries worldwide (Schoeman *et al.*, 2010). During this study, all the data from the Dorper Sheep Breeders Society were extracted from the INTERGIS and subjected to a number of analyses. Animal breeding data sets obtained from industry often pose a number of challenges to the analyst. Prior to any analysis being conducted the data should be subjected to a rigorous editing process. It is therefore appropriate to describe the nature of the various traits that were analyzed to allow readers a better insight into the distribution of the traits that were analysed.

3.2 Dorper live weight production data submitted to the NSIS

For many decades direct selection for weaning weight has been practiced in the Dorper sheep breed amongst other selection criteria. It has been reported that direct selection for weaning weight resulted in the fastest genetic gain in this trait in Dorpers (Neser *et al.*, 1995). It has also been suggested that selection for weaning weight ought to result in a concomitant increase in net reproductive rate and ewe productivity (Snyman *et al.*, 1997; Olivier *et al.*, 2001; Duguma *et al.*, 2002). Submission of Dorper live weight data to the NSIS over the years is depicted in Figure 3.2.1. It was evident that there was substantial fluctuation in the submission of live weight production data with only 384 records in 1983. Up to 1996 there were still fewer than 1000 records submitted per annum. The number of records steadily increased from 1 398 in 1997 to 21 546 in 2008. By 2009 the total number of live weight records had accumulated to 119 349. Weaning weight accounted for the bulk of live weight records submitted whereas pre-weaning, post weaning and yearling weights accounted for only 6, 3 and 9 percent of the available weight records respectively (Figure 3.2.2).

It was evident that initial uptake of livestock recording in the Dorper breed was slow. It could be perceived that some traditional breeders who believed for many generations in type scoring (selection for breed standards) were hesitant to commence performance recording. With the advent of the 21st century breeders became more aware of the need to submit production data to the NSIS due to the rapid gains commonly reported in other breeds and species, notably in the more intensive pig, chicken and dairy industries. However, the controversy of whether breed standards (subjectively assessed traits) have a role to play in overall genetic improvement has not been fully addressed despite the preliminary study conducted by Olivier & Cloete (2006). The present study attempted to resolve the uncertainty surrounding selection based on performance in the show ring. It is also essential to mention that the random entrance and exit of flocks into the NSIS is expected to impact on the genetic parameters to be derived. That feature was vividly evident between 2002 and 2004 (Figure 3.2.1). Zishiri (2009) reported that the random entrance and exit of flocks into and out of schemes results in loss of genetic links which impairs the capacity of analysts to partition maternal variation into its individual components while also resulting in biased estimates of the correlation between direct genetic and maternal genetic effects (r_{am}). It is thus sensible at this stage to state that regardless of knowledge of such attributes analysts have little influence on the quality of data that are submitted to livestock improvement schemes besides rational editing in an endeavour to attain meaningful results from genetic analyses.

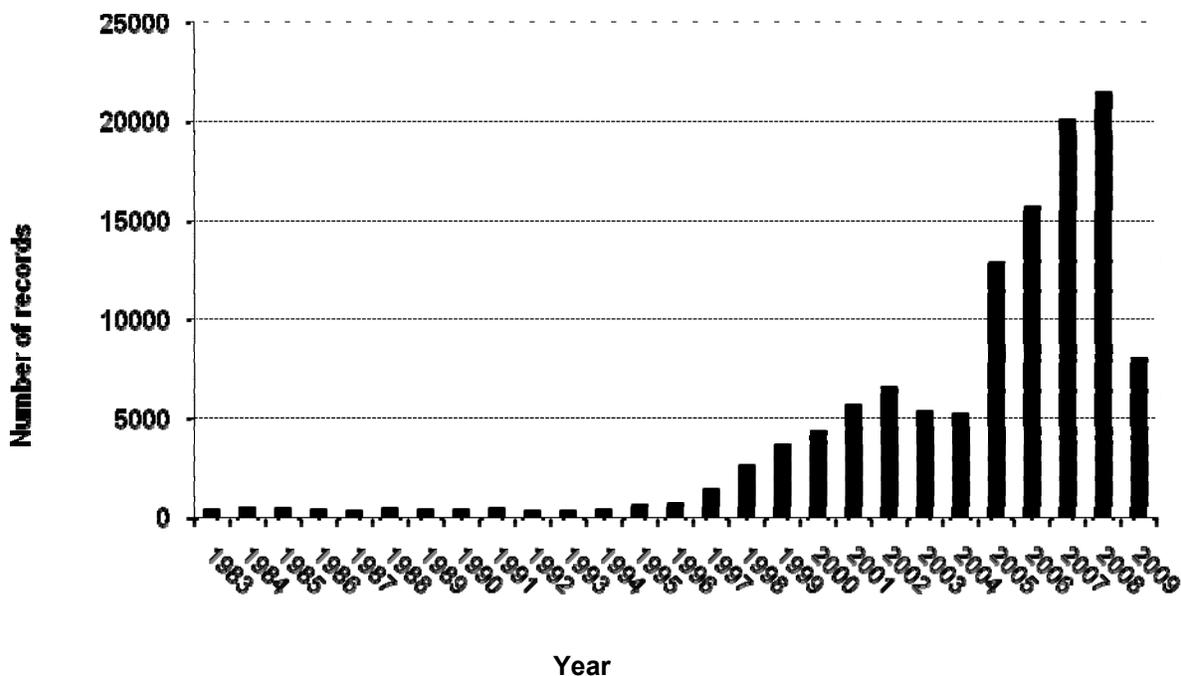


Figure 3.2.1 Annual submission of Dorper live weight production data to the NSIS

The live weight traits and their respective ages when recorded are presented in Table 3.2 and the magnitude is presented in Figure 3.2.2

Table 3.2 Dorper live weight traits recorded

Trait	No. records	Age (days)	Mean	SD	CV %
Pre-weaning weight (kg)	8 210	41 - 75	21.0	3.7	17.6
Weaning weight (kg)	111 012	76 -160	30.9	4.5	14.6
Post-weaning weight (kg)	4 043	161 - 270	45.1	4.5	10.0
Yearling weight (kg)	12 651	271 - 540	58.0	6.0	10.3

■ Prewaning Weight ■ Weaning weight ■ Post weaning weight ■ Yearling Weight

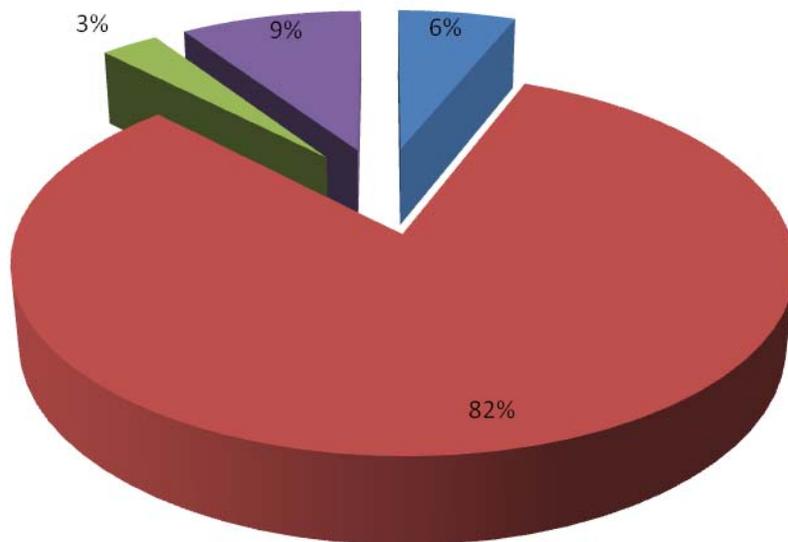


Figure 3.2.2 Dorper live weight traits recorded

3.3 Dorper reproduction and fitness data submitted to the NSIS

According to Simm *et al.* (2001), sheep improvement schemes are often hampered by relatively low use of performance recording, the relatively small size of recorded flocks in some breeds, and a frequent lack of genetic ties to facilitate across-flock genetic evaluations. Atkins *et al.* (1998) argued that the sheep

industry, especially the Merino industry in Australia, was slow to adopt an across-flock genetic evaluation, while the other major livestock industries (dairy cattle, beef cattle, meat sheep and pigs) have already developed evaluation schemes. Furthermore, Swan *et al.* (2009) reported that there have been outstanding genetic gains in Australian terminal sire sheep schemes such as Border Leicester, Terminal Sire and Coopworth between 1990 and 2005 due to sound performance recording. This progress has led to substantial improvements in productivity, with their estimates suggesting cumulated increases of \$10 to \$17 per ewe depending on breed. Merino sheep on the other hand made consistent but slow progress over the entire period of evaluation, with the rate of gain being only one third of the rate predicted in the simulation. This was attributed to the Merino being a very diverse breed, with a wide range of breeding objectives in use across flocks, and that this might be a limitation when estimating progress across the whole breed. These schemes primarily depend upon on-farm data collection and centralized processing for across-flock predictions of the breeding values of seed-stock animals. The South African Dorper Sheep Breeders Association has attempted for more than 2 decades to build a solid base of reproduction performance traits as depicted in Figure 3.3.1.

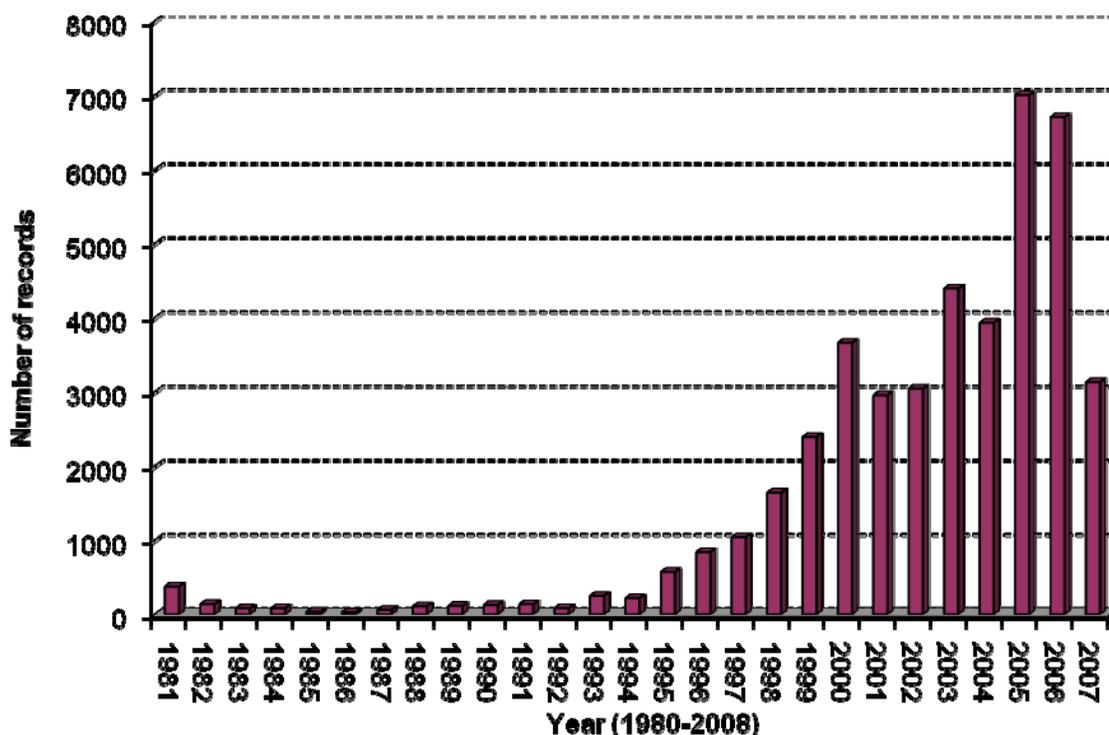


Figure 3.3.1 Reproduction data submitted to the NSIS per annum

The number of Dorper ewe records submitted to the NSIS was negligible between 1981 and 1994 (Figure 3.3.1). As from 1994, submitted ewe records steadily increased from 221 to a peak of 7003 in 2005.

However random entrance and exit of flocks into and out of the scheme remained prevalent in the new millennium. This is often a typical feature in across flock sheep genetic evaluation schemes. The inconsistent submission of data have apart from the previously stated complications, an effect during the estimation of genetic progress or lack thereof in national flocks, as reported by Zishiri (2009). Novel traits of reproduction were submitted to the NSIS by the Dorper Sheep Breeders Society. Figure 3.3.2 depicts the frequency of the cumulative Number of Lambs Born per Ewe Lifetime (NLB/EL) across parities. This information was extracted from the submitted data. The trait is quite novel because longevity, fecundity and fertility may be perceived as components thereof. The NLB/EL incorporates data from all the parities that had data collected.

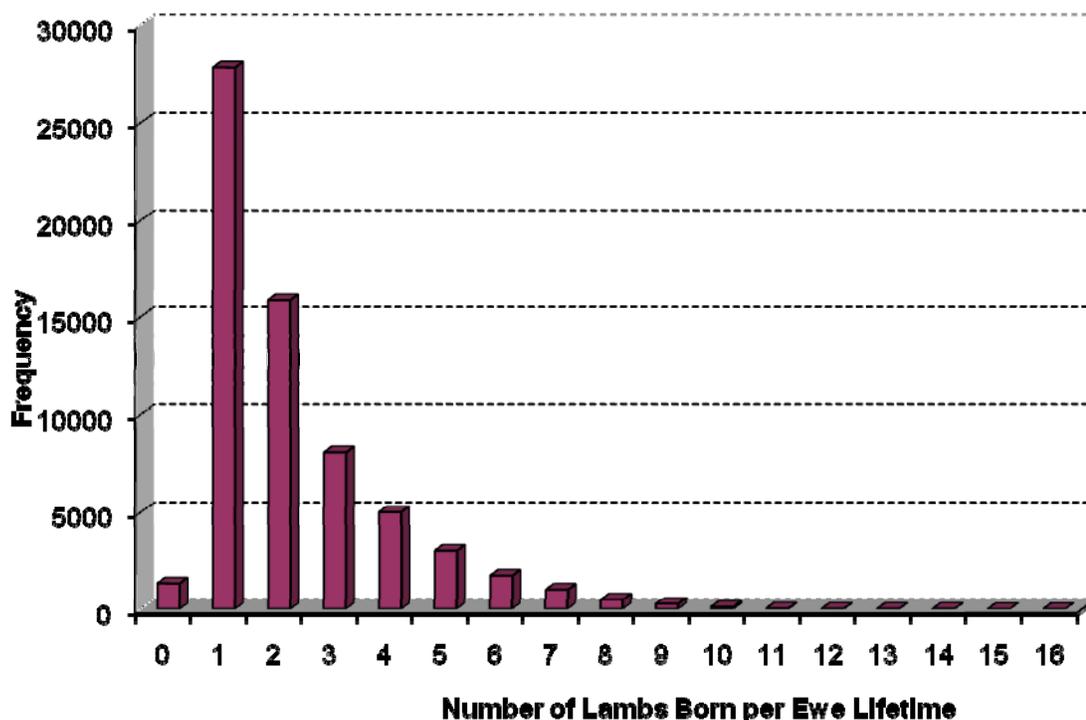


Figure 3.3.2 Frequency of the cumulative Number of Lambs Born per Ewe Lifetime in the data submitted to the NSIS

The mode for NLB/EL was 1. Approximately 43 % of the ewes gave birth to only one lamb in their entire lifetimes and 24 % bore 2 lambs. The maximum NLB/EL was 16 which were achieved by 0.002 % of the ewes. The relative poor performance of ewes intrigued the analysts because prior to any genetic analysis of the data being implemented, as it was perceived that this feature indicated poor reproduction performance in the Dorper breed. However, other attributes, like the personal preferences of the breeder,

as well as the cessation of recording in specific flocks could also have contributed. This trait can also be used to provide an indication of ewe longevity. Studies on ewe longevity are essential because of the high costs of rearing ewe replacements. Sheep breeding enterprises should endeavour to incorporate ewe longevity in their selection indices because it can significantly affect profitability (Borg *et al.*, 2009). However, it should be noted that sheep lambing annually generally have no problem to reach 5 – 6 years of age. The mere fact that it takes such a long period of time to accumulate longevity records makes the whole task of incorporating longevity difficult. Nevertheless, breeders can obtain records of early indicators of longevity, such as stayability at 2 and 3 years of age. Alternatively breeders can record ewe productive years. Ideally a prudent sheep breeder would desire to rear sheep that have a combination of high fecundity, high survival rate as well as a high longevity. Using the data that were availed by the NSIS, it was very critical for the benefit of the Dorper Sheep Breeders Society as well as the scientific community to utilize all the information in an innovative way to propose a lucid policy on how to improve the Dorper breed to maximize productivity. When the effect of lamb survival was accounted for in the Number of Lambs Born per Ewe Lifetime a new composite trait indicative of robustness or fitness was defined as the Number of Lambs Weaned per Ewe Lifetime (NLW/EL). This trait can be used effectively to assess net reproductive rate and ewe productivity. NLW/EL may result in genetic gains if selection objectives take it into cognizance. Figure 3.3.3 depicts the frequency of NLW/EL in the Dorper breed.

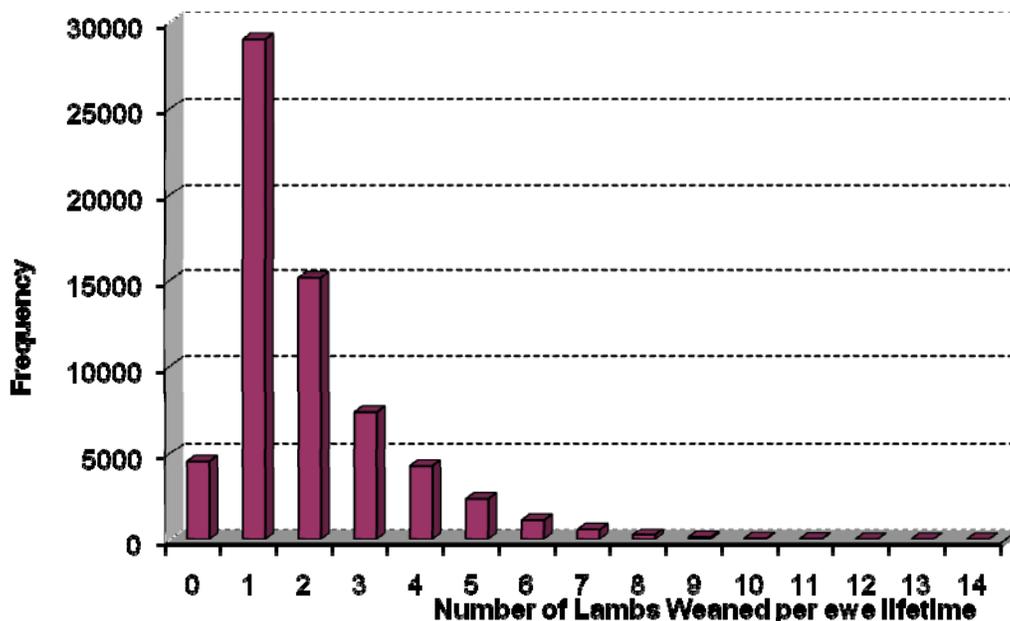


Figure 3.3.3 Frequency of the cumulative Number of Lambs Weaned per Ewe Lifetime (NLW/EL) in the data submitted to the NSIS

It is evident from Figure 3.3.3 that 7 % of the recorded ewes did not wean a lamb in their entire lifetimes, while 45 % weaned only 1 lamb. The maximum number of lambs that were weaned per lifetime was 14, which was achieved by 0.03 % of ewes. As stated previously it seemed as if rapid inspection of the Dorper reproduction data already hinted at poor reproduction capacity, although the factors stated previously could also have played a role. The current study aimed to assess the genetic basis of reproduction through considering all the traits that could be derived from the available data. The Number of Lambing Chances that each ewe was afforded in a lifetime is presented in Figure 3.3.4.

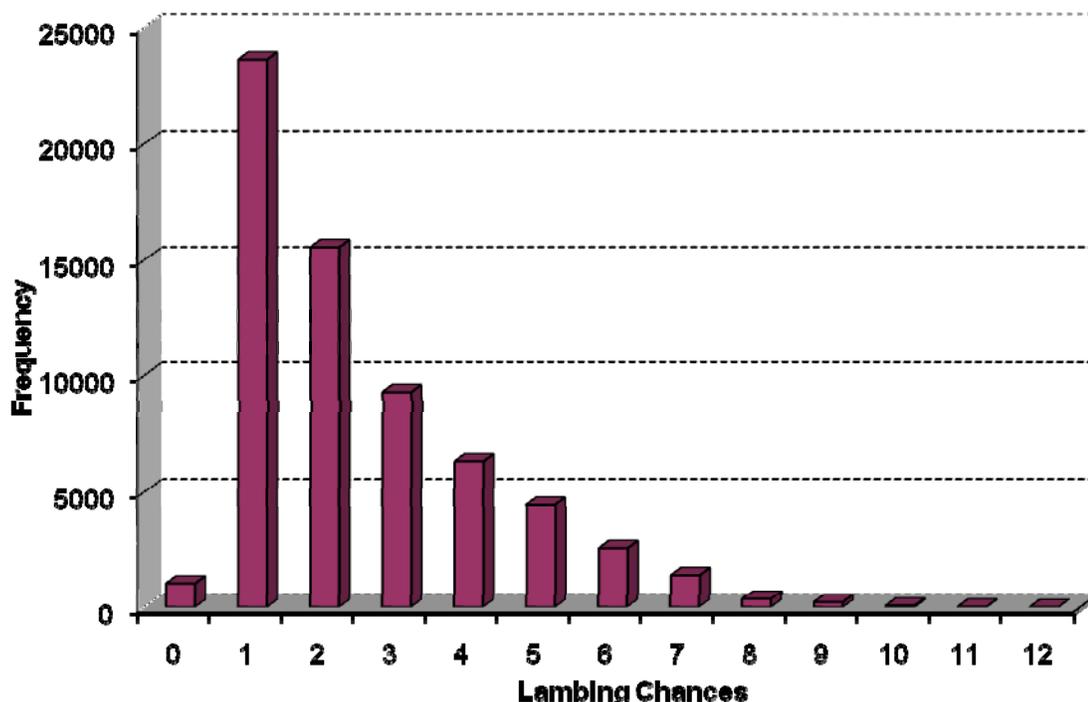


Figure 3.3.4 Number of Lambing Chances (LC/EL) afforded to a Ewe per Lifetime

The number of lambing chances afforded per ewe lifetime could be important to assess net ewe production. It is crucial to note that these ewes were selected as breeding ewes and were exposed to rams at least once. More than one third (36 %) of the ewes were afforded one lambing opportunity. The number of lambing chances decreased to 0.06 % at 8 opportunities and 0.002 % at 12 lambing opportunities. The data that was submitted to the NSIS suggested that after three lambing chances (which can happen in 2 years in an eight-monthly accelerated lambing system) less than 10 % of the ewes will manage to get the chance to lamb for the fourth time, which could be as young as four years of age, if ewes lamb for the first time at an age of 18 months. There could be a correlation between number of lambing chances and ewe productive life. If such a correlation is present it can add value because ewe

longevity has got a significant impact on fertility of sheep breeding enterprises. It is also worth mentioning that there is a dearth in literature on the genetic basis of ewe productive life (Borg *et al.*, 2009). Ewe stayability which reflects the underlying fitness characteristics that cause the removal of breeding animals from the flock was also studied and the distribution of age specific indicators of stayability are depicted in Figures 3.3.5 to 3.3.7. Data were truncated to include ewes born between they years 1998 to 2005. This was implemented to ensure that all the ewes were afforded an opportunity to stay in the flocks for at least four years up to the year 2009. The current study at least attempted in part to address this deficit in information by estimating parameters for novel traits of reproduction, fitness and longevity as well as their genetic and environmental correlations with other production traits.

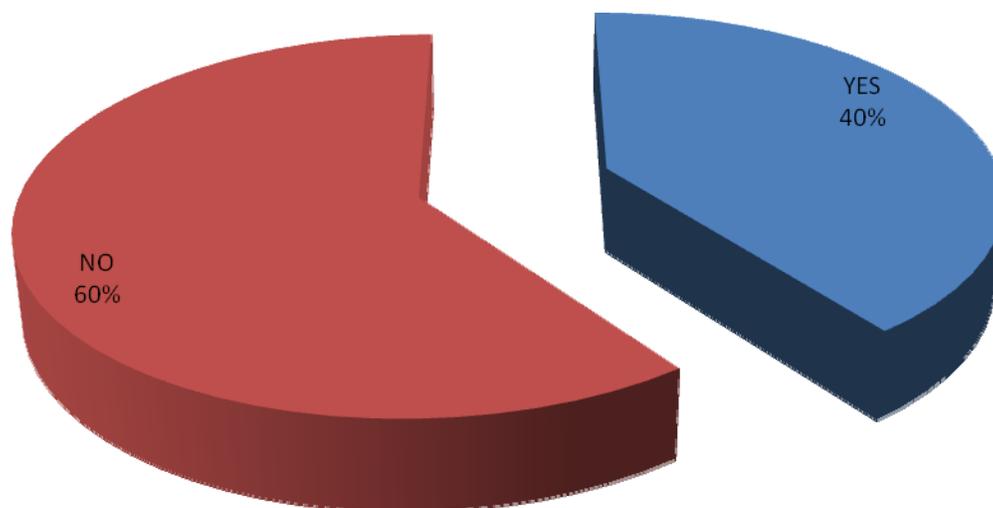


Figure 3.3.5 Ewe Stayability up to 2 years using data truncated between the years 1998 and 2005

Of the 43 262 stayability records that were derived from the submitted reproduction data it was evident that the likelihood of being available decreased with age from 2 to 4 years. Precisely 40 % of the ewes whose records were submitted to the NSIS stayed in the flocks to generate a record at 2 years of age, whereas respectively 22 and 12 % stayed up to 3 and 4 years. Reasons for 60 % of the ewes being absent from the flocks at only 2 years of age were unknown. Stayability is typically measured as a binary trait and has been evaluated with linear and threshold models. Results from alternative models are usually consistent as long as observations are approximately equally distributed across fixed effect categories (Mäntysaari *et al.*, 1991). Stayability of individual ewes can only be assessed after the ewe

leaves the flock, and, in extensive production systems, detailed information about time of ewe removal may be limited as encountered in the present study. Borg *et al.* (2009) reported that the incorporation of associations between stayability and other traits in multiple-trait evaluations could improve accuracy. Therefore, by considering the nature of data and little information available from literature, the estimation of genetic parameters for alternative measures of stayability as well as the estimation of relationships with live weight, reproductive and fitness traits in the Dorper sheep breed were stated as objectives of this study.

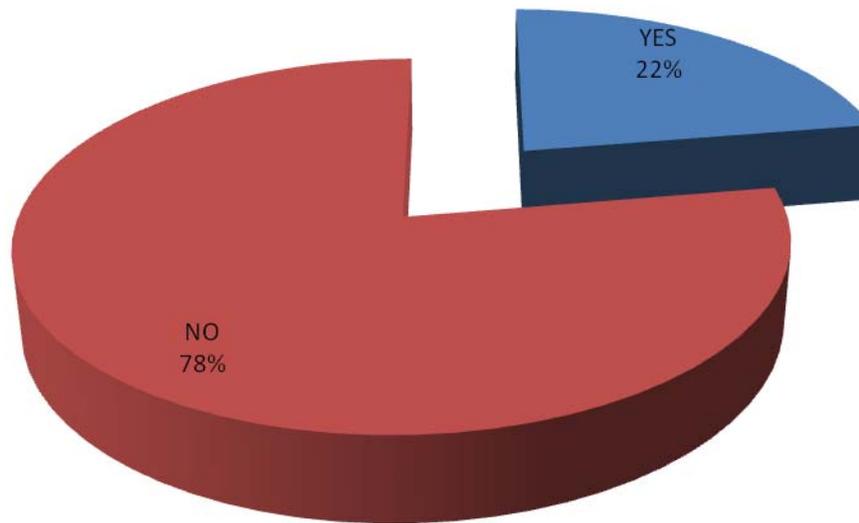


Figure 3.3.6 Ewe Stayability up to 3 years using data truncated between the years 1998 and 2005

The current study also aimed to evaluate the Dorper breed for lamb survival to weaning as a trait of the ewe. The trait assessed the ability of ewes to rear progeny up to weaning stage (ewe rearing ability). Haughey (1991) had highlighted that ovine lamb survival had by that time been recognized as a trait of economic importance. Cloete *et al.* (2009) further justified the significance of lamb survival by stating that apart from the obvious loss of monetary income incurred by lamb deaths, there is also an important animal welfare component associated with it. As previously reported in the literature review, lamb survival was treated as a binomial trait in many genetic evaluations where it was studied as a trait of the lamb (Piper & Bindon, 1977; Snyman *et al.*, 1998b; Lopez-Villalobos & Garrick, 1999; Morris *et al.*, 2000; Cloete *et al.*, 2004; Riggio *et al.*, 2008; Cloete *et al.*, 2009). In the current study, lamb survival to weaning was derived as a ratio of the number of lambs weaned over the number of lambs born alive (NLW/NLB). At this stage it is essential to note that assessment was on a per ewe basis and was indicative of ewe rearing ability. It is usually expressed on a per lamb basis, which will yield considerably different results.

Furthermore, it can be elaborated that lamb survival was considered as a continuous trait because individual probability measurements (Figure 3.3.8) were utilized in the genetic evaluation. A more detailed exploration of the ewe rearing ability data indicated that 6 % of the ewes totally failed to rear a lamb up to weaning despite having given birth at least once. Approximately 0.25 % of the ewes had a lamb survival rate of less than or equal to 20 % but higher than 0 %. Survival rate of between 20 and 40 % was achieved by a mere 2 % of ewes, 79 % of the ewes had a lamb survival of 80 to 100 %. Similarly ewe fertility was constructed from the 64 835 available records before any truncation as a ratio of the number of times lambed over the number of lambing chances afforded. It was analysed as a continuous trait as previously mentioned for lamb survival. Figure 3.3.9 depicts the frequencies of ewe fertility.

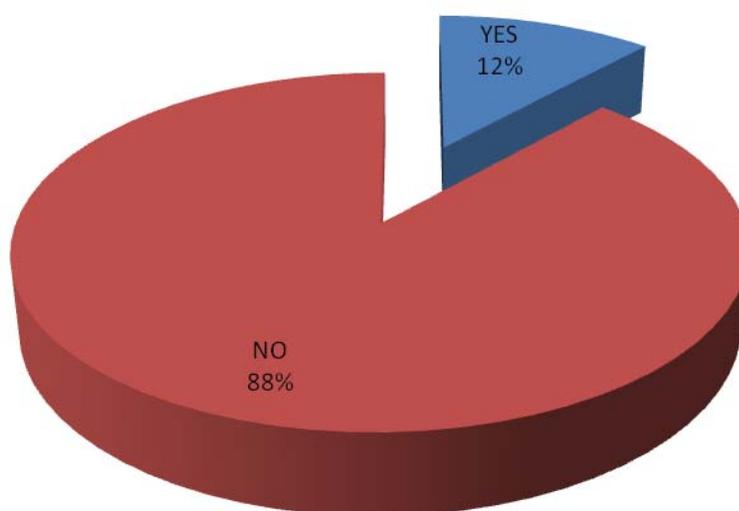


Figure 3.3.7 Ewe Stayability up to 4 years using data truncated between the years 1998 and 2005

Approximately 3 % of the ewes had a low fertility of below 2 %, and 9 % had a fertility between 2 and 4 %. There was a significant increment of up to 23 % of ewes that lambed at 40 to 60 % of their lambing chances. It was also quite clear that 49 % of the ewes had an 80 to 100 % chance of lambing when they were afforded an opportunity to do so. Ewe fertility was also measured as a binomial trait by assessing whether a ewe lambed at 2 years of age or not. Ewes that lambed at 2 years were assigned the number 1 and those that did not were assigned the number 0. These frequencies are depicted in Figure 3.3.10.

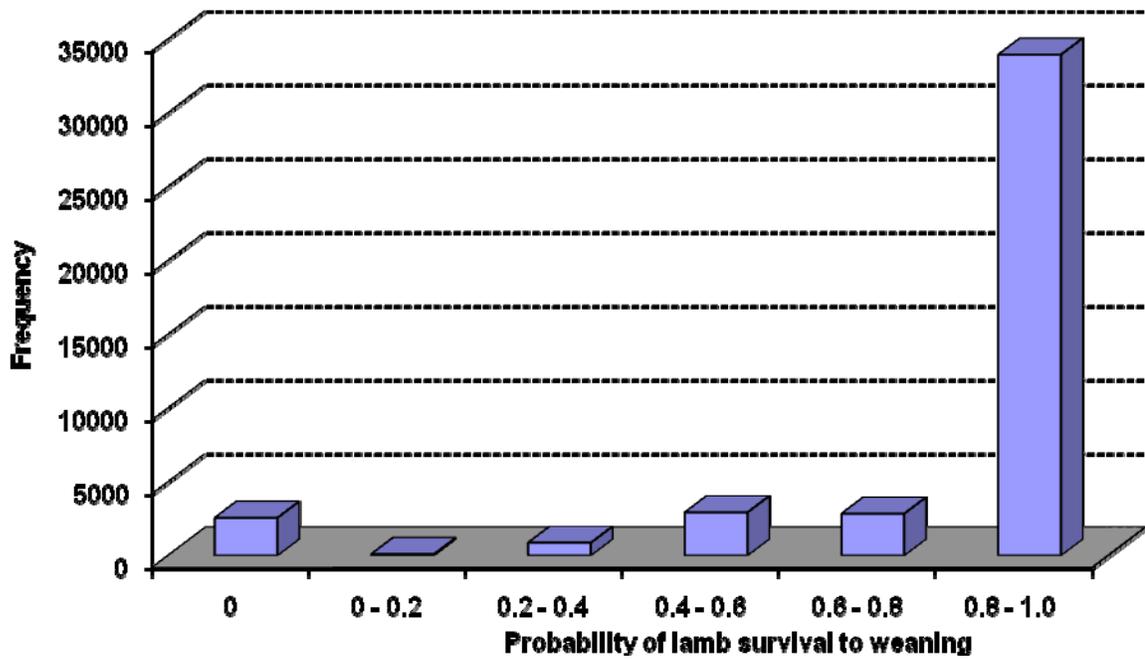


Figure 3.3.8 Frequency of lamb survival to weaning as a trait of the ewe

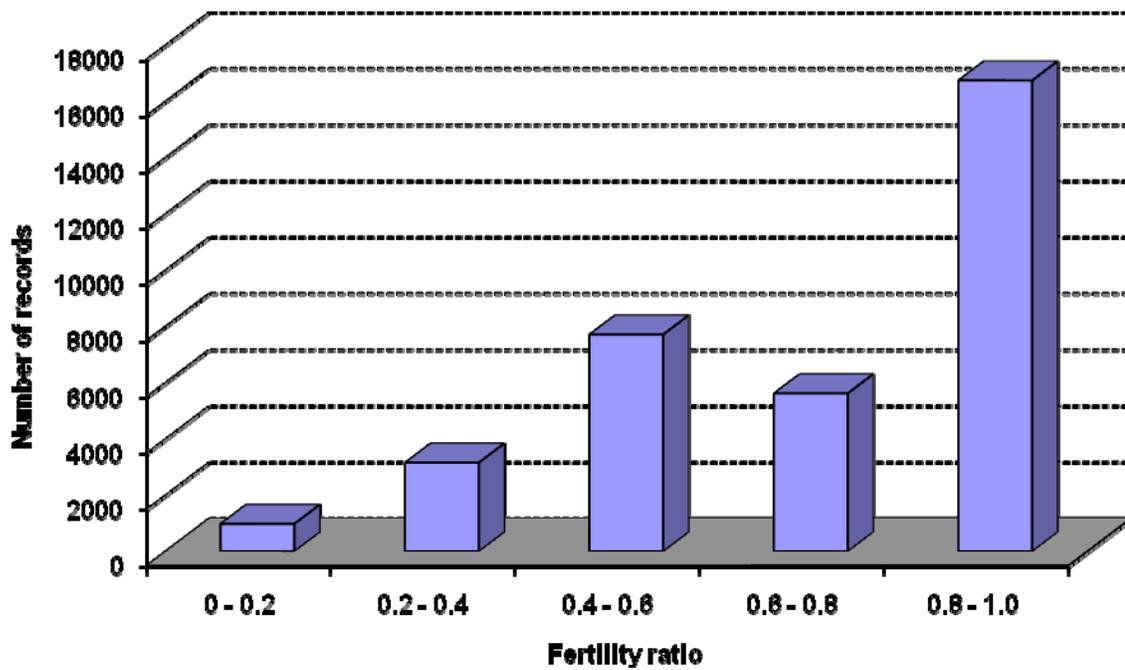


Figure 3.3.9 Frequency of Ewe Fertility as a ratio of number of times lambed on number of lambing chances afforded per Ewe Lifetime

It was evident from Figure 3.3.10 that 80 % of the ewes had lambed by the time they were 2 years old. This attribute was consistent with literature. Joubert (1962) reported that the Dorper is an early maturing breed. This was also confirmed by Greeff *et al.* (1988) when they reported that Dorpers on average exhibit their first oestrous activity at an average age of 213 days and a weight of 39 kg. The same workers also demonstrated that Dorper ewes lambed for the first time at an average age of 346 days, compared to 363 days in Romanovs. Furthermore, it was also reported by Schoeman & Burger (1992) that under an accelerated lambing system, Dorper ewes lambed for the first time at an average age of 19.6 months. Results from Snyman (1998) (unpublished) supported this by reporting that ewe fertility of 208 Dorper ewes mated to fertile rams at an age of 7 months was 0.58.

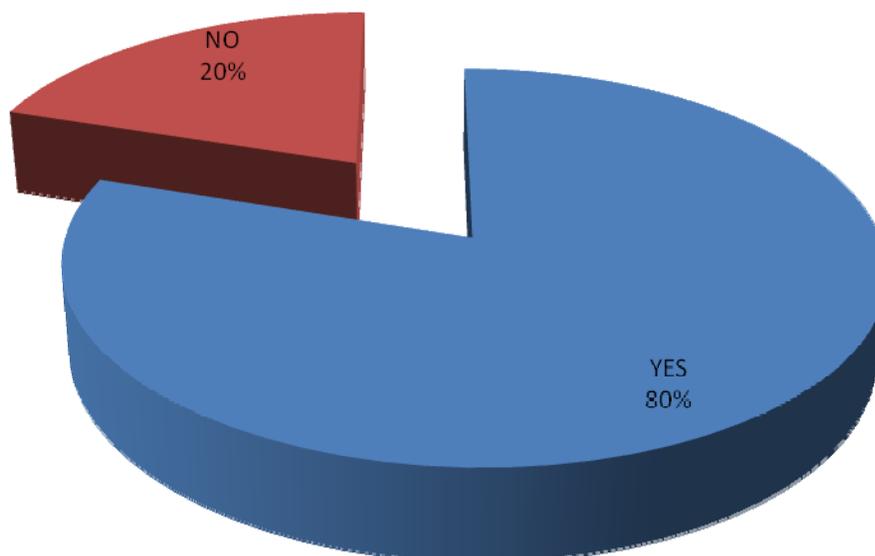


Figure 3.3.10 Frequency of Ewe Fertility at 2 years of age treated as a binomial trait

Dorpers were not extremely fecund because 68 % of the ewes bore single lambs and 32 % bore multiples (Figure 3.3.11). In recent years there has been a keen interest by animal breeders to breed robust sheep that are highly productive for many years. Analysts can use any traits that are indicative of longevity in an attempt to attain genetic improvement for traits that are difficult to measure. Genetic improvement in lifetime production efficiency depends on selection for traits known to be correlated with lifetime production on the genetic level. It would be prudent to breed ewes that have a high ewe production life to reduce costs of ewe replacement in the rapidly and drastically fluctuating micro and macro economy. In the current study 42 014 ewes born prior to the year 2005 had records for age at last lambing.

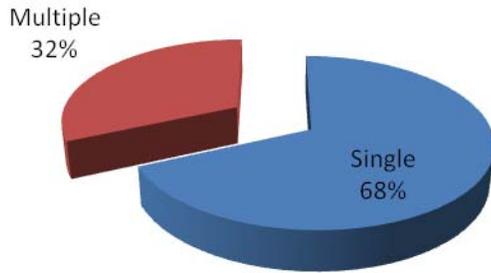


Figure 3.3.11 Frequency distribution of Litter Size in Dorper sheep based on ewe records

The frequency distributions of Ewe Productive Years are displayed in Figure 3.3.12. After truncating the ewe data to include only ewes born on or before the year 2005 it was established that one third (33%) of Dorper ewes had an official last lambing when they were between 2 and 3 years of age. Twenty six percent of the ewes were removed from the flocks when they were below 2 years of age. In summary, 59 % of the ewes lambed for the last time when they were 3 years or below. Sheep breeding enterprises would desire that their ewes lamb until they are at least 5-6 years of age. There have been a plethora of studies that have reported the effect of ewe age on production and reproduction traits (Cloete & De Villiers, 1987; Manyuchi *et al.*, 1991; Schoeman & Burger, 1992; Van Wyk *et al.*, 1993a; Cloete *et al.*, 2002; Zishiri, 2009).

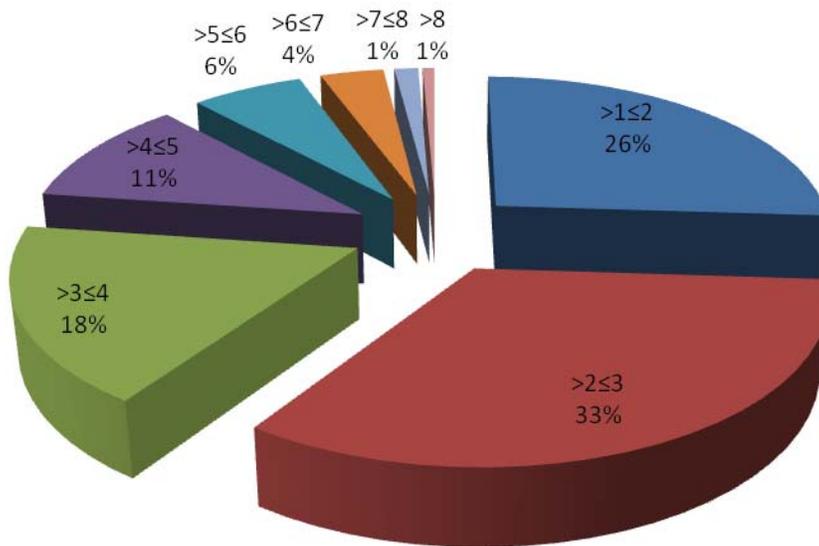


Figure 3.3.12 Frequency distributions for Ewe Productive Years truncated to ewes born before the year 2005

The relationships between subjectively assessed and objectively measured traits formed the one of the objectives of the current study. Breed standards are used to indicate the degree of excellence of the animal by means of a description and a score by points relative to visual appearance and performance to aid stud-breeding selection and for the benefit of new breeders. These values are recorded to give a true reflection of the positive or negative traits of the sheep and are used for comparative analysis within a flock. Traditionally the breed development of the Dorper has been mainly based on subjective assessment in the show ring with much less emphasis on objectively measured traits (Olivier & Cloete 2006). The Dorper Breeders Society is very strict to the adherence of mainly six standards of excellence namely: conformation, size or growth rate, distribution of fat, colour pattern and cover or fleece. It was therefore prudent to give an overview of the breed standards in terms of simple statistics and correlations amongst themselves in Table 3.3 and Table 3.4 from a well recorded flock that was utilized in the current study.

Table 3.3 Summary statistics of subjectively assessed traits in a Dorper flock

Trait	N	Mean	Std Dev	Median	Min	Max
Conformation	6609	3.402	0.818	4.0	1.0	5.0
Size	6608	4.257	0.807	4.0	1.0	5.0
Fat Distribution	6608	4.648	0.512	5.0	1.0	5.0
Colour	6608	3.666	0.862	3.0	1.0	5.0
Type	6609	3.251	0.909	3.0	1.0	5.0

Descriptive statistics demonstrated that the Dorper sheep in the flock that was evaluated exhibited a very good Size and very good Fat Distribution with no localization. It was also of interest to compute Pearson correlations amongst the subjective traits in order to clearly define the traits as distinctive from the given data. Such correlations are reported in Table 3.4 and demonstrate positive relationships amongst the subjective scores.

Table 3.4 Pearson correlations amongst subjectively assessed traits in a Dorper flock

	Conformation	Size	Fat Distribution	Colour	Type
Conformation	1.000	0.343	0.347	0.151	0.883
Size	0.343	1.000	0.629	0.174	0.528
Fat Distribution	0.347	0.629	1.000	0.161	0.434
Colour	0.151	0.174	0.161	1.000	0.187
Type	0.883	0.528	0.434	0.187	1.000

3.4 Conclusion

Animal breeding data sets of several thousands of records with well linked deep pedigrees are powerful sources of information that can be exploited by quantitative geneticists to assess traits of economic importance. However, organizing, editing and manipulating these databases should be done in such a way that deviations can be spotted and rectified before robust statistical machinery and analytical tools are used for analyses. Prior to genetic evaluation, it is essential to explore the data and contemplate on the possible aspects that can be rigorously edited and analysed to make a significant contribution to animal improvement. Across flock data sets can be challenging and unpredictable therefore, they should be edited carefully.

The quality of animal breeding performance data has a direct impact on the potential information that could be derived. There were several instances where genetic links were broken due to the random entrance and exit of flocks into the NSIS in the current study. This loss of links could potentially cause problems during ranking of the animals. The loss of links was further aggravated by the fact that the number of link sires used in more than one flock was not optimum, as is often experienced with industry data. This feature is a common feature in industry data utilized in across flock genetic evaluation programmes. Inspection of the reproduction data sets that accounted for the number of lambs born and weaned per ewe lifetime suggested poor reproductive performance in Dorpers, or an erosion of data due to other factors. However, that particular limitation can be redressed if the genetic basis of reproduction is demonstrated. Inspection of the data has also indicated that there could be underlying problems of fitness and robustness within the Dorper breed. This and other issues formed major focal points of these studies.

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CHAPTER 4

GENETIC PARAMETER ESTIMATES FOR SUBJECTIVELY ASSESSED AND OBJECTIVELY MEASURED TRAITS IN A DORPER FLOCK USING THE FREQUENTIST APPROACH

4.1 Abstract

Breed improvement in the Dorper sheep breed is based on subjectively assessed traits as determined in the show ring. There is a paucity of information on genetic parameters and relationships between subjectively assessed and objectively measured traits in the Dorper breed. In an endeavour to counteract the literature dearth, genetic analyses were conducted using REML procedures to determine the magnitude of additive direct and maternal effects as well as their correlation for live weights from weaning to yearling age, average daily live weight gains from weaning to yearling age as well as for Conformation, Fat distribution, Size, Colour and Type scores. The fixed effects that were significant ($P < 0.05$) for most models, included sex of animal, dam age, year of birth and birth status. The age at which the live weights and growth were taken was modeled as a linear covariate. The live weight and growth traits were moderately to highly heritable ranging from 0.18 ± 0.04 for post weaning weight to 0.54 ± 0.15 for yearling weight using single-trait analyses. However, when multi-trait analyses was implemented weaning weight and average daily gain to weaning assumed moderate h^2 of 0.30 ± 0.03 and 0.27 ± 0.03 respectively. Maternal effects were significant, although of fairly low magnitude with the exception of estimates for post weaning weight and average daily gain to post weaning. Heritabilities of subjectively assessed traits were fairly low, ranging from 0.07 ± 0.02 for Conformation and Type to 0.15 ± 0.03 for Size using both single-trait and multi-trait analyses. That indicated that genetic progress in these traits will be quite slow. There was very little or no direct genetic variation for Ewe Productive Life because its h^2 was 0.03 ± 0.03 and c^2 was 0.05 ± 0.04 . A series of two-trait analyses between all the twelve trait combinations confirmed the existence of positive genetic and environmental correlations between subjective and objective traits. Five-trait analyses led the conclusion that there are some moderate to high maternal genetic correlations as well as dam permanent environmental correlations between live weight, growth, Size and Type. A few negative direct genetic correlations were found for trait combinations of Colour with yearling weight, average daily gain to yearling age and Ewe Productive Life in the magnitude of -0.18 ± 0.19 , -0.05 ± 0.16 and -0.28 ± 0.32 respectively. It was concluded that despite most of the traits being positively correlated more emphasis should be put on breed improvement basing on objectively measured traits.

Keywords: log-likelihood, heritability, maternal, correlation, weight.

4.2 Introduction

The Dorper breed was developed as a result of the need for a sheep breed suitable for producing slaughter lambs in South African adverse arid environments (Cloete *et al.*, 2000). The breed has grown to be the second largest in South Africa after the Merino, and has been exported to other countries (Cloete *et al.*, 2000). To date, substantial numbers of Dorper ewes and rams have been exported as seedstock to

a number of countries abroad, including Australia, New Zealand, USA and Brazil. Dorper rams have been proven to be outstanding terminal meat sires, siring progeny with lamb growth rates, feed conversion efficiency ratios and carcass characteristics comparable to those of Suffolk crossbred lambs and Columbia purebred lambs (Snowder & Duckett, 2003).

The ultimate aim of sheep breeding research is to provide estimates of the genetic parameters required to construct breeding plans that could lead to an increment in viability, productivity and profitability of the specific enterprises (Snyman & Olivier, 2002). In numerous studies in the past, genetic parameters for objective production traits have been thoroughly reviewed (Fogarty, 1995; Safari & Fogarty 2003; Safari *et al.*, 2005b). In the South African Dorper breed, considerable emphasis is placed on subjectively assessed traits such as Conformation, Type, Size, Fat distribution and Colour during the selection of breeding sires and dams. In most instances, animals are culled on the basis of these traits. The possible expense of this selection criterion on economically important traits such as growth rate and reproduction is unknown. Traditionally the breed development of the Dorper has been based on subjective assessment in the show ring with much less emphasis on objectively measured traits (Olivier & Cloete, 2006).

Profit maximization in a sheep enterprise can be achieved mainly as a result of good net reproduction rate, maximum growth rate to slaughter and good quality carcasses produced under natural veld conditions. Dorper sheep are normally marketed as soon as possible after weaning. Therefore, live weight traits and average daily weight gain to weaning are crucial in a Dorper sheep enterprise (Neser *et al.*, 2001). In an endeavour to realize this profit objective, the South African National Small Stock Improvement Scheme (NSIS) has been mandated to record live weight traits such as weaning weights, post weaning weights, average daily body weight gain to 270 days and/or 365 days (Olivier & Cloete, 2006). Progressive sheep producers use selection as a tool to improve flock profitability by increasing lamb crop value and reducing production costs. Traits of economic importance typically include lamb growth, and lamb weights. Selection for these traits can also have indirect effects on other aspects of flock performance. Lasslo *et al.* (1985) reported an increase in mature ewe size as a correlated response to selection for weaning weight in a western range environment in the United States. Herd *et al.* (1993) reported similar results in a Merino population selected for lamb weaning weight. Changes in mature ewe weight have a direct influence on feed intake and energy requirements for the ewe flock and may also have indirect effects on lamb performance (Herd *et al.*, 1993).

Sophisticated computer software has been developed to derive unbiased estimates of genetic parameters (Meyer, 1993; Gilmour *et al.*, 2002; Misztal *et al.*, 2002). Such software among others enable the partitioning of genetic variances into direct additive and maternal additive effects, the covariance between direct and maternal animal effects, animal permanent environmental effects as well as maternal permanent environmental effects (Lewis & Beatson, 1998). The advent of these software packages

enabled researchers to conduct studies partitioning the respective random effects for various livestock species. A successful genetic improvement plan for economically important performance traits in meat sheep depends on selection for a specific trait and understanding the correlated responses in other traits because of selection for that specific trait. However, in many cases knowledge of correlations among traits is scant, thus often hampering livestock improvement programs.

There are a few studies on genetic parameters of subjectively assessed traits and their genetic and phenotypic correlations with quantitative production traits in South Africa, mostly on woolled sheep (Cloete *et al.*, 1992; Snyman & Olivier, 2002; Naidoo *et al.*, 2004; Olivier & Cloete, 2006 and Matebesi *et al.*, 2009). The usage of subjective traits as an integral part of the breeding objective without knowledge of their relationships with other economically important traits could be counter productive if correlations prove to be antagonistic. Knowledge of the genetic variation of visually assessed traits and their relationships with measured production traits will assist the predicting outcomes from breeding programmes, and is required for more accurate genetic evaluation of animals (Mortimer *et al.*, 2009). At the very least, selection based on subjective traits could be ineffectual if genetic correlations are favourable but low. It is crucial at this juncture to state that apart from the preliminary study conducted by Olivier & Cloete (2006), which investigated relationships between subjectively assessed and objectively measured traits in South African Dorper sheep, there is no other information for local meat sheep.

Ewe Productive Life can be used as a measure that reflects underlying fitness and robustness characteristics in sheep. Ewe Productive Life is an economically relevant trait due to its direct relationship with profitability of the production system. Increased ewe productive life is associated with a reduction in annual cost of the replacement of ewes, increased flock production and an increase in voluntary culling (Borg *et al.*, 2009). There is no published literature on any trait that explains the fitness and robustness in Dorper sheep despite the existence of several anecdotal reports purporting these capabilities in Dorsers. Despite the preliminary study having been undertaken by Olivier & Cloete (2006) in which they suggested the need for further investigations, there is a paucity of information on the genetic basis of subjectively assessed traits and their correlations with objectively measured traits in the Dorper breed. There is a literature dearth on estimates of genetic parameters in the breed (Cloete *et al.*, 2000). The hypothesis by Oliver & Cloete (2006) in which they attributed the slow genetic gains in Dorper production traits to over-accentuation of type traits needs to be validated. It is therefore of utmost vitality to unravel these relationships as genetic progress could be hampered by unfavourable genetic correlations among key traits contained in the selection objective. Against this background, the objectives of this study were to extract live weights, average daily weight gains, ewe productive life as well as subjectively assessed scores from the NSIS data base and to estimate genetic parameters for the recorded traits as well as genetic correlations between subjectively assessed and objectively measured traits.

4.3 Materials and Methods

Data were retrieved from the NSIS database and performance records accumulated by a single Dorper breeder over a period of 21 years (1983 to 2003) were utilized. The data came from progeny of 104 sires and 2 558 dams. The objectively measured production traits considered were weaning weight (WW), post-weaning weight (PWW), yearling weight (YW), average daily live weight gain to weaning (ADGW), average daily weight gain during the post weaning phase (ADGPW), average daily weight gain up to yearling age (ADGYW) and Ewe Productive Life (EPL). EPL was derived from age at last lambing after truncating the ewe data to include only records for ewes born on or before the year 1998. The subjectively assessed traits scored on a 5 point scale were Conformation (Conf) (1=poor to 5=excellent), Size (1=small to 5=large), Type (1=very poor to 5=excellent), Fat distribution (Fat) (1= excessive localization, 2= localized fat, 3= reasonable amount of localized fat, 4= good with slight localization and 5= good over the entire body with no fat localization) and Colour (1= cull excessive colour to 5= stud/ ideal amount of colour). A white sheep with a black head is regarded as the ideal for the breed. All subjective traits were recorded at weaning or shortly thereafter. Descriptive statistics of the data after editing are summarised in Table 4.3.1.

Table 4.3.1. Description of the raw data used after editing from a Dorper flock (n = number of records, CV% = coefficient of variation and SD = standard deviation)

TRAIT	N	MEAN	SD	CV%	RANGE
Weaning weight (kg)	7497	25.43	6.18	24.30	7 - 42
Post-weaning weight (kg)	1969	40.77	8.99	22.00	21 - 85
Yearling weight (kg)	1487	40.66	8.24	20.27	21 - 67
Weaning ADG (g/day)	7197	195.30	50.65	25.93	83 - 307
Post-weaning ADG (g/day)	1703	110.70	20.85	18.83	62 - 166
Yearling ADG (g/day)	1392	102.60	22.11	21.55	47 - 158
Ewe Production Life (EPL) (Years)	1611	4.28	1.61	37.62	1 - 9
Conformation	6609	3.403	0.8177	24.03	1 - 5
Size	6608	4.257	0.8071	18.96	1 - 5
Fat Distribution	6608	4.648	0.5123	11.02	1 - 5
Colour	6608	3.666	0.8620	23.51	1 - 5
Type	6609	3.252	0.9095	27.97	1 - 5

4.3.1 Data Editing

One-way frequency procedures were then implemented using the SAS programme (SAS, 2004) with the aim of obtaining a general overview of the data. The implementation of one-way frequencies determined the number of records contributed per year, the number of animals in each birth status group, the number of animals in each sex and the number of progeny that each sire and dam had respectively. Progeny records of sires with fewer than 15 progeny in the data set were omitted. Such animals would have become part of the base population if they had become parents in future. There were only 22 triplets,

therefore, triplets and the 2142 twins were pooled together as multiples. Dams aged eight years and above were also pooled together. The number of immature one-year-old dams was 572 hence, their records were discarded. Their progeny also had very low birth weights compared to those of their older contemporaries, since there is normally competition for the partitioning of nutrients between the developing embryo and the requirements for growth in the maiden ewe. There were also 13 cases in which there were contradictions in the pedigree by which some animals appeared as both sire and dam. In such cases it was attempted to resolve the duplicate pedigrees. If unsuccessful, such parents were regarded as unknown to avoid compromises.

The live weight and growth data was also scrutinised in an endeavour to eliminate outliers. In this regard the Univariate procedure in SAS was utilized to derive means, standard deviations, and 95 % confidence intervals. Only lambs with live weight and growth measurements within the 95% confidence interval were retained in the analyses. In total 564 weaning weight records were discarded because they fell below the lower limit of the 95 % confidence interval and 14 records were discarded because they fell above the upper 95 % confidence limit. Only 2 post-weaning weight records were discarded because they fell below the 95 % confidence interval lower limit and 80 records were eliminated because they were above the upper limit. In the case of yearling weights, 10 records were deleted for falling below the lower limit and 48 were discarded for being above the upper limit. When Ewe Productive Life (EPL) was assessed, only ewes that had been born on or before the year 1998 were incorporated into the analysis. With regards to the subjectively assessed scores, distribution analyses were conducted for each trait in SAS. The number of records that fell in each category per trait was noted. The Kolmogorov-Smirnov test, Cramer-von Mises test and the Anderson-Darling test, all confirmed that the five subjective traits assumed a normal distribution. The decision to utilize linear methods to analyze the data was therefore justified.

4.3.2 Statistical analysis

The ASREML program (Gilmour *et al.*, 2002) was used for the estimation of (co)variance components. The fixed effects that were found to be significant ($P < 0.05$) were incorporated into the operational models. Least squares mean estimates for the significant fixed effects were subsequently estimated but are not reported because they mostly conformed to expectations based upon literature results. Random terms were added to analytical models sequentially. Likelihood Ratio tests (LRT) were performed to assess the significance of the contribution of each random term to improvements in the model of analysis. The LRT is based on testing twice the increase in the Log-likelihood resulting from adding a random term to the model of analysis as a Chi-square statistic. Alternatively, for two models with the same number of different random terms, and assuming identical fixed effect modelling, the model with the higher value for the Log-likelihood fits the data best. During the first step of multi-trait analyses, the random effect of animal was fitted to the series of 66 two-trait analyses obtain starting values for multi-trait analyses as well as to estimate genetic, phenotypic and environmental correlations between all possible two-trait

combinations. The two-trait analyses were further modified initially into three-trait then finally five-trait analyses through the implementation of the most appropriate models that were adopted through the adoption of Likelihood Ratio tests (LRT). The models further incorporated the direct additive maternal and dam permanent environmental effects.

The first step in ASREML was to fit the following fixed-effects model for all for live weight traits:

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

Where:

Y_{ijklm} = Live weight trait $ijklm$ 'th (kg)

μ = population mean

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

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

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

C_m = effect of the m^{th} year of birth ($m = 1983, 1984, \dots, 2003$)

WA_{ijklm} = Age at which live weight was recorded fitted as a linear covariate (WW = 76-160 days, PWW = 161-270 days and YW = 271-365 days)

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

e_{ijklm} = random error

The fixed effects model for the average daily weight gain traits and subjective scores was similar to the one for live weight traits except that there was no covariate fitted. Fixed effects from the analyses were consistent with those reported in the literature, and were thus not presented and discussed further. The second step was the estimation of (co)variance components for each trait. This was obtained using the ASREML programme (Gilmour *et al.*, 2002) fitting single-trait animal models initially. These models include a combination of direct additive, maternal additive and maternal permanent environmental effects as well as the covariation between direct additive and maternal additive effects. It was attempted to fit sire by year interaction as an additional random term in an effort to model the various random sources of variation better, but there was no significant change in the Log-likelihood, hence it was dropped from the model. Six different forms of single-trait animal mixed models (in matrix notation) were fitted for all traits, namely:

Model 1 $Y = Xb + Z_1a + e$

Model 2 $Y = Xb + Z_1a + Z_2m + e$ {with cov (a, m) = 0}

Model 3 $Y = Xb + Z_1a + Z_2m + e$ {with cov (a, m) = $A\sigma_{am}$ }

Model 4 $Y = Xb + Z_1a + Z_2m + Z_3c + e$ {with cov (a, m) = 0}

Model 5 $Y = X\mathbf{b} + Z_1\mathbf{a} + Z_2\mathbf{m} + Z_3\mathbf{c} + e$ {with $\text{cov}(\mathbf{a}, \mathbf{m}) = \mathbf{A}\sigma_{am}$ }

Model 6 $Y = X\mathbf{b} + Z_1\mathbf{a} + Z_3\mathbf{c} + e$

Where Y = vector of observations,

\mathbf{b} = vector of fixed effects influencing traits,

\mathbf{a} = vector of direct additive effects,

\mathbf{m} = vector of random maternal additive (dam) effects,

\mathbf{c} = vector of random permanent maternal environmental effects,

σ_{am} = the covariance between additive direct genetic and additive maternal effects

e = randomly distributed vector of residuals;

Where X , Z_1 , Z_2 and Z_3 are considered as the corresponding incidence matrices relating observations to their respective fixed and random effects as well as the vector of residuals.

It was assumed that:

$V(\mathbf{a}) = \mathbf{A}\sigma_a^2$; $V(\mathbf{m}) = \mathbf{A}\sigma_m^2$; $V(\mathbf{c}) = \mathbf{I}\sigma_c^2$ and $V(\mathbf{e}) = \mathbf{I}\sigma_e^2$

Where \mathbf{A} is the numerator relationship matrix among animals in the pedigree file and \mathbf{I} being an identity matrix; with σ_a^2 , σ_m^2 , σ_c^2 and σ_e^2 being the direct genetic variance, maternal genetic variance, maternal permanent environmental variance and the environmental (residual) variance respectively.

4.4 Results and Discussion

4.4.1 Model selection

Log likelihood values were obtained for single-trait analyses on the respective traits. The inclusion of random factors such as direct additive effects, additive maternal effects, dam permanent environmental effects and the correlation between additive direct genetic and additive maternal effects resulted in significant increments in log likelihood values as presented in Table 4.4.1.1. When WW and ADGW were modeled in ASREML, the most appropriate models consisted of additive direct genetic effects, additive maternal effects, dam permanent environment effects and the correlation between additive direct and additive maternal effects as random terms. It was attempted to fit sire by year interaction as an additional random term in an effort to model the various random sources of variation better, but there was no significant change in the Log-likelihood, hence it was dropped from the model. The 7 497 weaning weight and 7 197 average daily weight gain to weaning records had reasonable genetic links and it was feasible to partition maternal effects into their individual components during multi-trait analyses. Genetic models including maternal effects and the covariance between direct and maternal genetic effects mostly fit data better than simple additive models (Maniatis & Pollott, 2002a). Exclusion of maternal effects results in biased direct heritability.

During the statistical modeling of PWW and ADGPW, the addition of extra random terms apart from the additive direct genetic effects did not result in significant increments in Log-likelihood values presumably because of data erosion, the haphazard distribution of progeny for dam (owing to the low level of recording for these traits) and the loss of genetic links between ewes, dams and granddams. The “best” model for yearling weight and ADGYW involved a model similar to the one used for WW and ADGW. The “best” models for subjective scores with the exception of Fat distribution and Conformation scores contained additive direct effects and either direct maternal or dam permanent environmental variances. The significant model for Ewe Productive Life contained both additive direct genetic and dam permanent environmental effects. It was attempted to fit the animal permanent environmental effect to ewe productive life but that particular random term was insignificant hence, the term was dropped.

4.4.2a Single-trait analyses

One of the fundamental objectives of genetic evaluation exercises is to partition the genetic variance in direct and maternal effects, where applicable. Variation was reasonably partitioned during the single-trait analyses of eight of the twelve traits in the Dorper flock. These results are presented in Table 4.4.1.3. The h^2 of WW was 0.43 ± 0.06 . Although the estimate was high it was consistent with some literature estimates. A similar estimate of 0.39 was obtained by Tosh & Kemp (1994) when they fitted exactly the same model to 5 601 records of the Hampshire meat sheep breed. Cloete *et al.* (2001) analysed 2 192 South African Mutton Merino weaning weight records that had descended from 50 sires and 423 dams and derived a h^2 estimate 0.32 ± 0.09 . Their model also accounted for the maternal effects as well as their correlation with direct effects (r_{am}). Brash *et al.* (1994c) reported a h^2 of 0.45 ± 0.07 using 7 030 records of Coopworth sheep. However, the model that they utilized incorporated only the direct additive genetic effects as a single random term. Snyman *et al.* (1995) obtained a high h^2 estimate of 0.33 when they fitted additive direct genetic and additive maternal effects to 4 325 weaning weight records of the dual-purpose Afrino sheep that had descended from 146 sires and 946 dams. Jara *et al.* (1998) reported a h^2 estimate of 0.37 ± 0.10 when they fitted direct additive, maternal additive and the correlation between direct and maternal effects to Corriedale sheep.

However, most h^2 estimates for WW in both meat and dual-purpose breeds in literature were reported to be moderate ranging from 0.15 to 0.29 (Fossceco & Notter, 1995; Hall *et al.*, 1995; Yazdi *et al.*, 1997; Wuliji *et al.*, 1998; Neser *et al.*, 2000; Rao & Notter 2000; Maniatis & Pollott, 2002a; Gizaw *et al.*, 2007; Miraei-Ashtiani *et al.*, 2007 and Rashidi *et al.*, 2008). A review of genetic parameters for various traits in diverse sheep breeds was subsequently conducted by Safari *et al.* (2005b). With regards to growth traits the authors concluded that the weighted means of heritability for growth traits ranged from moderate to high in magnitude (0.15 to 0.41) with very low standard errors (range 0.01–0.04) of the means. They also noted that heritability increased with age to post weaning and adult weights.

Table 4.4.1.1 Log likelihood ratios for the respective random effects models fitted to subjectively assessed and objectively measured traits in a Dorper flock. The model of choice is depicted in bold figures*

Effects	WW	PWW	YW	ADGW	ADGPW	ADGYW	Conf	Size	Fat	Colour	Type	EPL
Fixed effects only	-5134.53	-3680.31	-2679.27	-356.70	-5464.59	-4265.22	-1750.33	-688.34	-2370.55	-2253.30	-2309.70	-1342.08
Fixed + h^2	-4853.18	-3650.50	-2654.81	-141.53	-5438.93	-4247.93	-1730.36	-600.91	-2414.89	-2219.86	-2284.49	-1341.39
Fixed + h^2 + c^2	-4803.39	-3650.49	-2646.28	-92.66	-5437.85	-4232.13	-1729.69	-596.40	-2414.89	-2214.68	-2283.31	-1338.74
Fixed + h^2 + m^2	-4803.39	-3650.26	-2644.28	-79.78	-5438.75	-4232.13	-1729.16	-592.85	-2414.89	-2217.15	-2283.80	-1339.52
Fixed + h^2 + m^2 + c^2	-4795.73	-3650.26	-2646.28	-77.01	-5437.85	-4228.68	-	-	-	-	-	-1338.74
Fixed + h^2 + m^2 + r_{am}	-4781.56	-3650.26	-2643.71	-75.37	-5437.85	-4226.15	-	-	-	-	-	-1338.74
Fixed + h^2 + m^2 + c^2 + r_{am}	-4775.51	-3648.84	-2643.71	-50.74	-5438.66	-4223.43	-	-	-	-	-	-1338.74

* h^2 is the direct additive genetic effects, m^2 is the additive maternal genetic effect, c^2 is the dam permanent environment effects and r_{am} is the correlation between additive direct genetic and additive maternal effects

The maternal heritability (m^2) estimate for WW was 0.11 ± 0.06 . This estimate was similar to the ones reported in previously cited literature. This feature also clearly indicates the role played by maternal effects on early growth traits in sheep. Maternal effects were further partitioned into c^2 (0.08 ± 0.02) and r_{am} (-0.73 ± 0.07). It is noteworthy to state that genetic evaluation schemes therefore attempt to separate direct and maternal effects. However, accurate evaluation requires accurate estimates of genetic variances for direct and maternal effects and their correlation. Such estimates may differ according to breed or production system (Robinson, 1996b). Accounting for maternal effects also increases the accuracy of selection. Although the r_{am} estimate was within the range of estimates in the literature, more recent research indicated that such correlations may not always be a function of the underlying biological processes, and may rather be caused by not fitting all the relevant terms in the model (Robinson, 1996b; Maniatis & Pollot, 2002a; Heydarpour *et al.*, 2008).

It was attempted to fit sire by year interaction as an additional random term in an effort to model the various random sources of variation better, but there was no significant change in the Log-likelihood, hence it was dropped from the model. In this context, Dodenhoff *et al.* (1999) reported that including grand-maternal effects in models for genetic analysis of weaning weight in beef cattle seems to be important for populations with large maternal effects. The same workers demonstrated that grand-maternal effects exist in some beef populations and furthermore reported that when grand-maternal effects exist, maternal heritabilities may be underestimated and correlations between direct and maternal effects may be biased downward with models typically used to estimate maternal effects for weaning weight. Similar to Robinson (1996b), Lee & Pollak (1997) focused on the effect of sire x year interactions on the correlation between direct and maternal effects and found the correlation to be biased downward if sire x year interactions are ignored in the model. Meyer (1997), who applied the model and additionally included a sire x herd-year interaction, found direct-maternal genetic correlations to be considerably less negative compared to the "usual" model in cattle.

The moderate h^2 estimate of 0.18 ± 0.04 for PWW was in concordance with values reported in the literature for meat and dual-purpose breeds (Atkins, 1991; Gilmour *et al.*, 1994; Fossceco & Notter, 1995; Al-Shorepy & Notter, 1996; Analla, 1997; Notter & Hough, 1997; Maniatis & Pollott, 2002a; 2002b and Simm *et al.*, 2002). These moderate estimates are also consistent with those published in a review by Safari *et al.* (2005b). There was substantial reduction in the number of records from weaning to post-weaning because only 26 % (1 969 records) of the weights that were available at weaning had corresponding post weaning weights. This feature is very common in across-flock genetic evaluations as reported by Zishiri (2009). It is crucial to point that erosion of data results in the loss of genetic links which in turn result in difficulties in partitioning genetic variation further.

Table 4.4.1.2 (Co)variance components and genetic parameters for subjectively assessed and objectively measured traits in a Dorper flock

Variance components	Traits											
	WW	PWW	YW	ADGW	ADGPW	ADGYW	Conf	Size	Fat	Colour	Type	EPL
σ_a^2	9.28	5.11	12.37	840.39	59.15	99.45	0.042	0.068	0.024	0.063	0.052	0.058
σ_m^2	2.44	-	3.18	288.04	-	52.43	-	0.019	-	-	-	-
σ_c^2	1.79	-	-	104.49	-	-	-	-	-	0.027	0.013	0.093
σ_p^2	21.60	28.18	22.78	1814.58	242.51	193.75	0.603	0.477	0.176	0.717	0.723	1.877
σ_{am}	-3.46	-	-3.18	-364.94	-	-52.45	-	-	-	-	-	-
σ_e^2	11.55	23.07	10.00	946.60	183.35	94.32	0.560	0.360	0.152	0.627	0.659	1.726
Variance ratios												
$h^2 \pm s.e$	0.43±0.06	0.18±0.04	0.54±0.15	0.46±0.06	0.24±0.06	0.51±0.15	0.07±0.02	0.15±0.03	0.13±0.02	0.09±0.02	0.07±0.02	0.03±0.03
$m^2 \pm s.e$	0.11±0.03	-	0.16±0.08	0.16±0.03	-	0.27±0.09	-	0.04±0.01	-	-	-	-
$c^2 \pm s.e$	0.08±0.02	-	-	0.06±0.02	-	-	-	-	-	0.04±0.01	0.02±0.01	0.05±0.04
$r_{am} \pm s.e$	-0.73±0.07	-	-0.48±0.19	-0.74±0.06	-	-0.73±0.12	-	-	-	-	-	-

Where σ_a^2 , σ_m^2 , σ_c^2 , σ_e^2 and σ_{am} being the direct genetic variance, maternal genetic variance, maternal permanent environmental variance, the environmental (residual) variance and the correlation between direct genetic and maternal effects respectively.

The h^2 of YW (0.54 ± 0.15) was higher than most literature estimates although it was within the range of estimates reported in the review by Safari *et al.* (2005b). Brash *et al.* (1992) reported a high 14-month weight h^2 of 0.40 ± 0.10 in dual-purpose Coopworth sheep. However, their model only incorporated the additive direct genetic effects as the only random effect. Atkins *et al.* (1991) also obtained a high h^2 of 0.21 ± 0.03 in the Poll Dorset meat sheep breed with a similar model to that implemented by Brash *et al.* (1992). The high estimates obtained in our study suggest that yearling weight is highly heritable and significant selection progress can be attained if directed selection is applied to the trait. The m^2 estimate for YW was moderate (0.16 ± 0.08) and higher than most literature estimates in the range 0.05 to 0.08. There are several reports that have shown inflated direct heritability (h^2) estimates and consequently inflated breeding values when maternal effects were not included in the model of analysis (Nashom & Danell, 1996; Maniatis & Pollott, 2002a). The importance of maternal effects in livestock species is well known. Such effects arise from the ability of the dam to produce the milk needed to sustain their offspring and possibly maternal behaviour during the post-natal phase (Snyman *et al.*, 1995).

The r_{am} estimate for YW was -0.48 ± 0.19 . Although this correlation was within the range of estimates in the literature, published research indicated that such correlations may not always be a function of the underlying biological process, and may rather be related to model construction (Robinson, 1995; Robinson, 1996b; Maniatis & Pollot 2002a; Heydarpour *et al.*, 2008). There is conflicting evidence in literature on the magnitude and direction of r_{am} according to Van Wyk *et al.* (2003). It was attempted to take into cognizance other random effects such as sire x year and sire x birth status into the model for YW in an effort to counteract the high and negative r_{am} but the modeling was fruitless because the Likelihood Ratio Test selection criteria for model building was not adequately fulfilled hence, the additional terms were discarded, as for weaning weight.

The heritabilities (h^2) of average daily gain to weaning or yearling ages were 0.46 ± 0.06 and 0.51 ± 0.15 respectively and closely resembled those of the respective liveweights. These estimates were higher than expected, but nevertheless consistent with a few literature estimates available (Notter & Hough, 1997; Yazdi *et al.*, 1997; Mousa *et al.*, 1999; Bromley *et al.*, 2000; Rao & Notter, 2000; Matika *et al.*, 2003). The h^2 of post weaning average daily weight gain was 0.24 ± 0.06 . Although this estimate is consistent with the estimates in previously cited literature, it could be biased because the model failed to partition the variation further into additive maternal effects and dam permanent environmental effects due to excessive data erosion. However, it should be noted that the dam permanent environmental effect does not play a very important role after weaning because it has been thoroughly reported that maternal effects diminishes with an increment in age (Snyman *et al.*, 1995). The moderate to high m^2 estimates for average daily gain weight to weaning and yearling age amounted to 0.16 ± 0.03 and 0.27 ± 0.07 respectively. The estimates were consistent with those in previously cited literature. The correlation between direct additive effects and maternal additive effects (r_{am}) was high and negative when fitted to

average daily weight gain to weaning and average daily gain to yearling age (-0.74 ± 0.06 and -0.73 ± 0.12 respectively).

The five subjectively assessed traits in the Dorper sheep demonstrated that there is comparatively little genetic variation for type traits in Dorper sheep. The h^2 of Conf, Fat, Colour and Type were all low (0.07 ± 0.02 , 0.13 ± 0.02 , 0.09 ± 0.02 and 0.07 ± 0.02 respectively). Apart from the estimates from the preliminary study conducted by Olivier & Cloete (2006) there are no other literature estimates to compare with. Olivier & Cloete (2006) also reported low h^2 estimates for Conf and Type (0.10 and 0.11 respectively) although they did not attempt to further partition the genetic variance of type into maternal effects. However they reported a moderate h^2 estimate of 0.25 for size which was somewhat higher than the one obtained in this study (0.15 ± 0.03). The present study also attempted to partition the variation of Size into maternal genetic effects (m^2) and the derived estimate amounted to 0.04 ± 0.01 . There was a lack of literature estimates for comparison. Animal variation was further partitioned into dam permanent environment (c^2) for Colour and Type, and the resulting estimates were low (0.04 ± 0.01 and 0.02 ± 0.01 respectively). There was also a lack of literature estimates to compare with these estimates. The current study also reported very low genetic variation for Ewe Productive Life (EPL).

The apparent lack of genetic variation for EPL suggested that ewes can arguably be kept in the flock for longer periods through good management. However, the variance components obtained in this study for EPL could be biased due to the data structure. There is also some evidence from Muller (2005) that there is some genetic variation in age at last kidding in Saanen dairy goats. This result could hint at some genetic variation in sheep as well. A series of all possible multi-trait, analyses were conducted using the most appropriate models as implemented in single-trait analyses to estimate the genetic, phenotypic, maternal and environmental correlations between subjectively assessed and objectively measured traits in the Dorper flock and the results are presented in Tables 4.4.1.3 to Table 4.4.1.5

4.4.2b Multi-trait analyses

The direct h^2 estimates obtained for objectively measured traits as a consequence of the implementation of multi-trait analyses differed from the ones derived through single trait analyses although they concurred with estimates from previously cited literature. The multiple-trait h^2 estimates for weaning weight (0.30 ± 0.03), ADGW (0.27 ± 0.03) and ADGYW (0.40 ± 0.06) were lower than the single trait estimates (Table 4.4.1.2). However, the estimates for post-weaning weight (0.30 ± 0.04), ADGPW (0.40 ± 0.06) and yearling weight (0.55 ± 0.07) were significantly higher than the single-trait estimates. The multiple-trait estimates for live weights and growth have got better and positive implications and are more reasonable because information in traits with more records benefited those traits with fewer records as a result of relationships amongst all the 12 traits were taken into account. It was also evident that direct heritability

estimates increased with age as is commonly reported in the literature (Tosh & Kemp, 1994; Maniatis & Pollott, 2002a; Simm *et al.*, 2002; Rashidi *et al.*, 2008). The multi-trait direct h^2 estimates obtained for subjectively assessed traits did not differ much from the single-trait estimates.

Correlations amongst traits are interesting to discuss although there may be some controversial aspects. In most cases the correlations depend on the type of models that have been fitted to the data. In our study the most fascinating and relieving of all the genetic correlations are those among the five subjectively assessed traits. Type traits in Dorper sheep were all positively (i.e. favourably) correlated to each other. The highest positive r_g was between Conformation and Type (0.94 ± 0.04), suggesting that selecting Dorper sheep basing on Type alone would be equivalent to selecting on Conformation. Type scores involve judging the degree to which the sheep conform to breed characteristics and is in fact a combination of all other type traits. Emphasis is placed on Conformation, Size and Fat distribution and Color when determining Type. Type was also genetically highly correlated to Size and Fat distribution (0.84 ± 0.06 and 0.63 ± 0.12 respectively). There were no literature estimates to compare these correlations except those reported in the preliminary study by Olivier & Cloete (2006). In their study they accordingly reported high genetic correlations between Type, Size and Conformation. The genetic correlation between Type and Colour was lower, at 0.40 ± 0.16 . Selecting on Type would thus not necessarily result in marked changes in Colour scores. Colour was also genetically moderately correlated to Conformation, Size and Fat distribution (0.24 ± 0.15 , 0.30 ± 0.14 and 0.30 ± 0.12 respectively). In view of our observations it is essential to note that Snyman *et al.* (1998a) noted that genetic correlations are notorious for their inconsistency and high standard errors, unless data sets of substantial magnitude were available.

Despite the fact that estimates for direct maternal effects (m^2) for live-weight and growth traits were lower than single-trait estimates (Table 4.4.1.4), multi-trait analyses unequivocally concurred with single-trait analyses in that maternal effects are of cardinal importance. It has been reported by Safari *et al.* (2005b) amongst other authors that the role of maternal effects diminishes with age from birth to adulthood in sheep. Similar estimates of low maternal effects have been reported in literature (Tosh & Kemp, 1994; Fossceco & Notter, 1995; Notter & Hough, 1997; Lewis & Beatson, 1999; Matika *et al.*, 2003). The current study also demonstrated that the maternal genetic correlation (r_g) between size and live weights and average daily weight gain was high and positive. High and positive maternal genetic correlations between live weight and growth traits have been reported numerous times in literature (Yazdi *et al.*, 1997; Simm *et al.*, 2002; Duguma *et al.*, 2002b). It was therefore concluded that selecting Dorper rams and ewes on the basis of size does not have detrimental effects on live weight and growth traits.

Table 4.4.1.3 REML estimates (SE in brackets) of direct heritability (h^2) on diagonal genetic (r_g) (above diagonal), and environmental (r_e) (below diagonal) correlations between objectively measured and subjectively assessed traits in a Dorper flock using multi-trait analyses

	Conformation	Size	Fat	Colour	Type	WW	PWW	YW	ADGW	ADGPW	ADGYW	EPL
Conformation	0.07(0.02)	0.65(0.11)	0.51(0.16)	0.24(0.15)	0.94(0.04)	0.45(0.13)	0.39(0.15)	0.32(0.18)	0.32(0.12)	0.22(0.17)	0.25(0.17)	0.27(0.31)
Size	0.30(0.01)	0.15(0.03)	0.71(0.06)	0.30(0.14)	0.84(0.06)	0.88(0.04)	0.81(0.07)	0.67(0.11)	0.84(0.05)	0.60(0.11)	0.63(0.11)	0.52(0.26)
Fat	0.27(0.02)	0.55(0.01)	0.11(0.02)	0.30(0.12)	0.63(0.12)	0.64(0.07)	0.69(0.10)	0.60(0.11)	0.66(0.07)	0.43(0.14)	0.50(0.12)	0.38(0.27)
Colour	0.14(0.01)	0.14(0.02)	0.13(0.01)	0.09(0.02)	0.40(0.16)	0.14(0.12)	0.01(0.14)	-0.18(0.19)	0.20(0.12)	0.20(0.15)	-0.05(0.16)	-0.28(0.32)
Type	0.87(0.01)	0.43(0.01)	0.33(0.01)	0.16(0.02)	0.07(0.02)	0.55(0.10)	0.46(0.13)	0.34(0.19)	0.52(0.10)	0.40(0.15)	0.39(0.15)	0.23(0.30)
WW	0.23(0.02)	0.58(0.01)	0.41(0.02)	0.15(0.02)	0.32(0.02)	0.30(0.03)	0.87(0.04)	0.71(0.06)	0.94(0.01)	0.70(0.07)	0.73(0.07)	0.62(0.22)
PWW	0.13(0.03)	0.46(0.02)	0.33(0.02)	0.10(0.02)	0.17(0.03)	0.69(0.01)	0.30(0.04)	0.95(0.08)	0.83(0.05)	0.84(0.05)	0.89(0.10)	0.56(0.26)
YW	0.10(0.05)	0.25(0.05)	0.27(0.02)	0.06(0.05)	0.12(0.05)	0.42(0.04)	0.39(0.05)	0.55(0.07)	0.72(0.06)	0.99(0.09)	0.87(0.04)	0.27(0.28)
ADGW	0.22(0.01)	0.54(0.01)	0.42(0.01)	0.13(0.02)	0.31(0.01)	0.91(0.01)	0.63(0.01)	0.52(0.02)	0.27(0.03)	0.62(0.09)	0.68(0.07)	0.65(0.23)
ADGPW	0.04(0.03)	0.34(0.02)	0.22(0.03)	0.09(0.02)	0.11(0.03)	0.51(0.02)	0.78(0.01)	0.42(0.05)	0.47(0.02)	0.40(0.06)	0.96(0.8)	0.39(0.31)
ADGYW	0.11(0.03)	0.26(0.05)	0.28(0.03)	0.06(0.03)	0.18(0.03)	0.50(0.01)	0.42(0.05)	0.85(0.02)	0.58(0.03)	0.35(0.05)	0.40(0.06)	0.60(0.34)
EPL	0.03(0.03)	-0.06(0.04)	-0.02(0.03)	0.03(0.03)	0.02(0.03)	-0.10(0.04)	0.08(0.04)	-0.05(0.08)	-0.13(0.04)	0.08(0.04)	0.03(0.04)	0.04(0.03)

The current finding is quite novel because Olivier & Cloete (2006) did not partition the genetic variance of Size into direct and maternal components. The phenotypic correlation (r_p) between size and weaning weight as well as ADGW was also high and positive similar to the findings of the former authors. However, the phenotypic correlation between Size and yearling weight as well as ADGYW was moderate. This can be attributed to data erosion between weaning and yearling ages as reported previously as well as the fact that scoring was conducted closer to weaning than yearling age.

Table 4.4.1.4 REML estimates (SE in brackets), maternal heritability (m^2) (on diagonal), maternal genetic (r_m) correlation (above diagonal), phenotypic (r_p) correlation (below diagonal) between objectively measured and subjectively assessed traits from a five-trait analysis in a Dorper flock

	WW	SIZE	ADGW	YW	ADGYW
WW	0.05(0.01)	0.95(0.04)	0.98(0.01)	0.95(0.02)	0.98(0.07)
SIZE	0.66(0.01)	0.03(0.01)	0.91(0.05)	0.83(0.07)	0.48(0.06)
ADGW	0.92(0.01)	0.61(0.01)	0.04(0.01)	0.99(0.01)	0.99(0.07)
YW	0.54(0.02)	0.34(0.03)	0.51(0.02)	0.04(0.01)	0.84(0.06)
ADGYW	0.62(0.02)	0.34(0.03)	0.65(0.02)	0.85(0.01)	0.14(0.03)

Multi-trait analyses further demonstrated that the dam permanent environmental effect (c^2) influenced live-weight, growth, Type and Colour with similar magnitudes to single-trait analyses (Table 4.4.1.5). The dam permanent environmental correlation (r_{pe}) between live-weight and growth traits was high and positive. These correlations were in concurrence with literature (Yazdi *et al.*, 1997; Mousa *et al.*, 1999; Duguma *et al.*, 2002b). Inconclusive r_{pe} estimates between colour and live-weight as well as growth traits were derived (ranging from negative to positive). This further endorses our previous assertion that the incorporation of Colour in Dorper selection objectives should be reviewed.

The environmental correlations (r_e) between Conformation and Size, Fat distribution and Colour were positive but low ranging from 0.14 ± 0.01 to 0.30 ± 0.01 . However, the r_e between Conformation and Type was high and positive (0.87 ± 0.01). The r_e estimates among Colour and Conformation, Size, Fat and Type was positive and low ranging from 0.13 ± 0.01 to 0.18 ± 0.01 . The low r_e suggests that an environment sustaining any of the subjectively assessed traits could have a low but positive influence on the others. The r_e between size and fat distribution was positive and high (0.55 ± 0.01) implying that a favourable environment for an improvement in size will also result in an increase in fat. The genetic correlations between Colour and objectively measured traits such as live weights, average daily gains and Ewe Productive Life were low. Their magnitudes were less than or equal to 0.20 and variable in sign. Furthermore the environmental correlations between Colour and all the objectively measured production traits were lowly negative to lowly positive, ranging from 0.01 ± 0.03 to 0.16 ± 0.01 . It will be judicious if

Dorper sheep breeders would desist from paying much attention on Colour because most Dorper sheep have reached the desirable phenotypic level of colour. There is therefore very little ability to discriminate and little effect on selection intensity. Furthermore, Colour has a low heritability and is lowly positively correlated to other subjective and growth traits and will not have any significant impact on genetic gains.

Table 4.4.1.5 REML estimates (SE in brackets), dam permanent environment(c^2)(on diagonal), dam permanent environmental (r_{pe}) correlation (above diagonal) and phenotypic (r_p) correlation (below diagonal) between objectively measured and subjective subjectively assessed traits from a five-trait analyses in a Dorper flock

	WW	ADGW	TYPE	COLOUR	EPL
WW	0.05(0.01)	0.95(0.02)	0.47(0.30)	0.15(0.23)	-0.55(0.27)
ADGW	0.92(0.01)	0.04(0.01)	0.57(0.10)	-0.01(0.31)	-0.61(0.06)
TYPE	0.35(0.01)	0.31(0.01)	0.01(0.01)	-0.22(0.52)	-0.18(0.14)
COLOUR	0.16(0.01)	0.13(0.01)	0.18(0.01)	0.03(0.01)	0.55(0.20)
EPL	0.05(0.03)	0.03(0.03)	0.02(0.03)	0.02(0.03)	0.04(0.04)

Conformation was positively genetically correlated with weaning weight, post-weaning weight and yearling weight (0.39 ± 0.11 , 0.39 ± 0.15 and 0.41 ± 0.16 respectively). The only comparable estimates were reported in the preliminary study conducted by Olivier & Cloete (2006), in which weaning weight and post weaning weight were moderately and positively genetically correlated with conformation. The positive correlations suggest that selection for Conformation will not result in deleterious correlated responses in live-weight traits. Average daily weight gain traits were moderately positively to lowly positively correlated with conformation. Environmental correlations between conformation and live weight and average daily weight gain traits were low, ranging from 0.04 ± 0.03 to 0.24 ± 0.01 . The only anomaly was the genetic correlation between Conformation and ewe productive life which was (0.27 ± 0.31). The environmental correlation between Conformation and Ewe Productive Life did not differ from zero (0.03 ± 0.03). This attribute has to be further validated when more data that is indicative of longevity becomes available.

Size was highly genetically correlated with all live weight and average daily gain traits with a range of r_g estimates of 0.60 ± 0.11 to 0.88 ± 0.04 . Olivier & Cloete (2006) also reported that weaning weight and post weaning weight were highly positively correlated with Size implying that heavy animals would have high scores for Size (0.98 ± 0.01 and 0.71 ± 0.09 respectively). The environmental correlations between Size and live weight and average daily gain traits were positive and varied from moderate to high (0.34 ± 0.02 to 0.65 ± 0.01). These correlations further infer that selecting Dorper sheep on the basis of Size will result in faster growing animals with higher mature weights. Simple logic also dictates that larger animals are also heavier animals. The Dorper sheep breeders society emphasizes that a sheep with a good weight for its

age is ideal. Discrimination against extremely small or extremely big animals is routinely exercised. The society further recognizes and acknowledges that larger animals are not as able to produce during extreme conditions due to the burden of maintaining their body weight (DorperSA, 2011).

The genetic correlation between Fat distribution and the objectively measured live weight and average daily weight gain traits were positive and varied from moderate to high (0.43 ± 0.14 to 0.69 ± 0.10). However, there are no literature estimates for comparison of these estimates. These positive correlations indicate that selecting Dorper sheep on the basis of the Fat distribution scores does not have a negative impact on growth traits. Likewise one would also infer that selecting animals that have good live weights and fast growth will result in animals that have a reasonable fat distribution according to the scoring system utilised. It is also critical to mention that fat distribution scores should be treated with caution as too fat animals could be undesirable, although they may have desirable growth patterns. It should however be borne in mind that Fat distribution is not about the amount of fat in an animal but rather the distribution. It was prompted by the very localized fat depots in the Blackhead Persian which was used as the dam breed during breed development. The environmental correlations between Fat distribution and objectively measured live weight and average daily weight gain traits were positive and low ranging from 0.22 ± 0.03 to 0.45 ± 0.01 .

All the genetic correlations between all live weight and all average daily gain traits were high and positive. This feature was consistent with a plethora of literature estimates (Brash *et al.*, 1994c; Lewer *et al.*, 1995; Al-Shorepy & Notter, 1996; Nasholm & Danell, 1996; Analla *et al.*, 1997; Yazdi *et al.*, 1997; Notter, 1998; Snyman *et al.*, 1998a; Mousa *et al.*, 1999; Wuliji *et al.*, 2001; Duguma *et al.*, 2002b). The current results are also in concordance with very high genetic correlations for comparable traits reported in the review by Safari *et al.* (2005b). Another interesting attribute unearthed by the current study was that genetic correlations of ewe productive life with most of the live weight and average daily gain traits were fairly high, with estimates being 0.65 ± 0.19 , 0.56 ± 0.26 , 0.65 ± 0.19 and 0.60 ± 0.34 for WW, YW, ADGW and ADGY respectively. The environmental correlations between ewe productive life and live weight and growth traits were ranging from zero to very positively low.

4.5 Conclusion

The low levels of genetic variation and heritability estimates for derived for subjective traits suggest that genetic progress in such traits is feasible although genetic gains will be quite slow. Fortunately all subjectively assessed traits except Colour have favourable genetic relationships with objectively measured traits. There is a need to maintain the minimum standard for colour in the Dorper breed. Selection based on colour would not result in marked gains in traits of economic importance to the breed, but would at least ensure that the colour pattern that was established over decades remain stable. It can

also be concluded that selection on Type score alone is also sufficient based on very high and favourable genetic correlations with Conformation, Fat distribution and Size. This will facilitate the process of selection, as judges will be allowed to score more animals within a shorter time span. On the other hand, emphasis should be placed on recording objective traits as these have a more pronounced impact on profitability. More focus should be directed to recording performance related traits and deriving breeding values for such traits. Selection indices should also be compiled to include conformation traits together with objectively measured traits such as growth, reproduction and carcass traits.

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CHAPTER 5

GENETIC PARAMETER ESTIMATES FOR SUBJECTIVELY ASSESSED AND OBJECTIVELY MEASURED TRAITS IN A DORPER FLOCK USING THE BAYESIAN APPROACH

5.1 Abstract

Bayesian inference is a robust statistical tool for utilization in quantitative animal breeding. There is often a conflict of ideology amongst quantitative geneticists as to whether Bayesian or the linear methods results in the most accurate genetic parameters. In an attempt to resolve this issue, (co)variance components, posterior standard deviations, 95 % highest posterior density confidence intervals and variance ratios of subjectively assessed and objectively measured traits in a Dorper flock were estimated using a series of multi-trait analyses through the implementation of threshold-linear and threshold-threshold models. The software that was used was THRGIBBSF90, which is suitable for the estimation of variance components and genetic parameters in threshold-linear and threshold-threshold animal mixed models for any combination of categorical and continuous traits. The estimates of direct heritability (h^2) for subjectively assessed traits differed from those obtained using Residual Maximum Likelihood (REML). The mean h^2 for Conformation ranged from 0.12 ± 0.08 to 0.29 ± 0.09 depending on the trait combination. Size had a mean moderate to high h^2 of between 0.17 ± 0.07 and 0.21 ± 0.09 . The h^2 of Fat distribution also ranged from low to moderate in the range, namely from 0.13 ± 0.09 to 0.25 ± 0.10 . Colour was moderately heritable in the range 0.15 ± 0.09 to 0.16 ± 0.09 . Type was lowly heritable in the range 0.07 ± 0.04 to 0.10 ± 0.05 . Genetic, maternal, dam permanent environmental and environmental correlations between subjectively assessed and objectively measured traits computed using Gibbs sampling differed mainly in magnitude but seldom in direction with those computed using REML. There were high and positive genetic correlations between Size and all the live weight traits and low to moderate genetic correlations between Colour and yearling weight.

Keywords: Bayesian, threshold, posterior density, significant, subjectively, heritability, objectively genetic, correlation

5.2 Introduction

The most prominent methods that have been utilised by animal breeders for the estimation of genetic parameters have been based on linear methods through the implementation of Residual Maximum Likelihood (REML). However, the implementation of linear methods for some threshold traits does not always result in accurate variance components and ratios (Gianola & Foulley, 1982). The application of alternative methods of inference has however, garnered significant momentum following the demonstration of their potential in solving animal breeding problems by several workers (Gianola & Foulley, 1983; Gianola & Fernando, 1986; Harville, 1990; Pretorius & Van der Merwe, 2000). In the recent past, user friendly software that is underpinned by Bayesian methods and is capable of doing a series of multi-trait analyses of a combination of linear and threshold traits in any combination has been developed

for use in the estimation of genetic parameters (Misztal *et al.*, 2002). Pretorius & Van der Merwe (2000) reported that animal breeding inference usually assumes that the data follows a normal distribution. When the values of the variance components are not known, the classical approach to the problem of predicting linear combinations of fixed and random effects has been to estimate the variance components using restricted maximum likelihood (REML), and to proceed thereafter as if these estimates were the true values. The authors further noted that the Bayesian approach has several practical advantages over the classical (REML) approach. Firstly, the estimates from the Bayesian approach for a variance are always within the allowed parameter space (i.e. positive for a variance). An interval estimate such as a highest posterior density region will thus not include negative values.

This is in contrast to the REML estimates. Although REML estimates are defined inside the appropriate parameter space, their asymptotic distributions can generate interval estimates that include negative values (Gianola & Foulley, 1990). This statistical limitation is often overlooked in discussion of likelihood-based methods. Secondly, highest posterior density regions using the Bayesian approach are never empty, whereas confidence intervals for the ratio of variances can be empty in the case of the classical approach in the event that the analyses fail to converge and it becomes impossible to reliably estimate the appropriate standard errors. Finally, one can report the whole of the posterior probability distributions of the parameters in the Bayesian approach visually (Van der Merwe & Botha, 1993; Wright *et al.*, 2000).

Blasco (2001) highlighted the major argument against Bayesian methods in statistical inference. This involves the practical sterility of such methods with regards to the fact that they did not always produce the desired results. The methodology is characterized by the resolution of complicated multi-dimensional integrals or the use of more or less accurate approximations. The recent use of MCMC techniques has solved most of these problems, although it has generated new issues. However, most of these new problems are related to the convergence of these chains, and easier to handle, particularly when the distribution of the data is normal. These MCMC methods provide random samples of the joint and marginal posterior distributions, and thus the mean, standard deviation, and confidence intervals can be calculated directly from the samples without the need of integration. New variables such as ratios, squares, and so on can be derived from the components of the joint posterior distribution samples obtained, and confidence intervals can be derived from these distributions without the need of any approximation.

Pretorius & Van der Merwe (2000) further elaborated that, while the variance components are fixed at a single value for the REML estimates, ignoring uncertainty associated with estimating their values, the Bayesian approach incorporates this uncertainty by averaging over plausible values of the variance components. This is accomplished through the choice of appropriate prior distributions. Statistical confidence intervals for the estimates can easily be obtained, and all the available information about the

random effects to be predicted is contained in the posterior distribution of these random effects. They further on noted that critics of the Bayesian approach have often debunked Bayesian methodology by alleging that it was computer intensive. This might have been a valid criticism in the past before the advent more user friendly statistical software and fast algorithms became available (Misztal *et al.*, 2002). Against this background, this study aimed to demonstrate that Bayesian methods are more appropriate for the estimation of genetic parameters for categorical traits than linear methods. It was also intended to add value to the (co)variance components and ratios derived using REML procedures in Chapter 4 by applying Bayesian methods to estimate (co)variance components, posterior standard deviations, 95 % highest posterior density confidence intervals, variance ratios of subjectively assessed and objectively measured traits in a in Dorper flock as well as genetic, maternal, dam permanent environmental and environmental relationships between these traits.

5.3 Materials and Methods

The origin of the data, description of the subjectively assessed and objectively measured traits, data editing as well as the descriptive statistics of the data were given in section 4.3.

5.3.1 Statistical analysis

The data were analyzed using multi-trait linear-threshold and threshold-threshold animal models. The fixed effects that were fitted were year of birth (21 levels), age of dam (7 levels), sex (2 levels) and birth type (2 levels). Furthermore, the ages at which live weights were recorded were fitted as linear covariates for the respective live weight traits. These fixed effects had been shown to be significant ($P < 0.05$) using the ASREML program (Gilmour *et al.*, 2002) as described in section 4.3.2. The fitted models included a combination of direct additive, maternal additive and maternal permanent environmental effects as was demonstrated through the implementation of the Likelihood ratio test in the REML analyses. It is however essential to state at this juncture that the parameters generated are dependent on the models that are implemented. The following multi-trait models were therefore implemented:

Model 1 $y_{ijklm} = f_{ij} + a_{ik} + e_{ijklm}$

Model 2 $y_{ijklm} = f_{ij} + a_{ik} + m_{ik} + e_{ijklm}$

Model 3 $y_{ijklm} = f_{ij} + a_{ik} + c_{il} + e_{ijklm}$

Model 4 $y_{ijklm} = f_{ij} + a_{ik} + m_{ik} + c_{il} + e_{ijklm}$

In this model, y was a vector of observations for underlying values for i th trait; f_{ij} was the fixed effect j for the i 'th trait; a_{ik} was the additive genetic effect of the k th animal for the i 'th trait; m_{ik} was the maternal genetic effect of the k 'th animal for the i 'th trait, c_{il} was the dam permanent environmental effect of the l 'th animal for the i 'th trait and e_{ijklm} was the vector of randomly distributed residual effects.

The software used was THRGIBBSF90 (Misztal *et al.*, 2002). This software was reported by Lee *et al.* (2002) to be suitable for the estimation of variance components and genetic parameters in threshold animal mixed models for any combination of categorical and continuous traits. The software is robust enough to handle multiple-trait analyses efficiently regardless of the presence of missing observations. The program POSTGIBBSF90 was used for post-Gibbs analysis (Misztal *et al.*, 2002). The use of such software has been applied in the estimation of genetic parameters for lamb survival in South African Merino sheep by Cloete *et al.* (2009). Our study generated single chains of 1 000 000 samples with the first 250 000 samples being discarded as the burn-in period. For all analyses, convergence was assessed using methodology presented by Raftery & Lewis (1992). Convergence of the analyses was confirmed the attainment of a stationary stage by graphical through graphical inspection after plotting the post Gibbs sample values against the iterations. Every 10th sample was stored after 250 000 iterations, giving a total of 75 000 samples for the computation of posterior means and posterior Standard Deviations (PSD), as well as 95% Highest Posterior Density (HPD) confidence intervals. Based on results from the analysis, 95% HPD confidence intervals were also computed for the (co)variance components when applicable. Point estimates were calculated as the posterior mean of the specific variance component, using the results from the final 75 000 samples as set out above. Direct genetic, maternal, dam permanent environmental and environmental (residual) correlations were derived from these analyses.

5. 4 Results and Discussion

Only a few random samples of 95 % confidence intervals of the Highest Posterior Densities (HPD) histograms for the assessed traits are discussed and presented in (Figures 5.4.1 to 5.4.4). However, it should be noted at this stage that several hundreds of 95 % confidence interval (HPDs) were generated in the different multi-trait combinations. The ones that are reported in this section are purely for demonstrative purposes. The difference in the skewedness of the additive genetic variance distributions for the categorical subjectively assessed traits was vividly clear from the sample graphs. It was demonstrated that subjectively assessed traits approximated normal distributions and exhibited very low additive genetic variation. This observation is in concordance with the observations reported in Table 4.4.1.3. However, the magnitudes of the additive genetic variations differed depending on whether the method of inference was either the Bayesian or REML. Gibbs sampling generally reported higher genetic variation than REML for threshold traits because of its better statistical properties for analysing data that does not observe a normal distribution. Bayesian methods took into cognizance the fact that all the five subjective traits had 5 categories and 4 thresholds. The distributions of the additive genetic variances were quite informative because in our view thorough diagnostic tests were conducted as per the guidelines of Raftery & Lewis (1992) to confirm convergence when the post Gibbs samples approached a stationery phase. It can thus be said in a nutshell that the subjective trait that exhibited the most additive

genetic variation was Conformation which ranged from 0.1059 to 0.9496 depending on the trait combination and the least was Fat distribution which ranged from 0.022 to 0.096.

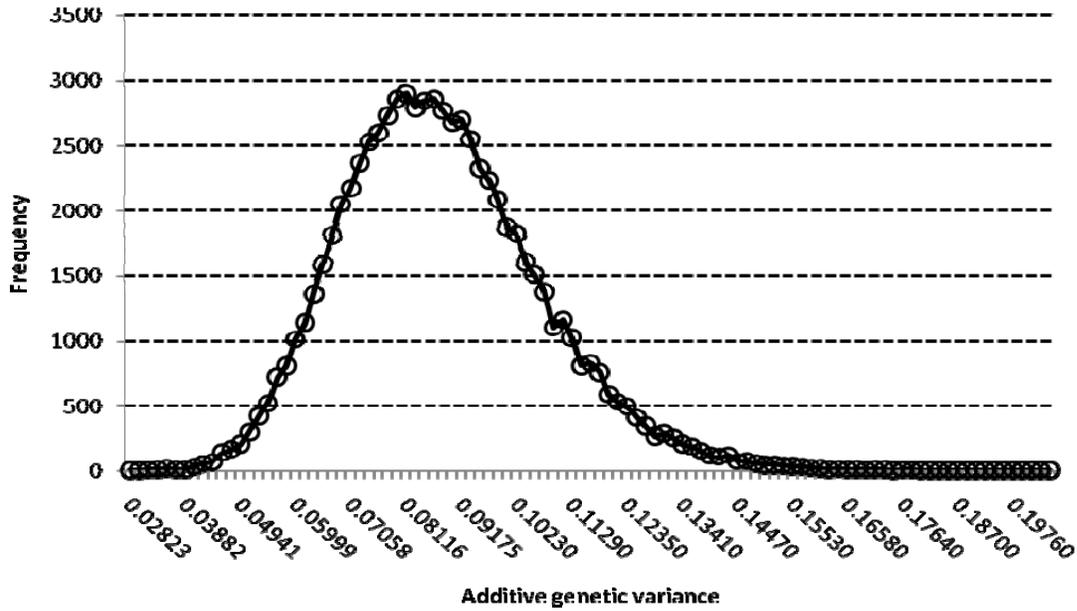


Figure 5.4.1 Posterior density distribution for the additive genetic variance of Size

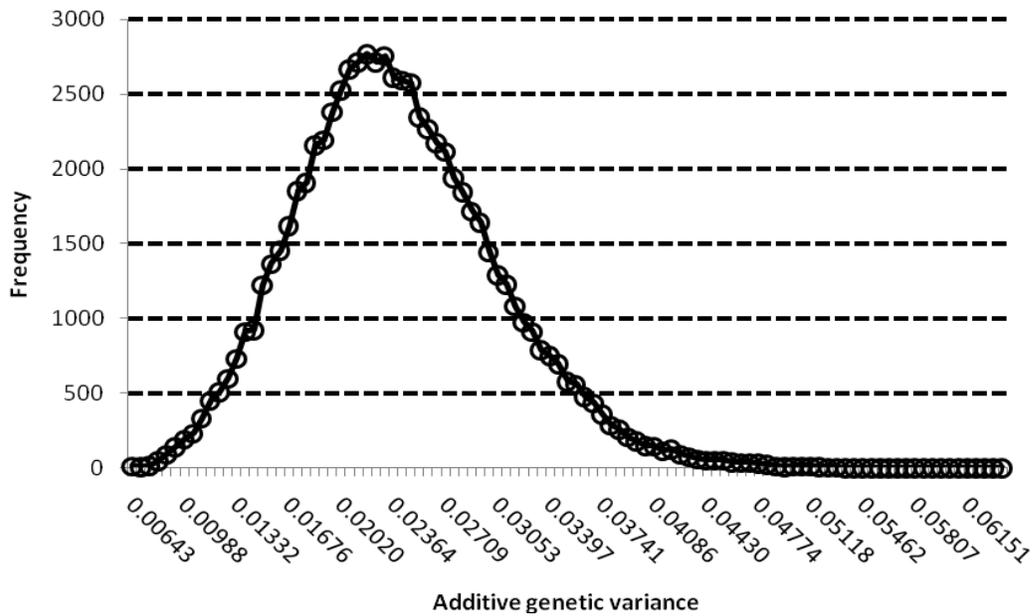


Figure 5.4.2 Posterior density distribution for the additive genetic variance of Colour

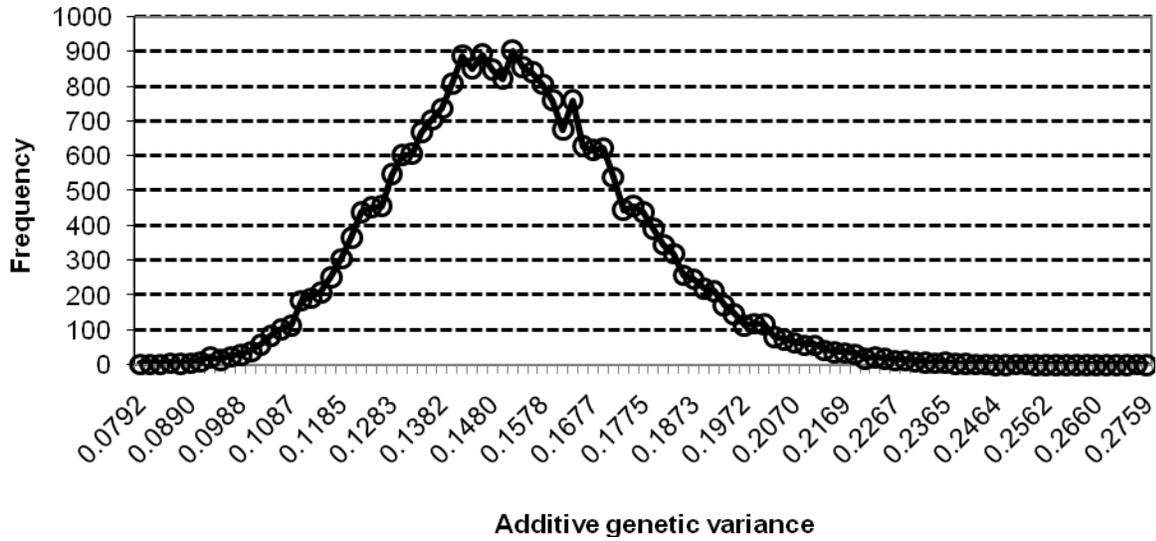


Figure 5.4.3 Posterior density distribution for the additive genetic variance of Type

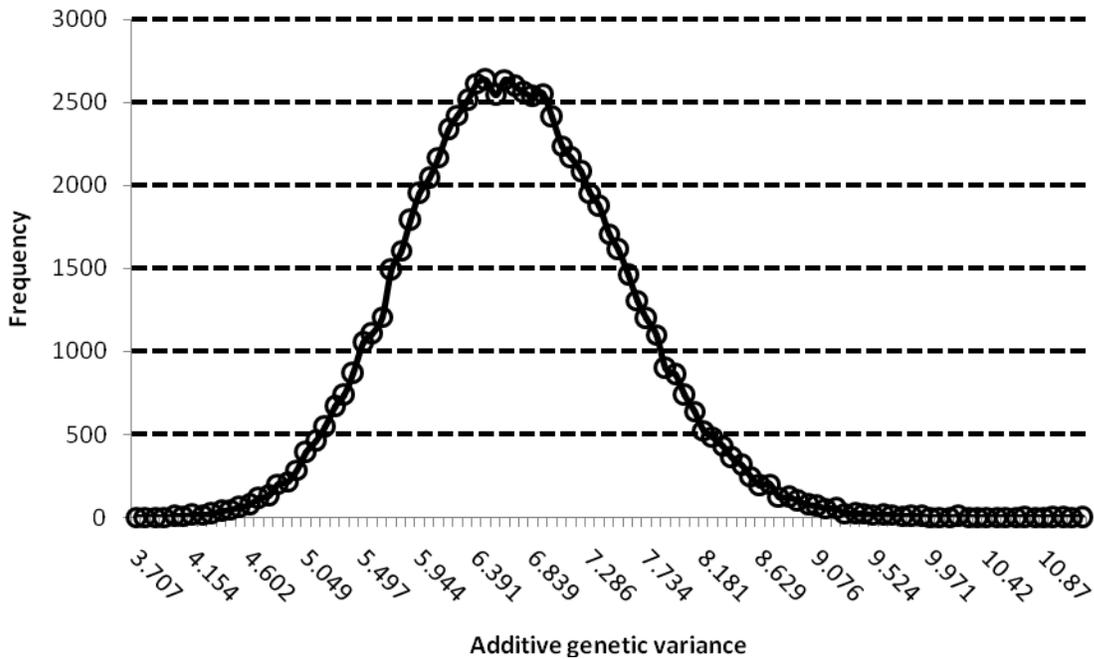


Figure 5.4.4 Posterior density distribution for the additive genetic variance of weaning weight

The genetic parameters that were derived from a series of two-trait analyses that fitted only the additive genetic effect as the random term are reported in Table 5.4.1. Parameters from three-trait analyses that accounted for direct, maternal and dam permanent environmental effects are presented in Tables 5.4.3 to 5.4.6. Although it is easy to analyse more traits in a single run with THRGIBBSF90 (Misztal *et al.*, 2002), the present study was confined to a series of three-trait analyses to compare parameters with those obtained from linear models. It was clearly evident that the mean direct heritability (h^2) estimates that culminated from the implementation of Gibbs sampling were generally higher than the ones generated by REML (see Chapter 4). Furthermore, in addition to point estimates, Gibbs sampling also reported some informative highest posterior density (HPD) confidence intervals that can be useful during the design and implementation of animal breeding plans. The highest posterior density (HPD) confidence interval for conformation (Conf) additive genetic variance ranged from a minimum of 0.1072 to a maximum of 0.6975 depending on the two-trait combination. The additive genetic variance (0.042) that was computed through REML for Conf fell below the lower HPD limit. The mean h^2 of Conf ranged from 0.12 ± 0.08 to 0.29 ± 0.09 depending on the two-trait combination. These estimates are significantly higher than the estimate obtained using REML (0.07 ± 0.02) and that reported by Olivier & Cloete (2006) in the magnitude of 0.10. In their study the former authors also demonstrated that the additive genetic variance of Conf is quite low. The low genetic variance of Conf led to the conclusion that although it is feasible to genetically improve Dorper sheep on the basis of subjective conformation scores, genetic progress would take a long time to lead to appreciable genetic gains. It might not be very economic and prudent to select animals on the basis of these scores.

Highest posterior density (HPD) confidence interval for Colour additive genetic variance ranged from 0.0106 to 0.0366 as depicted in Table 5.4.4 and Table 5.4.5. The additive genetic variance (0.063) that was computed through REML for Colour fell outside the HPD interval. The mean h^2 of Colour was 0.16. The estimate was significantly higher than the estimate obtained using REML (0.09 ± 0.02) regardless of the fact that the REML five-trait analyses and the Gibbs three-trait analyses operational models accounted for the very low dam permanent environmental effect (c^2) which did not differ much from zero (0.03 ± 0.01 vs 0.01 ± 0.01 respectively). The environmental (residual) variation (σ_e^2) ranged from 0.1085 to 0.1368 in the three-trait analyses which included the dam permanent environmental effect, and was greater than the mean additive genetic variance. The environmental correlations (r_e) between correlations between Colour, Size and yearling weight were demonstrated to be low using a three-trait analysis that accounted for maternal effects. That implied that there were other aspects, apart from genetics, that had an impact on Colour that were not addressed by this study. It could have been measurement error or difficulty in scoring fairly uniform animals. The h^2 estimates for Colour computed in this study are quite novel because there is no other literature estimate to compare with. Be that as it may have been, genetic improvement of Dorper sheep on the basis of Colour should be no longer be a major focus since the desired phenotypic colour of a black head as and white body has stabilized in the breed. Furthermore,

Colour was observed to exhibit a low genetic correlation with Size, Type and weaning weight (0.28 ± 0.14 , 0.36 ± 0.14 and 0.06 ± 0.02 respectively) when models that accounted for maternal effects were fitted using three-trait analyses. More focus should be diverted towards improving objectively measured traits of economic importance, while the objective should be to maintain the existing standards as pertaining to colour.

Table 5.4.1 Mean (co)variance components, posterior Standard Deviations (PSD), 95% highest posterior density (HPD) confidence intervals and variance ratios of live weights and subjective scores in a Dorper flock using a series of two-trait analyses

Objective traits	Item	Conformation	Fat Distribution
Weaning Weight	PSD	0.0989	0.0105
	Lower HPD	0.1587	0.0100
	Higher HPD	0.5462	0.0512
	σ_a^2	0.3525	0.0306
	σ_e^2	2.3890	0.2045
	σ_p^2	2.7415	0.2351
	$h^2 \pm SE$	0.13 ± 0.07	0.13 ± 0.09
Post-weaning weight	PSD	0.0891	0.0135
	Lower HPD	0.1757	0.0110
	Higher HPD	0.5251	0.0637
	σ_a^2	0.3504	0.0373
	σ_e^2	2.2900	0.1883
	σ_p^2	2.6404	0.2256
	$h^2 \pm SE$	0.13 ± 0.07	0.17 ± 0.12
Yearling Weight	PSD	0.0960	0.0133
	Lower HPD	0.1834	0.0140
	Higher HPD	0.5597	0.0660
	σ_a^2	0.3716	0.0400
	σ_e^2	2.3740	0.1893
	σ_p^2	2.7456	0.2293
	$h^2 \pm SE$	0.14 ± 0.07	0.17 ± 0.11

Table 5.4.2 Genetic and environmental correlations between live weights and subjective scores in a Dorper flock using two-trait analyses

Objective traits	Type of correlation	Conformation	Fat Distribution
Weaning Weight	Genetic	0.25±0.05	0.65±0.02
	Environmental	0.31±0.03	0.60±0.01
Post-weaning weight	Genetic	0.17±0.07	0.71±0.04
	Environmental	0.67±0.04	0.25±0.02
Yearling weight	Genetic	0.36±0.06	0.80±0.02
	Environmental	0.07±0.06	0.37±0.03

Table 5.4.3 Mean (co)variance components, posterior Standard Deviations (PSD), 95% highest posterior density (HPD) confidence intervals and variance ratios of Size, Type and Weaning Weight in a Dorper flock using a three-trait analysis

	(Co)variance		95 % HPD interval			
TRAITS	Component	PSD	Lower	Upper	Item	Ratio±SE
Additive direct genetic variance (σ_a^2)						
Size	0.0871	0.0192	0.0495	0.1246	h^2	0.17±0.07
Type	0.1225	0.0307	0.0624	0.1826	h^2	0.10±0.05
WW	6.6270	0.8468	4.9670	8.2870	h^2	0.31±0.08
Maternal genetic variance (σ_m^2)						
Size	0.0484	0.0113	0.0263	0.0705	m^2	0.10±0.04
WW	1.6580	0.3800	0.9133	2.4030	m^2	0.08±0.03
Dam permanent environmental variance (σ_c^2)						
Type	0.0230	0.0113	0.0010	0.0451	c^2	0.02±0.02
WW	0.8475	0.3107	0.2384	1.4570	c^2	0.04±0.03
Environmental variance (σ_e^2)						
Size	0.3665	0.0243	0.3189	0.4140	-	-
Type	1.0270	0.0648	0.9000	1.1540	-	-
WW	12.530	0.5789	11.4000	13.6600	-	-
Additive covariance (σ_a)						
Size, Type	0.0752	0.0201	0.0357	0.1146	r_g	0.73±0.19
Size, WW	0.6149	0.1092	0.4009	0.8289	r_g	0.81±0.03
Type, WW	0.2931	0.1225	0.0530	0.5332	r_g	0.33±0.03
Maternal covariance (σ_m)						
Size, WW	0.2257	0.0580	0.1121	0.3394	r_m	0.80±0.07
Dam permanent environmental covariance (σ_c)						
Type, WW	0.0747	0.0549	-0.0329	0.1823	r_c	0.53±0.12
Environmental covariance (σ_e)						
Size, Type	0.3429	0.0225	0.2988	0.3870	r_e	0.56±0.03
Size, WW	1.4710	0.0877	1.2990	1.6430	r_e	0.69±0.01
Type, WW	1.3600	0.1074	1.1500	1.5710	r_e	0.38±0.02

Table 5.4.4 Mean (co)variance components, posterior Standard Deviations (PSD), 95% highest posterior density (HPD) confidence intervals and variance ratios of Colour, Size and Yearling Weight in a Dorper flock using a three-trait analysis

	(Co)variance		95 % HPD interval			
TRAITS	Component	PSD	Lower	Upper	Item	Ratio±SE
Additive direct genetic variance (σ_a^2)						
Colour	0.0226	0.0065	0.0099	0.0354	h^2	0.15±0.09
Size	0.1089	0.0245	0.0508	0.1569	h^2	0.21±0.09
YW	9.5750	2.3450	4.9780	14.1700	h^2	0.43±0.20
Maternal genetic variance (σ_m^2)						
Size	0.0427	0.0117	0.0197	0.0657	m^2	0.08±0.04
YW	4.6090	1.1820	2.2910	6.9260	m^2	0.21±0.10
Dam permanent environmental variance (σ_c^2)						
Colour	0.0041	0.0025	0.0000	0.0089	c^2	0.03±0.03
Environmental variance (σ_e^2)						
Colour	0.1233	0.0071	0.1094	0.1373	-	-
Size	0.3768	0.0300	0.3179	0.4356	-	-
YW	8.2480	1.5130	5.2820	11.2100	-	-
Additive covariance (σ_a)						
Colour, Size	0.0141	0.0092	-0.0039	0.0321	r_g	0.28±0.14
Colour, YW	0.0153	0.0975	-0.1759	0.2064	r_g	0.03±0.02
Size, YW	0.6530	0.1797	0.3008	1.0000	r_g	0.64±0.04
Maternal covariance (σ_m)						
Size, YW	0.2237	0.0852	0.0567	0.3907	r_m	0.50±0.10
Environmental covariance (σ_e)						
Colour, Size	0.0472	0.0078	0.0319	0.0625	r_e	0.22±0.03
Colour, YW	0.0513	0.0858	-0.1169	0.2195	r_e	0.05±0.02
Size, YW	0.4540	0.1540	0.1522	0.7557	r_e	0.26±0.03

Table 5.4.5 Mean (co)variance components, posterior Standard Deviations (PSD), 95% highest posterior density (HPD) confidence intervals and variance ratios of Colour, Type and Weaning Weight in a Dorper flock using a three-trait analysis

	(Co)variance		95 % HPD interval			
TRAITS	Component	PSD	Lower	Upper	Item	Ratio±SE
Additive direct genetic variance (σ_a^2)						
Colour	0.0236	0.0066	0.0106	0.0366	h^2	0.16±0.09
Type	0.1124	0.0291	0.0553	0.1694	h^2	0.10±0.05
WW	6.6570	0.8409	5.0090	8.3060	h^2	0.31±0.08
Dam permanent environmental variance (σ_c^2)						
Colour	0.0020	0.0011	0.0000	0.0041	c^2	0.01±0.01
Type	0.0234	0.0106	0.0026	0.0442	c^2	0.21±0.10
WW	0.8493	0.3087	0.2442	1.4540	c^2	0.04±0.03
Maternal variance (σ_m^2)						
WW	1.6570	0.3727	0.9263	2.3870	m^2	0.08±0.03
Environmental variance (σ_e^2)						
Colour	0.1227	0.0072	0.1085	0.1368	-	-
Type	1.0070	0.0647	0.8802	1.1340	-	-
WW	12.4800	0.5734	11.3600	13.6100	-	-
Additive covariance (σ_a)						
Colour, Type	0.0188	0.0103	-0.0015	0.0391	r_g	0.36±0.14
Colour, WW	0.0249	0.0515	-0.0761	0.1258	r_g	0.06±0.02
Type, WW	0.2800	0.1198	0.0452	0.5149	r_g	0.32±0.03
Environmental covariance (σ_e)						
Colour, Type	0.0828	0.0102	0.0628	0.1027	r_e	0.24±0.02
Colour, WW	0.2803	0.0404	0.2012	0.3594	r_e	0.23±0.01
Type, WW	1.3430	0.1077	1.1320	1.5540	r_e	0.38±0.02

Table 5.4.6 Mean (co)variance components, posterior Standard Deviations (PSD), 95% highest posterior density (HPD) confidence intervals and variance ratios of Type, Weaning Weight and Yearling Weight in a Dorper flock using a three-trait analysis

	(Co)variance		95 % HPD interval			
TRAITS	Component	PSD	Lower	Upper	Item	Ratio±SE
Additive direct genetic variance (σ_a^2)						
Type	0.0500	0.0142	0.0222	0.0777	h^2	0.07±0.04
WW	6.5760	0.8321	4.9450	8.2070	h^2	0.31±0.08
YW	11.460	2.5960	3.3710	16.5500	h^2	0.50±0.22
Maternal genetic variance (σ_m^2)						
WW	1.5430	0.3634	0.8308	2.2550	m^2	0.07±0.03
YW	4.4530	1.1520	2.1930	6.7140	m^2	0.19±0.10
Dam permanent environmental variance (σ_c^2)						
Type	0.0111	0.0045	0.0022	0.0199	c^2	0.02±0.01
WW	0.8650	0.2971	0.2826	1.4470	c^2	0.04±0.03
Environmental variance (σ_e^2)						
Type	0.6192	0.0161	0.5876	0.6508	-	-
WW	12.5600	0.5702	11.4500	13.6800	-	-
YW	7.0210	1.5910	3.9030	10.1400	-	-
Additive covariance (σ_a)						
Type, WW	0.1941	0.0803	0.0367	0.3514	r_g	0.34±0.02
Type, YW	0.21920	0.1361	-0.0475	0.4860	r_g	0.29±0.02
WW, YW	5.6200	1.1510	3.3640	7.875	r_g	0.65±0.13
Maternal covariance (σ_m)						
WW, YW	1.6890	0.5235	0.6626	2.7150	r_m	0.64±0.17
Environmental covariance (σ_e)						
Type, WW	0.9477	0.0687	0.8131	1.0820	r_e	0.34±0.01
Type, YW	0.3685	0.1420	0.0901	0.6469	r_e	0.18±0.04
WW, YW	3.6840	0.8176	2.0810	5.2860	r_e	0.39±0.08

The highest posterior density (HPD) confidence interval for Fat distribution (Fat) additive genetic variance ranged from a minimum of 0.01002 to a maximum of 0.0660 depending on the two-trait combination (Table 5.4.1). The additive genetic variance (0.024) that was computed through REML for Fat fell within the HPD interval. This attributes confirms the traditional belief that linear methods are also useful in the estimation of genetic parameters. The mean h^2 of Fat ranged from 0.13±0.09 to 0.17±0.12 depending on the two-trait combination. These lowest estimate is quite similar to the estimate obtained using REML

(0.13±0.02) although the standard error for the former is quite high. The mean environmental (residual) variation (σ_e^2) ranged from 0.1410 to 0.2045 and was greater than the mean additive genetic variance. This implied that there were other aspects apart from genetics that had an impact on Fat distribution.

Additive genetic variance highest posterior density (HPD) confidence interval for Size ranged from a minimum of 0.0495 to a maximum of 0.1246 depending using three-trait analyses (Table 5.4.3 and Table 5.4.4). The additive genetic variance (0.068) that was computed through REML for Size fell within the HPD 95 % confidence interval. The mean h^2 of Size was 0.17±0.07 when maternal effects were taken into account using the three-trait analyses. This moderate estimate although slightly higher than the ones derived using linear methods are in concordance with the h^2 reported by Olivier & Cloete (2006) of 0.25. The mean maternal heritability estimate that was derived using Bayesian inference (0.10±0.04) was low and in agreement with the REML estimate although they differed in magnitude. There are no comparable estimates reported in literature except to mention that Olivier & Cloete (2006) fitted a model that only accounted for the additive direct effects for Size and they derived an inflated direct heritability estimate. The mean environmental (residual) variation (σ_e^2) ranged from 0.3567 to 1.331 and was greater than the mean additive genetic variance implying that there were other aspects apart from genetics that have an effect impact on Size. It can be concluded that that (co) variance components and ratios generated in this study for Size add value and precision to the preliminary study conducted by Olivier & Cloete (2006).

Confidence intervals of the highest posterior density (HPD) for Type additive genetic variance ranged from a minimum of 0.0222 to a maximum of 0.1826 depending on the three-trait combination (Table 5.4.3, Table 5.4.5 and Table 5.4.6). The additive genetic variance (0.052) that was computed through REML for Type fell within the HPD interval although the mean σ_a^2 were higher than the point REML estimates. The mean h^2 of Type ranged from 0.11±0.05 to 0.29±0.09 depending on the three-trait combination. The estimates were higher than those obtained using REML (0.07±0.02). However it must be further stipulated that both Gibbs sampling and REML analyses managed to partition the additive genetic variation into both direct effects and dam permanent environmental effects despite the fact that the dam permanent environmental estimate for Type did not differ much from zero (0.02±0.02 and 0.02±0.01) when Type was modeled in conjunction with Size, Weaning weight and Yearling weight. However, when Type was modeled with Colour and Weaning weight the dam permanent environment estimate was moderate (0.21±0.10). It was also noted that the mean environmental (residual) variation (σ_e^2) ranged from 0.1173 to 1.301 and was far much greater than the mean σ_e^2 as well as the point estimate derived through REML procedures. The h^2 estimates generated by the three-trait analyses were more accurate than the 0.11 which was reported by Olivier & Cloete (2006) because maternal effects were taken into account. The low to moderate heritability estimates accompanied by low additive genetic variance for subjective traits suggest that genetic progress in such traits is feasible although genetic gains may be quite slow.

The genetic parameters computed for objectively measured traits in the Dorper flock using a series of threshold-linear models closely resembled those generated by REML. It is crucial to note that there is a paucity of literature estimates using Bayesian methods hence most comparable estimates were derived through the implementation of REML. The h^2 estimates of weaning weight (WW) in different combinations with the three subjectively assessed traits that accounted for maternal effects were all 0.31 ± 0.08 . These estimate differed from the moderate one of 0.19 that was obtained in the preliminary study by Olivier & Cloete (2006). Although the estimate was high it was consistent with some literature estimates. Brash *et al.* (1994b and c) reported a h^2 of 0.45 ± 0.07 using 7 030 records and 0.34 ± 0.07 using 3 202 records respectively of Coopworth sheep through the application of REML procedures.

However, it is worth mentioning that most h^2 estimate for WW in both meat and dual purpose breeds were reported in literature to be moderate (Fossceco & Notter, 1995; Hall *et al.*, 1995; Yazdi *et al.*, 1997; Wuliji *et al.*, 1998; Naser *et al.*, 2001; Rao & Notter 2000 and Maniatis & Pollott, 2002a). The current study also derived HPD confidence intervals for additive genetic variance of WW in the range 6.352 to 9.752. This interval contained the point σ_a^2 of 9.28 that was computed using ASREML. Direct maternal and dam permanent environmental effects for weaning weight were demonstrated to be low using Bayesian inference. The genetic correlation between weaning weight and Size was high (0.81 ± 0.03) and it was moderate with Type. The mean residual variation (σ_e^2) that was derived ranged from 11.36 to 13.68 using Gibbs sampling was fairly comparable with the value of 11.55 generated by REML. It is however essential to state at this juncture that the estimates generated are dependent on the models that are implemented. A review of genetic parameters for various traits in diverse sheep breeds was subsequently conducted by Safari *et al.* (2005b). With regards to growth traits the authors concluded that the weighted means of heritability for growth traits were generally moderate in magnitude and ranged from 0.15 to 0.41 with very low standard errors (range 0.01–0.04) of the means. They also noted that heritability increased with age to post-weaning and adult weights.

Table 5.4.4 and Table 5.4.6 report that the h^2 estimates of yearling weight (YW) in combination with subjectively assessed traits ranged from 0.43 ± 0.20 to 0.50 ± 0.22 using three-trait analyses. The increment in additive genetic variation from weaning age to yearling age confirms early literature reports (Tosh & Kemp, 1994; Maniatis & Pollott, 2002a; Simm *et al.*, 2002; Safari *et al.*, 2005; Zishiri, 2009). The high h^2 estimates generated with the Gibbs sampler are in concordance with other literature estimates Brash *et al.* (1992) reported a high 14 month weight h^2 of 0.40 ± 0.10 in the dual purpose Coopworth sheep. However, their model incorporated the additive direct genetic effects as the only random effect. Atkins *et al.* (1991) also obtained a high h^2 of 0.31 ± 0.04 in the Poll Dorset meat sheep with a similar model. The high estimates obtained in our study suggest that yearling weight is highly heritable and significant selection progress can be attained if the trait is incorporated into selection indices. HPD confidence intervals for additive genetic variance in the range 3.371 to 16.550 were also derived. This interval

included the point σ_a^2 estimate of 12.37 that was computed using ASREML. Three-trait analyses that accounted for maternal effects resulted in high maternal genetic correlations between weaning weight and yearling weight. However, the environmental correlation between yearling weight with Size and Colour were low when models that accounted for maternal effects were implemented. The mean residual variations (σ_e^2) that were derived ranged from 3.9030 to 11.2100 using Gibbs sampling and were therefore in concordance with the one generated by REML of 10.00.

Genetic and environmental correlations (Table 5.4.2) between objectively measured and subjectively assessed traits generated in this study through the implementation of Gibbs sampling are quite novel and contribute to existing knowledge. The genetic correlation (r_g) between Conf and WW was 0.25 ± 0.05 . This low positive correlation was different from 0.43 ± 0.09 that was derived in the preliminary study by Olivier and Cloete (2006) using REML procedures. This current study also derived a r_g of 0.39 ± 0.11 using REML procedures using the same data and models. The environmental correlation (r_e) from this study using Gibbs sampling was not very different from the one derived through REML (0.31 ± 0.03 vs 0.24 ± 0.01). Conf was also lowly genetically correlated with PWW (0.17 ± 0.07) but the environmental correlation was high (0.67 ± 0.04). The r_g and r_e generated using REML were in the same direction but different in magnitude (Table 4.4.1.4). The current estimates differ from the one derived by Olivier & Cloete (2006) because their r_g varied from negative through zero to lowly positive (0.12 ± 0.16). The Bayesian r_g estimate between Conf and YW was positive and moderate (0.36 ± 0.06). This was in concordance with the REML estimate derived in this study (0.41 ± 0.16). The environmental correlations were low using both methods (0.07 ± 0.06 and 0.14 ± 0.03 respectively). In summary Conf was lowly but positively genetically and environmentally correlated with average daily weight gains. Selecting Dorper sheep on the basis of Conf does not have a deleterious effect on live weights due to lack of antagonisms. However more emphasis should be placed on recording objective measurements and selecting animals on the basis of breeding values.

Bayesian inference concluded that Colour had little or no genetic correlation with YW (0.03 ± 0.02). However the residual correlations were low and positive in both cases. It can therefore be concluded that breeders should not put much effort on selection for Colour because the trait has reached its desired phenotype of a black head and a white body in the national flock. Much focus should be placed on selection on the basis of objective traits of economic importance, while the current standards for colour is maintained.

High genetic correlations in the magnitude of 0.65 ± 0.14 to 0.80 ± 0.02 (Table 5.4.2) were derived for the relationships between Fat distribution and WW and YW respectively. It can thus be said that heavy and fast growing animals have the potential to be fat. However, there are no literature estimates for comparison of these estimates except the similar REML correlations that were unearthed as part of this study. These positive correlations indicate that selecting Dorper sheep on the basis of the Fat distribution

score does not have a negative impact on the growth traits. Likewise one would also infer that selecting animals that have good average daily gains to weaning, during post-weaning and up to yearling age will result in animals that have a reasonable fat distribution although the exact magnitude of the fat distribution is unknown.

It is also critical to mention that Fat distribution scores should be treated with caution as too fat animals may be undesirable although having desirable growth patterns. Size was also highly positively genetically correlated with live weight traits. This attribute confirmed the similar findings that were derived using REML procedures in both this study as well as the preliminary study by Olivier & Cloete (2006). Although the results that were obtained with regards to Size are favourable, there is a need for scientists and breed societies to design efficient selection objectives that take into cognizance the economic values associated with each trait. It would be injudicious for Dorper sheep to be too big because originally the Dorper breed was developed as a culmination of the need for a sheep breed suitable for the production of slaughter lambs under South African adverse arid environments (Cloete *et al.* 2000). The breed should be able to thrive during times of under-nutrition. This implies that very huge Dorpers would have huge nutritional demands and might cost dearly to rear

Type was basically positively correlated with all the other traits that were considered because Type is judged according to the degree to which the sheep conforms to the general requirements of the breed. Emphasis is placed on Conformation, Size and Fat distribution when determining type. Therefore, Type tried to generalize all the subjectively assessed traits that we have been studying. However, scientific studies would not like to underpin their findings on generalizations when enough detail can be obtained by scrutinizing every single detail and parameter at our disposal.

5.5 Conclusion

Animal breeders should not over concentrate on the philosophical problems associated with statistical inference but in tools to solve problems. Both Bayesian and frequentist schools of inference are well established and it is not necessary to justify why one or the other school is preferred. It has been demonstrated in this study that both schools to provide solutions to animal breeding problems. However, it has been established in this study that Bayesian methods are more appropriate than linear methods for the estimation of variance components and ratios of categorical traits because of their desirable statistical properties. Therefore, to preferentially choose one school to the other should be related to whether there are solutions in one school that the other does not offer and how easily the problems are solved. Both schools present formal problems and paradoxes, although problems and paradoxes with methods of greater familiarity are often better tolerated (Blasco, 2001). The low to moderate heritability estimates for

subjective traits suggest that genetic progress in such traits is feasible although genetic gains will be quite slow. Fortunately all subjectively assessed traits except Colour have reasonable genetic relationships with objectively measured traits. It is no longer necessary to exert great emphasis on Colour because this study has demonstrated that selection based on Colour will have little or no effect on the breeding soundness of Dorpers since the desired phenotype of a black head and white body has already stabilized in the national flock. Breeders should emphasize performance recording of objective traits with the overall objective of selecting their animals on the basis of breeding values for traits of economic importance.

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CHAPTER 6

GENETIC TRENDS

FOR OBJECTIVELY MEASURED AND SUBJECTIVELY ASSESSED TRAITS IN A DORPER FLOCK

6.1 Abstract

Genetic trends were constructed to monitor genetic change for subjectively assessed and objectively measured traits using data emanating from complete records from the NSIS database and performance records accumulated by a single breeder over a period of 24 years. The objectively measured production traits considered were weaning weight (WW), post-weaning weight (PWW), yearling weight (YW), average daily weight gain to weaning (ADGW), average daily weight gain during post-weaning phase (ADGPW), and average daily weight gain up to yearling age (ADGYW). The subjectively assessed traits (scored on a 5-point scale) were Conformation, Fat distribution, Size, Type and Colour. Direct breeding values were derived for each trait by using the data from the most appropriate single-trait animal model in ASREML. Maternal genetic trends were included where appropriate. Genetic trends were calculated as the regression of average predicted breeding value on year of birth using standard regression techniques. Direct genetic trends for live weight and growth traits (with the exception of ADGPW) were positive. All the objectively measured traits where maternal effects were significant except PWW registered small declines in maternal breeding values. The fastest genetic progress was attained by ADGW which amounted to 0.29 % of the overall phenotypic mean per annum. Conformation and type exhibited positive but slow increments in direct breeding values at an equivalent annual rate amounting to 0.12 % and 0.09 % of the overall phenotypic mean respectively. Size was demonstrated a negative genetic trend of -0.14 % of the overall phenotypic mean per annum. Genetic trends for Fat distribution and Colour were negligible. It was concluded that breeders should focus more on performance recording of objective traits as they are likely to respond favourably to selection pressure.

Keywords: Direct, maternal, regression, selection response, EBV, trend, progress

6.2 Introduction

Livestock breeding programmes must be revisited regularly to ensure genetic change in the desired direction takes place. Genetic trends indicate the extent of genetic change in a population. In order to determine the effectiveness of genetic selection, genetic trends in the population under consideration need to be monitored on a regular basis (Van Wyk *et al.*, 1993b). Selection on best linear unbiased prediction (BLUP) of breeding values derived through the implementation of Henderson's mixed model methodology is generally recommended for livestock improvement at present, since the correlation between the predicted and true breeding value is optimized. An added advantage is that the response to selection can be determined without the use of a control population. The outcome of selection in a commercial population can therefore be monitored, as demonstrated for the Grootfontein Merino stud (Olivier *et al.*, 1995) among other studies. It is generally accepted that the partitioning of genetic and

environmental effects by an appropriate BLUP animal model that incorporates all known relationships in the population is the most effective way of quantifying genetic change. Breeding values derived from such analyses can be averaged within birth years and used to depict genetic trends.

The complexity of the production and market environment of Dorper sheep result in many factors that need consideration during the assessment of genetic change. However, many changes are affected in animal breeding plans without thorough evaluation of their effects on farm profitability. General perception suggests that Dorper sheep breeders have emphasized subjectively assessed traits, as defined in the show ring, in their breeding strategy. It was established early in the study that submission of Dorper animal performance data to National Small Stock Improvement Scheme (NSIS) was very low until around 1994. The unavailability of data suggested that Dorper breeders relied heavily on subjective scores in the show ring when they selected their breeding stock prior to 1994 (see Figure 3.2.1 in Chapter 3). The direction of genetic trends in Dorpers has not been thoroughly verified, despite early work by Olivier & Cloete (2006). It was against this background that this study extracted breeding values from a well managed and recorded commercial Dorper flock and constructed genetic trends for objectively measured and subjectively assessed traits to monitor genetic progress over two decades.

6.3 Materials and Methods

Data emanating from complete records that were used in single-trait analyses from the NSIS data base and performance records accumulated by a single Dorper breeder over a period of 24 years (1980 to 2003) were utilised. The data represented progeny of 104 sires and 2 558 dams. The objectively measured production traits considered were described in Chapter 4 in section 4.3. Descriptive statistics of the data after editing were summarised in Table 4.3.1. Direct breeding values were derived for each trait by using the data from the most appropriate single-trait animal model in ASREML (Gilmour *et al.*, 2002). Although multiple-trait breeding values would have been preferred under most conditions, such breeding values were not used to construct genetic trends in this study. The erosion of data (for instance only 26 % of the sheep with weaning weights also had post-weaning weights) resulted in inconsistencies in the data structure, singularities in the average information matrices and difficulty in achieving convergence. If the data structure had been perfect, multiple-trait breeding values would have been used to estimate the genetic trends.

Solutions depicting maternal breeding values were also included for traits where the inclusion of such effects resulted in a better fit. However, they were excluded in subjectively assessed traits owing to their low magnitude. Genetic trends were calculated as the regression of average predicted breeding value on year of birth using the Regression Procedure (REG) in the Statistical Analysis System software (SAS, 2004). Regression coefficients and their standard errors ($b \pm SE$), correlations (r) and the goodness of fit

(R^2) values were also derived as part of the procedure. Since the flock was a well-recorded commercial population, regressions were forced through the origin at all instances because the first year represented the genetic level when selection commenced. The genetic gain or loss per annum was derived by expressing the regression coefficient (b) of the particular trait genetic trend line as a percentage of the overall phenotypic mean of the particular trait.

6.4 Results and Discussion

Genetic trends for all the subjectively assessed and objectively measured traits for the period 1980 to 2003 are presented in Table 6.4.

Table 6.1 Regression coefficients (b), standard errors (SE), correlations (r), goodness of fit (R^2), overall Least Square Means (LSM) and annual genetic change (as %) for subjectively assessed and objectively measured traits in a Dorper flock. Regressions were forced through the origin.

Trait	b±SE	r	R^2	LSM	Annual genetic change (%)
WW ^a	0.073±0.004	0.76	0.50	25.4	0.29
WW ^b	-0.026±0.004	-0.83	0.69	25.4	-0.10
PWW	0.019±0.001	0.66	0.28	40.8	0.05
YW ^a	0.026±0.03	0.79	0.32	40.7	0.06
YW ^b	-0.013±0.003	-0.65	0.42	40.7	-0.03
ADGW ^a	1.183±0.080	0.92	0.82	195	0.61
ADGW ^b	-0.574±0.040	-0.95	0.90	195	-0.29
ADGPW	-0.058±0.035	-0.19	0.08	110	-0.05
ADGYW ^a	0.190±0.021	0.91	0.76	102	0.19
ADGYW ^b	-0.142±0.015	-0.89	0.79	102	-0.14
Conf	0.004±0.001	0.83	0.68	3.40	0.12
Fat	0.0009±0.0005	0.03	0.11	4.65	-0.02
Size	-0.006±0.002	-0.63	0.28	4.26	-0.14
Type	0.003±0.0006	0.78	0.54	3.25	0.09
Colour	-0.001±0.0003	0.04	0.45	3.67	-0.03

^abeing the additive direct genetic trends and ^bbeing the additive direct maternal genetic trends for specific traits

6.4.1 Genetic trends for live weight traits in a Dorper flock

The genetic trends for weaning weight, post-weaning weight and yearling weight are shown in Figure 6.4.1.

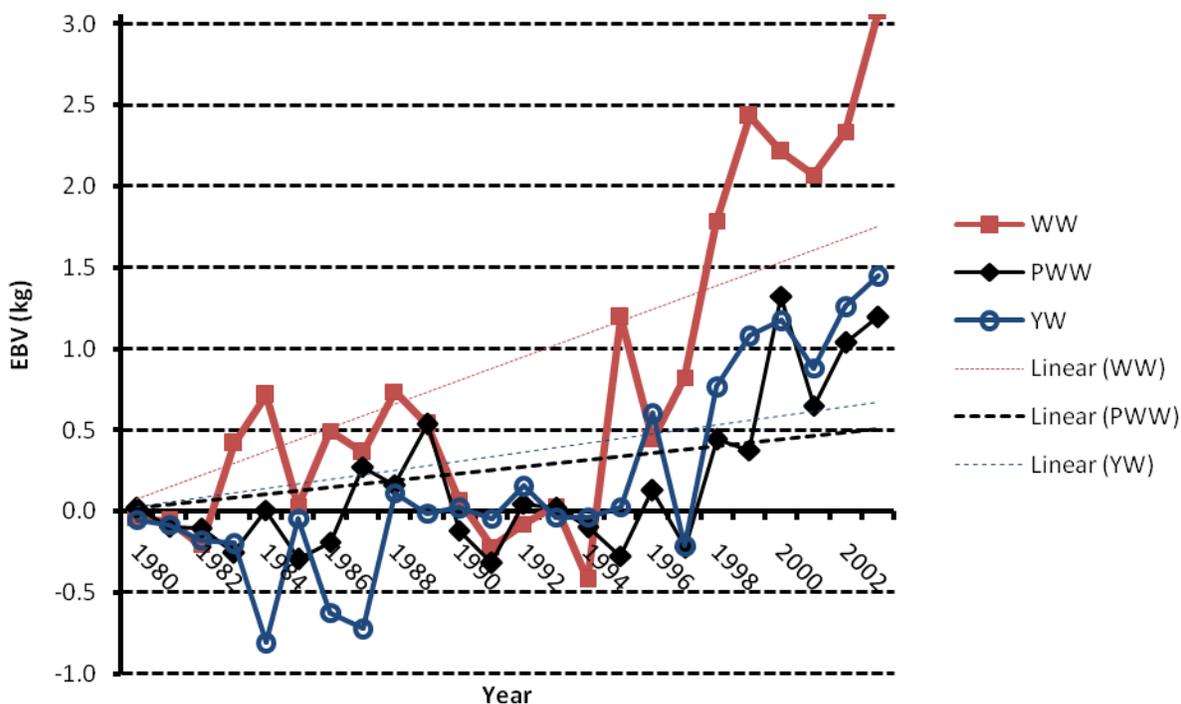


Figure 6.4.1 Additive direct genetic trends for live weight traits in a Dorper flock. Regressions were forced through the origin in all instances

It was evident that there was generally some genetic progress in weaning weight direct breeding values over 24 years of evaluation that amounted to 0.29 % per annum on average (Table 6.4). However between 1980 and 1994 the estimated direct breeding values (EBVs) oscillated from the lowest of approximately -0.50 kg through 0 kg to a maximum of approximately 0.75 kg. As from 1995 to 2003 there was a conspicuous increment in direct EBVs from 0 kg to a peak of just over 3 kg in 2003 which could probably be attributed to change in breeding strategy in the flock. It is essential to stipulate that these different trends in the graph between the stated time intervals imply that there were probably different selection criteria in the flock. A high regression correlation (r) value of 0.76 can be used to confirm this. However, there was no absolute knowledge pertaining to selection criterion afforded to the analysts by the time this chapter was written. It could have been that breed standards were emphasized prior to 1995, with more emphasis being paid to objectively measured weaning weight in later years.

It was conceded to fit the regression lines through the origin because the Dorper flock that was used in the study closely resembled an experimental flock in which subjective scores and objective measurements were recorded since 1983. It has however, already been reported that the uptake of performance recording was very slow in the entire breed until the mid 1990s. When separate regression

lines were fitted for WW between 1980 and 1993, it was evident that there was no genetic change ($b = -0.001 \pm 0.001$ and $R^2 = 0.00$). The lack of genetic change during that period implied that no selection pressure was applied on the trait. Furthermore, fitting a separate regression line between 1994 and 2003 resulted in a significant genetic progress ($b = 0.32 \pm 0.02$ and $R^2 = 0.82$). Therefore WW increased at an annual rate of 1.26 % per annum between 1994 and 2003. This positive trend could have only resulted from selection pressure being applied to the trait. On the contrary it was also evident from Figure 6.4.2 that as the direct EBVs for weaning weight increased, the propensity of the dam's genes to rear heavy progeny decreased because there was a reduction in maternal EBVs in the 24 years of evaluation which amounted to -0.10 % per annum. This further confirmed that there was an antagonistic relationship between direct additive and direct maternal effect as was reported in section 4.4.2 (see Table 4.4.1.3).

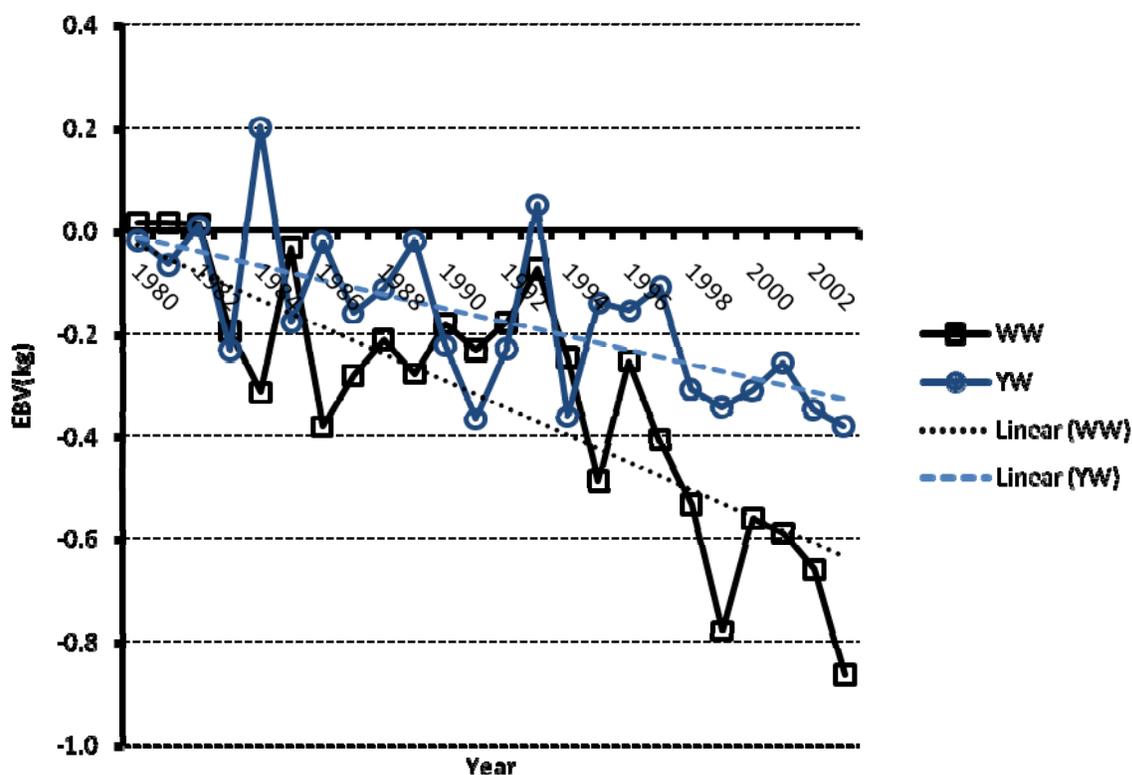


Figure 6.4.2 Maternal genetic trends for live weight traits in a Dorper flock. Regressions were forced through the origin in all instances

There is a paucity of relevant literature to compare to our current findings. However, Olivier & Cloete (2006) conducted preliminary genetic analyses for the entire Dorper breed and reported that, when the annual direct additive breeding values for WW were regressed on birth year to depict a genetic trend, the derived genetic trend amounted to 0.009 ± 0.006 kg per annum. The corresponding regression for maternal breeding values was 0.009 ± 0.005 kg per annum. Both trends did not differ from zero and

represented an annual improvement of only 0.03% when expressed relative to the overall phenotypic mean. Nesper *et al.* (1995) computed direct genetic trends for weaning weight of Dorpers on natural pastures that amounted to 0.087 kg per year, which compares well with the value in Table 6.1. In that study, positive gains were also observed for maternal breeding values (0.016 kg per year). The direction of the maternal genetic trends estimated in the current study different from that of Nesper *et al.* (1995) because different data sets had differences in pedigree depth, selection criteria and origins.

Gray *et al.*, (1999) obtained a low increment in direct EBVs for South African Mutton Merinos group breeding scheme that were assessed between 1984 and 1995. Their maternal genetic trends were decreasing slightly, possibly resulting from high negative correlations between direct additive and direct maternal effects as in the present study. Zishiri *et al.* (2010) derived direct genetic increments of weaning weight in the Dorper and Ile de France terminal sire sheep breeds amounting to 0.12 % and 1.21 % respectively. Furthermore, Olivier *et al.*, (1995) observed an increment in direct EBVs in body weight of Merino sheep amounting to 7.2 % between 1966 and 1985 (0.36 % per annum) and 22.3 % between 1985 and 1990 (3.7 % per annum) when they quantified genetic trends in the Grootfontein Merino stud. It is crucial to note that trends emanating from experimental flocks with specific breeding objectives and those from industry are difficult to compare due to conflicting breeding objectives.

Direct genetic trends for post-weaning weight were slow but in the desired direction (Figure 6.4.1). There was an annual increment in direct EBVs amounting to 0.05 % during the 24 years of evaluation (Table 6.1). This increment is quite slow especially considering that post-weaning weight has been reported to be highly heritable in previously cited literature. Olivier & Cloete (2006) reported a higher annual response to selection in PWW of 0.25 % in their preliminary analyses of the Dorper breed. The annual increment is lower than the 0.32% that was reported by Zishiri *et al.* (2010) for the Dorper breed as a whole. It was also noted that similar to trends for weaning weight, EBVs were oscillating from a minimum of approximately -0.35 kg through 0 kg to a maximum of approximately 0.5kg between 1980 and 1994. After 1994 there was an obvious incline to reach a peak of 1.2 kg in 2003. Similar inferences to those articulated for weaning weight thus can be reiterated. There were probably two different breeding policies for the time intervals. When a separate regression lines were fitted for PWW between 1980 and 1993, it was evident that there was negligible genetic change ($b = 0.01 \pm 0.01$ and $R^2 = 0.04$). The lack of genetic change during that period implied that no selection pressure was applied on the trait. Fitting a separate regression line between 1994 and 2003 resulted in a significant genetic progress ($b = 0.17 \pm 0.01$ and $R^2 = 0.77$). Therefore PWW increased at an annual rate of 0.42 % per annum between 1994 and 2003. No maternal breeding values were constructed because the model only incorporated the direct additive effects.

Direct genetic trends for Yearling weight increased at a rate of 0.06 % per annum between 1980 and 2003 (Table 6.1). The trends were quite low ranging from approximately -0.75 kg through 0 kg to a maximum of about 0.2 kg between 1980 and 1994 (Figure 6.4.1). This probably resulted as a consequence of the over emphasis on subjective traits such Conformation and Type as demonstrated by the trends derived at the expense of objectively measured traits. This is supported by the data description that was given in section 3.2 of this manuscript (see Figure 3.2.1). It was clear that the number of production records that was submitted to the NSIS was very low until 1995 when they commenced steadily increasing. However, the flock size in this data remained relatively stable over the evaluation period. Prior to 1995 most stud breeders were selecting their Dorper sheep on the basis of breed standards (Olivier & Cloete, 2006). When separate regression lines were fitted for YW between 1980 and 1993, it was evident that there was negligible genetic change ($b = 0.02 \pm 0.01$ and $R^2 = 0.09$). The slight genetic change during that period implied that insufficient or no selection pressure was applied on the trait. Fitting a separate regression line between 1994 and 2003 resulted in a significant genetic progress ($b = 0.17 \pm 0.01$ and $R^2 = 0.75$). Therefore YW increased at an annual rate of 0.42 % per annum between 1994 and 2003. However, it was demonstrated in the current study using REML procedures that there is a weak negative correlation between Colour and yearling weight (-0.18 ± 0.19).

Prior to 1994, colour probably was (and still is) an essential breed standard to Dorper stud breeders. Regardless of the fact that the selection criterion for this flock was unknown by the time of publishing these research findings, the data description, trends as well as the relationships between subjective and objectively measured traits infer that proper selection objectives were not clearly defined for a long time because of too much emphasis on breed standards at the expense of performance testing (Olivier & Cloete, 2006). The current findings further endorse the significance of basing most of our selection decisions on objectively measured traits whose effects can be easily assessed by the statistical methods and software that are available to quantitative geneticists.

There is a paucity of literature to debate the trends in yearling weights. However, in a study conducted by Cloete *et al.* (1998b) the genetic improvement in body weight of the Kromme Rhee Dohne Merino nucleus flock amounted to 0.145 kg per annum ($R^2=0.85$). Olivier *et al.* (1995) calculated the genetic trend in hogget weight of Merinos from the Grootfontein stud for BW at 0.205 kg per annum ($R^2=0.82$) from 1966 to 1984 and at 0.631 kg per annum ($R^2=0.94$) from 1985 to 1991. In the recent past, Swanepoel (2006) computed a direct breeding value for body weight in the Dohne Merino breed, amounting to 0.27 % (0.13 kg) per annum between 1992 and 2003. The maternal genetic trends for yearling weight decreased at a very slow annual rate of -0.03% ($r=-0.65$).

6.4.2 Genetic trends for growth traits in a Dorper flock

Genetic trends for growth traits are presented in Figure 6.4.3, while statistical information can be found in Table 6.1. It was evident that direct EBVs for average daily gain to weaning (ADGW) exhibited the fastest response to selection over the 24 years of evaluation which amounted to 0.61 % per annum. Contrary to live weight traits, ADGW increased consistently between 1980 and 2003 from 0 grams to approximately 38 grams ($r=0.92$). The maternal EBVs (Figure 6.4.4) exhibited an antagonistic relationship with the direct EBVs because they decreased at a steady rate of -0.29 % per annum ($r=0.95$). The reasons that led to this antagonistic behaviour in breeding values are exactly the same that was given with regards to live weight performance data. The only disparity was the explanation that was given about some negative genetic correlations between subjectively assessed and objectively measured traits.

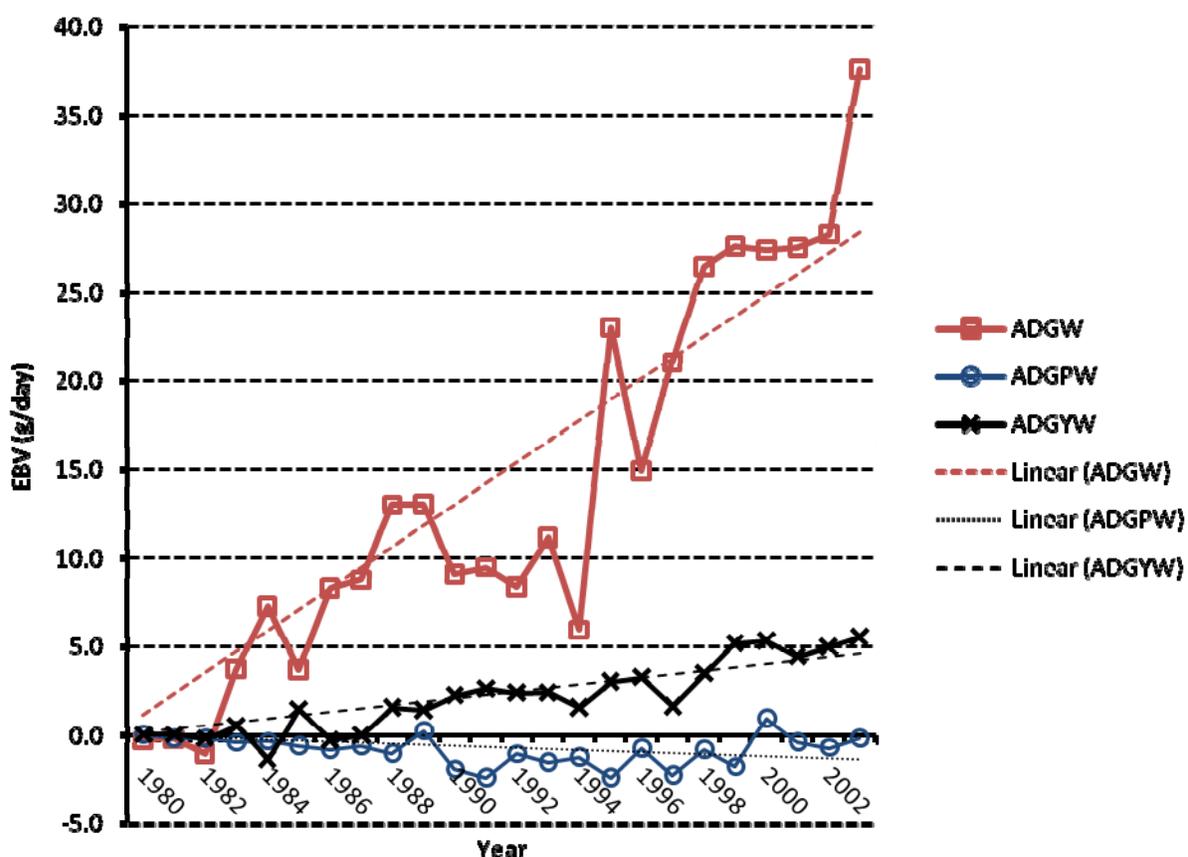


Figure 6.4.3 Additive direct genetic trends for average daily body weights in a Dorper flock. Regressions were forced through the origin in all instances.

Colour was once one of the most important selection criteria in the early formation of the Dorper breed. Early crosses of Dorper sheep were pied sheep with variable amounts of black. Currently the desired phenotype of a white body and a black head has been achieved. Selection pressure on the basis of colour can thus be relaxed and effort should be diverted to objectively measured traits. In previous discussions, Colour was noted to have some negative genetic correlation with some objectively measured traits and was elucidated to be lowly but positively correlated with ADGW using linear methods. There is not much literature to compare our findings except to mention that Gray *et al.* (1995) reported that there was a lack of selection response in post-weaning average daily gain (PWADG) in the South African Mutton Merino between 1984 and 1995. Interestingly our study also demonstrated that there was negligible genetic trend (-0.05 % per annum) for average daily gain during post weaning (ADGPW) ($r=-0.19$). This intriguing attribute is difficult to explain since a high and positive genetic correlation amounting to 0.62 ± 0.09 was derived between ADGW and ADGPW using REML procedures. ADGW was also demonstrated to have positive genetic and environmental correlations with live weight traits (Table 4.4.1.3). Under normal circumstances, and based on our previous findings, the genetic trend for ADGPW should follow a similar trend as other live weight and growth traits.

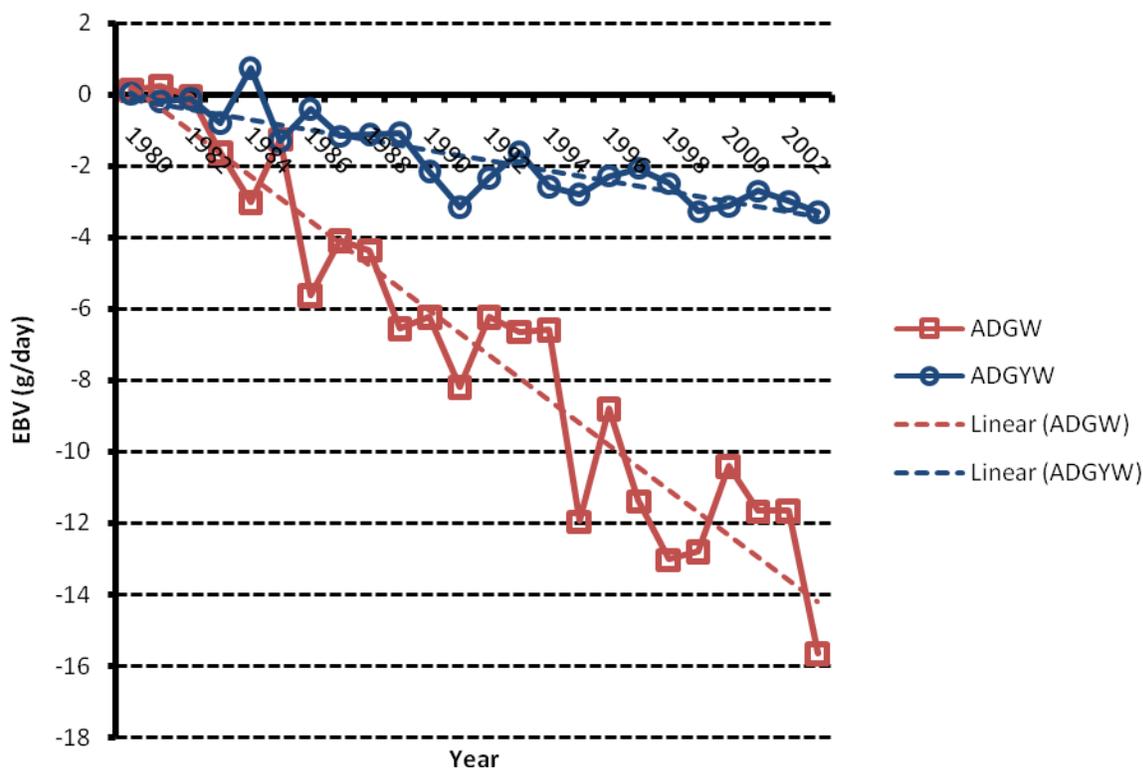


Figure 6.4.4 Maternal genetic trends for average daily body weights in a Dorper flock. Regressions were forced through the origin in all instances

Coincidentally it was also evident that the direct EBVs for average daily gain to yearling weight (ADGYW) followed a similar path although of different magnitude in comparison with ADGW. The derived genetic trend over the 24 years of evaluation amounted to 0.19 % per annum. Similar to ADGW, ADGYW increased consistently between 1980 and 2003 from 0 grams to approximately 6 grams ($r=0.91$). Although this trend was in the desired direction, its magnitude was quite low. Maternal EBVs exhibited an antagonistic relationship with the direct EBVs because they decreased at a steady rate of -0.14 % per annum ($r=-0.89$). By 2003 the average maternal EBVs for ADGYW were approximately -3.25 grams. This antagonistic behaviour in breeding values follows earlier reasoning for live weight data. It is worth mentioning that there are no published genetic trends for average daily weight gains to yearling stage that could be used for comparison with our findings.

6.4.3 Genetic trends for subjectively assessed traits in a Dorper flock

There is an absolute dearth in literature pertaining to genetic trends in subjectively assessed traits in both wool and meat sheep breeds in South Africa, despite several genetic evaluation exercises having been undertaken as cited previously. It has been highlighted previously that Dorper stud breeders have relied on breed standards that have been assessed by well-trained judges for many decades. It was therefore necessary to monitor the genetic progress that has been achieved in subjectively assessed traits by constructing genetic trends for a period covering more than 2 decades. Genetic trends for subjectively assessed traits are presented in Figure 6.4.5, with statistical information in Table 6.1. Figure 6.4.5 demonstrates that Conformation scores increased at a rate of 0.12% per annum ($r=0.83$) over the 24 years of evaluation. This response to selection was in the desired direction because Conformation was found to be positively correlated with all the objectively measured traits that were evaluated. It can thus be said that the genes that code for Conformation could be partly similar to those coding for live weight and growth.

Despite these positive trends, there is a need to further explore the nature of the relationship between Conformation and reproduction and fitness traits when sufficient data becomes available, because Olivier & Cloete (2006) reported that despite the existence of positive genetic and phenotypic correlations with WW and PWW there was a negative correlation with reproduction (assessed as Total Weaning Weight) amounting to -0.51 ± 0.28 . Table 6.1 and Figure 6.4.5 suggest an annual decline amounting to -0.14% in the EBVs for Size score. Unfortunately there is absolutely no relevant literature to compare our results with. This reduction in Size is difficult to explain because high positive correlations were reported in this study between Size and all the live weight and growth traits.

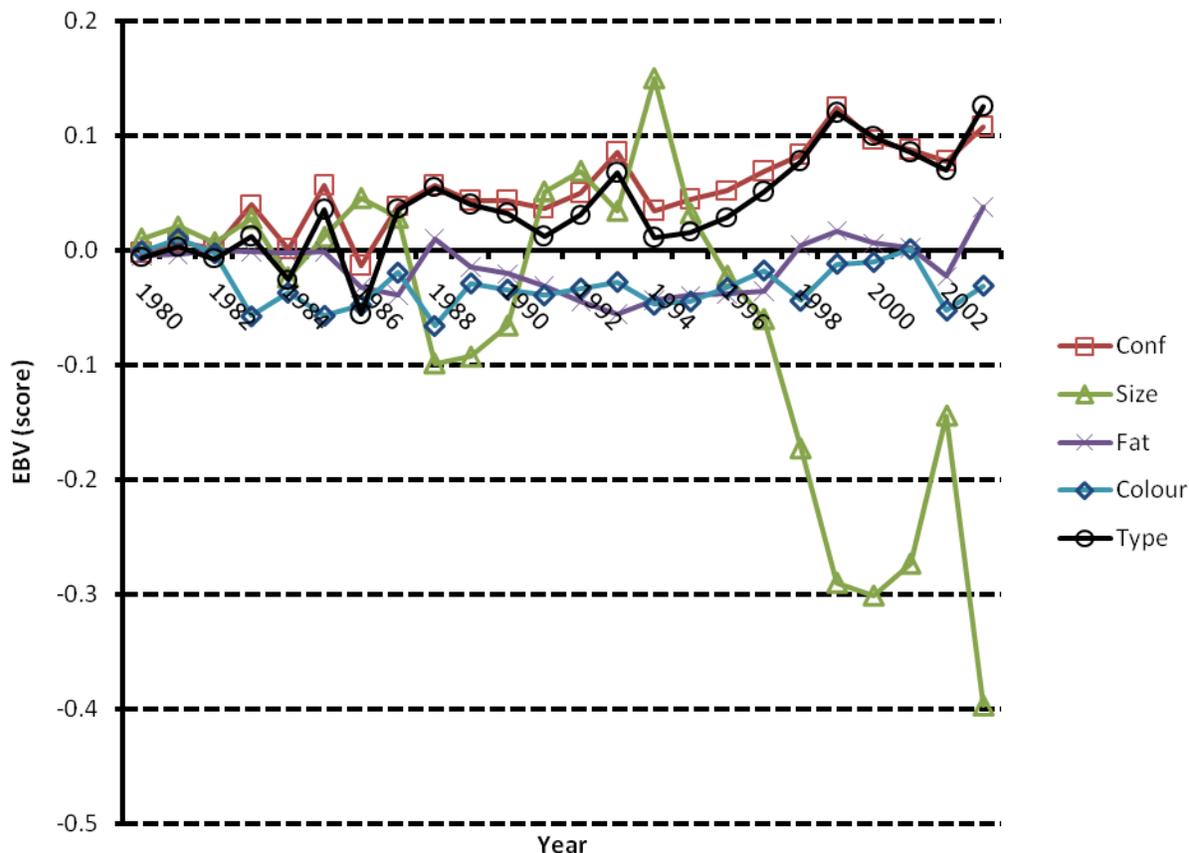


Figure 6.4.5 Direct genetic trends for subjectively assessed traits in a Dorper flock. Regressions were forced through the origin in all instances

Furthermore, positive direct genetic trends were derived for all the live weight and growth traits except ADGPW. The possibility of biased scoring can be nullified by taking into cognizance the fact that only well trained judges were used to score the animals using well set standards and procedures. It should be noted that despite the existence well trained judges, the lack of reference points comparable to previous years of assessment can result in haphazard genetic trends. This conflicting evidence further endorses previous assertions that the incorporation of subjective traits into selection objectives should be treated with extreme caution until thorough verification has been conducted.

There was no evident genetic change in Fat Distribution (Figure 6.4.5). No comparable results were found in literature. However, a small increment was anticipated based on the favourable genetic correlations (0.43 to 0.69) with live weight and growth traits (Chapter 4). Figure 6.4.5 reports that there was negligible or no response to selection in Colour between 1980 and 2003. The current observation further endorses the proposition that Dorper breeders should no longer exert much effort with regards to Colour since the

desired phenotypic standards of a black head and white body have been stabilized. The objective is thus to maintain the existing standards, as demonstrated in this chapter. Contrary to Colour and Size, Type responded to selection in a positive way although at a relatively slow rate of 0.09 % per annum ($r=0.78$). This was probably caused by the fact that Type is positively correlated with all the objectively measured traits. There was no literature to compare our findings with.

6.5 Conclusion

The genetic trends derived in this study indicated that significant and sustained genetic progress in the desired direction has been achieved in live weight and growth traits in the Dorper flock studied between 1980 and 2003, and particularly since 1993. It needs to be stressed that faster progress would theoretically be feasible if selection pressure is applied because high heritability estimates were derived for objectively measured traits. It is thus clear that these traits were not the sole objective in the selection strategy. Compared to the objective traits, genetic progress in subjective traits was only evident in Conformation and Type scores. The lack of response to selection for Fat distribution and Colour is probably rather caused by a lack of directed selection pressure capable of bringing about genetic change in these traits.

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CHAPTER 7

ACROSS FLOCK GENETIC EVALUATION OF THE DORPER BREED FOR PRODUCTION, REPRODUCTION AND FITNESS TRAITS USING THE FREQUENTIST APPROACH

7.1 Abstract

Across flock genetic parameter estimates for production, reproduction and fitness traits were derived using Residual Maximum Likelihood (REML) procedures for the Dorper breed. Data were retrieved from the NSIS data base from breeders that were constantly submitting performance data for a period spanning 30 years (1980 to 2009). Weaning weight and post-weaning weight were moderately heritable. Maternal effects were significant, although of fairly low magnitude in live weight traits. There was an increment in additive genetic variation as well as heritability as age increased. Maternal effects declined with age, as both the additive maternal effects as well as the dam permanent environmental effects were reduced between weaning and post-weaning. It was demonstrated that reproductive and fitness traits such as Total Weaning Weight per Ewe Lambing (TWW/L), Number of Lambs Born per Ewe Lifetime (NLB/EL), Number of Lambs Weaned per Ewe Lifetime (NLW/EL), lamb survival to weaning and litter size were lowly heritable. Selection of Dorpers to improve reproduction and fitness is feasible although relatively low heritability estimates indicate that annual progress may be slow. Low heritabilities for Ewe Productive Life (EPL) and stayability at two, three and four years of age indicated that these traits are, to some extent, influenced by genetics. Lambing Chances per Ewe Lifetime (LC/EL) and Times Lambled per Ewe Lifetime were demonstrated to have a moderate heritability and would also result in a correlated selection response in both reproduction and longevity. No genetic basis was found for inter-lambing period (ILP). It was therefore deduced that ILP can be improved through sound management. Live weight traits were positively correlated with reproduction and fitness traits. TWW/L was genetically and environmentally positively correlated with survival, litter size and EPL. It was concluded that despite the low additive genetic variances for reproduction and fitness, genetic improvement is feasible. Therefore, breeders should incorporate these traits in their selection strategies to achieve maximum production.

Keywords: Heritability, genetic, correlation, environmental, reproduction, longevity, stayability, survival, fitness

7.2 Introduction

Performance in sheep reflects the genes that an animal has inherited from both its parents as well as a mixture of seasonal and husbandry factors peculiar to the environment an animal finds itself in (Lewis & Beatson, 1999). Reproduction and survival rate are key factors determining the efficiency of lamb production in any environment (Snyman *et al.*, 1997). Other traits vary in significance and can, in some circumstances be of minute value or of no value at all (Snyman *et al.*, 1998b). It has been demonstrated by Falconer & Mackay (1996) that several components influence ewe productivity and that each of these components can be used independently as a selection criterion, as each has a direct impact on total ewe

productivity. Improved ewe productivity can be accomplished in part by increasing the number of lambs weaned and weight of lambs weaned per ewe per year (Cloete *et al.*, 2002). For instance in situations where lambing percentages are already high, an increment in the number of lambs born may be undesirable. Furthermore, the production of weaned lambs of inferior quality may often be encountered. Some of the factors determining total weight of lamb weaned per ewe are ovulation rate, embryo survival, mothering ability and milk production of the ewe, as well as growth rate and viability of the lamb (Falconer & Mackay, 1996).

Genetic improvement of reproductive performance could be achieved either by direct selection for a composite trait (total weight of lamb weaned) or by selection for one of the component traits. It is important to determine whether direct selection for total weight of lamb weaned per ewe joined is more efficient than selection for number of lambs born, number of lambs weaned or weaning weight (Olivier *et al.*, 2001). Until recently, emphasis has mostly been placed on the individual component traits of reproduction such as fertility, litter size, lamb survival rate and the number of lambs born and weaned per ewe joined (Duguma *et al.*, 2002a). Fogarty *et al.* (1995) reported that the number or total weight of lamb weaned per ewe joined, which comprises of several component traits has not received sufficient attention. The 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 individual lamb weight at weaning. According to Snyman *et al.* (1997), there is 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 (Olivier *et al.*, 2001). This predicted correlated response has in fact been confirmed by Cloete *et al.* (2003). 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 the growth potential of the lamb (Snyman *et al.*, 1997).

Despite Dorper germplasm having been widely distributed across the world, there is very little published information on the breed's reproduction, longevity and fitness. In recent years there have been some scholars who have stressed the need to embark on studies to evaluate the longevity and/or stayability of sheep in flocks because of the great impact of these traits on profitability and welfare. Borg (2007) reported that breeding ewes that stay in the flock for longer periods of time typically produce more lambs than ewes that leave the flock at younger ages. Therefore, the length of time a ewe remains productive influences profitability. Breeding ewes may be voluntarily removed from the flock if they fail to breed, have poor production, or reach a predetermined fixed culling age, or may be removed due to illness or death. However, consideration of the productive life of the breeding ewe in flock breeding objectives has been limited by the lack of information regarding genetic control of this trait.

Hudson & Van Vleck (1981) defined stayability as the probability of survival to a specific age, given the opportunity to reach that age. Stayability reflects the underlying fitness characteristics that contribute to the removal of a breeding animal from the production system. Genetic variation in stayability has been identified in cattle and pigs (Van Vleck, 1980; Snelling *et al.*, 1995; Lopez-Serrano *et al.*, 2000). However, information on stayability in breeding ewes is limited. Stayability is typically measured as a binary trait and has been evaluated by using both linear and threshold models. Borg *et al.* (2009) concluded that genetic variation in stayability implies that breeding objectives could incorporate selection for ewes that stay in the flock for a longer period of time. It should however, be born in mind that stayability is a trait that is measured late in life, therefore limited data might be available for genetic evaluation. The lack of data can be countered by measuring stayability at early ages and deriving correlations between early and late ages. Furthermore, the genetic relationships between stayability and other production traits are unclear and currently do not provide a good indicator for early life traits for selection on stayability. There is therefore an urgent need to assess the stayability and longevity of Dorper sheep to consider incorporating them into selection decisions with an overall intention of maximizing profits.

In spite of the Dorper breed being very popular, little if not nothing is known about the genetic basis of lamb survival in the breed. Haughey (1991) reported that decreased and variable lamb survival is generally considered a major constraint to efficient sheep production. Furthermore, it was noted that a core level of lamb losses remains, even if managerial inputs are optimized. Apart from the direct loss of production and income to farmers, lamb losses have also become an emotional issue involving animal welfare. Studies involving the possible genetic improvement of lamb survival have found limited genetic variation (Snyman *et al.*, 1998b; Lopez-Villalobos & Garrick, 1999).

The lack of genetic variation has led to recommendations that the improvement of lamb survival should rather be based on modification of the environment to create conditions suitable for survival of lambs (Morris *et al.*, 2000; Everett-Hincks *et al.*, 2005). In contrast, some previous studies suggested differences between lines within breeds that were brought about by selection (Haughey, 1983; Knight *et al.*, 1988). Gudex *et al.* (2005) more recently reported significant variation in survival of the progeny of respective sires. However, Gudex *et al.* (2005) also suggested that it would be fruitless to study lamb mortality without considering lamb birth weight. The latter sentiments were shared by Morris *et al.* (2000). In view of all these deficiencies of information, studies were undertaken to estimate across flock genetic parameters for production, reproduction, survival and fitness in the Dorper breed using Residual Maximum Likelihood (REML) procedures. It was also of cardinal importance to estimate genetic and environmental relationships (correlations) between growth, reproduction and fitness traits.

7.3 Materials and Methods

Data were retrieved from the NSIS data base from breeders that were constantly submitting performance data for a period spanning close to 30 years (1980 to 2009). All the progeny were descended from a pedigree spanning 15 generations out of 4 064 sires and 76 952 dams. Furthermore, the progeny emanated from 713 great grand sires and 16 613 great grand dams. The descriptive statistics are given in Table 7.3.1. An in-depth description of the raw data before editing was given in Chapter 3. Weaning weight was recorded between 76 and 160 days whereas post-weaning weight was recorded between 161 and 270 days. Ewe productivity was defined as the Total Weight of Lamb Weaned per Ewe Lambing (TWW/L) after correction for age and sex. The actual number of lambing chances afforded to ewe and the actual times a ewe lambled per ewe lifetime were assessed as traits indicative of reproduction and longevity.

Number of Lambs Born/ Weaned per Ewe Lifetime (NLB/EL and NLW/EL respectively) were taken as component traits of ewe productivity and as indicators of longevity. The proportion of the actual number of times lambled over the lambing chances that were afforded were used to calculate fertility. Fertility and precociousness were also computed as a binary trait by assessing whether a ewe lambled at 2 years of age or not (Two-Year Lambing). Fitness was derived through the computation of lamb survival to weaning as a proportion of the number of lambs weaned over the number of lambs born alive expressed as a trait of the ewe. The trait also indicated the ability of a ewe to rear a lamb up to weaning. Litter size was computed as a proportion of the number of lambs born per ewe lifetime over the actual number of times lambled per ewe lifetime (across parities, as appropriate for individual ewes). Inter-lambing period was taken as the number of days between successive lambings. Ewe Production Life was derived from the age of the ewe at last lambing and was indicative of longevity for ewes born on or before the year 2005. Finally, stayability at 2, 3 and 4 years of age for ewes born on or before the year 2005 was assessed as binary traits also indicative of longevity.

7.3.1 Data Editing

The data was exported from dBase to data1 format that could be analysed by the Statistical Analysis System (SAS, 2004). One-way frequency procedures were then implemented using the SAS programme with the aim of obtaining a general overview of the data. The implementation of one-way frequency procedures yielded the number of records contributed per year, the number of contemporary groups, the number of animals in each birth status group, the number of animals in each sex group and the number of progeny that each sire and dam had respectively. Routine and standard editing techniques for sheep breeding data were applied.

Table 7.3.1 Description of the raw data used after editing for the Dorper breed (n = number of records, CV% = coefficient of variation and SD = standard deviation)

TRAIT	N	MEAN	SD	CV%	RANGE
Weaning weight (WW) (kg)	111 011	30.9	4.5	14.6	12.4 - 49.6
Post-weaning weight (PWW) (kg)	16 694	45.1	4.5	10.0	30.8 - 59.6
Total Weaning Weight per Ewe Lambing (TWW/L) (kg)	42 831	31.9	12.4	38.9	6 - 134
Lambing Chances per Ewe Lifetime (LC/EL)	42 831	2.45	1.65	67.4	1 - 11
Times Lambed per Ewe Lifetime (TL/EL)	42 831	1.73	1.11	64.2	1 - 10
Number of Lambs Born per Ewe Lifetime (NLB/EL)	42 831	2.14	1.54	72.0	1 - 14
Number of Lambs Weaned per Ewe Lifetime (NLW/EL)	42 831	1.83	1.36	74.3	1 - 13
Litter Size (Litter)	42 831	1.23	0.38	30.9	1 - 5
Fertility	42 831	0.80	0.26	32.5	0.1 - 1.0
Lamb survival to weaning (Survival)	42 831	0.88	0.27	30.6	0 - 1
Inter-lambing Period (ILP) (days)	11 260	298	44.4	14.9	184 - 740
Ewe Productive Life (EPL) (years)	42 831	2.2	1.5	68.2	1 - 14
Two Year Lambing (TYL)	42 831	0.80	0.40	50.0	0 - 1
Stayability at 2 years (STAY2)	42 831	0.41	0.49	-	0 - 1
Stayability at 3 years (STAY3)	42 831	0.23	0.42	-	0 - 1
Stayability at 4 years (STAY4)	42 831	0.12	0.32	-	0 - 1

Each dam contemporary group included progeny of at least two sires after editing. Progeny records of sires with fewer than 20 progeny in the data set and sires with progeny in only one flock were omitted. One way of compensating for the unpredictable environment inherent to genetic analyses in extensive sheep flocks is to assign similarly raised animals to uniform groups referred to as contemporary groups. A contemporary group is a group of animals of similar breed composition, age and sex that are reared under the same managerial conditions and have had an equal opportunity to perform. Contemporary groups form the basis for all genetic evaluations, which depend on all animals in a contemporary group being subjected to similar conditions (Lofgren & Wood, 2001). The size of each contemporary group must be balanced with uniformity in each group, which is why single-sire contemporary groups are avoided. The general rule that is followed in genetic evaluations is to include offspring of at least three sires in each contemporary group, with offspring from several litters per sire.

The occurrence of triplets was low. Triplets and twins were thus pooled together as multiples when data were edited for live-weight traits. Dams which were eight years and older were pooled, because only 30 dams were greater than eight years of age. The number of immature one-year old dams was limited hence, their records were discarded. There were also many cases in which there were contradictions in the pedigree by which some animals appeared as both sire and dam. In such cases it was attempted to resolve the duplicate pedigrees. If unsuccessful, such parents were regarded as unknown to avoid compromises. The live weight and ewe productivity data was also scrutinized in an endeavour to eliminate outliers. In that regard the single-trait procedure in SAS was utilized to derive means, standard deviations, and 95 % confidence intervals. Only lambs with live weight measurements within the 95%

confidence interval were retained in the analyses. With regards to reproduction records, 1 280 records were discarded because they were not afforded a lambing opportunity. Furthermore, 646 and 7 760 reproduction records were discarded because the dam age was unknown or the ewes were immature (year-old) respectively.

7.3.2 Statistical analysis

The ASREML program (Gilmour *et al.*, 2002) was used for the estimation of (co)variance components. The fixed effects that were found to be significant ($P < 0.05$) were incorporated into the operational models. Least square mean estimates for the significant fixed effects were derived, but are not reported because they conformed to all literature standards. Random terms were added to analytical models sequentially. Likelihood Ratio tests (LRT) were performed to assess the significance of the contribution of each random term to improvements in the model of analysis. The LRT is based on testing twice the increase in Log-likelihood resulting from adding a random term to the model of analysis as a Chi-square statistic. Alternatively, for two models with the same number of different random terms, and assuming identical fixed effect modelling, the model with the higher value for the Log-likelihood fits the data best. Initially single-trait analyses were implemented with the most appropriate model. All Binomial reproduction, longevity and fitness traits were analysed using logit link functions to link binomially distributed data to the normal distribution (Gilmour *et al.*, 2002). Finally, a series of two-trait and three-trait analyses were conducted to estimate genetic and environmental correlations amongst reproduction and fitness traits.

The weaning age (76-160 days) was fitted as a covariate to weaning weight and fixed effects that were fitted were contemporary group (3 700 levels, consisting of year-season-property effects), sex (male/female), birth type (single/multiple), dam age (2-8 years and over i.e. 7 levels), and rearing status (3 levels i.e. born single and raised as a single, born multiple but raised as a single and born as multiples and raised as multiples). The model for post weaning weights was similar to that of weaning weight except that it had 574 contemporary groups and the post-weaning age (161-270 days) was fitted as a covariate. The fixed effects models that were fitted reproduction and fitness traits differed from the live weights models in that it contained fewer contemporary groups (1 841 levels). Furthermore, a number of covariates were fitted depending on the trait that was being evaluated such as the number of production years as a covariate to NLB/EL, NLW/EL and TWW/L. Other effects that were fitted were year (29 levels), dam age and birth type.

Fixed effects from the analyses were consistent with those reported in the literature, and were thus not presented and discussed further. The second step was to estimate (co)variance components for each trait. This was obtained using the ASREML program (Gilmour *et al.*, 2002) fitting single-trait animal

models initially. These models include a combination of direct additive, maternal additive and maternal permanent environmental effects as well as the covariation between direct additive and maternal additive effects. Genetic and environmental correlations between reproduction and fitness traits were fitted using the most appropriate single-trait animal models that were satisfied the LRT model selection criteria using a series of two-trait and three-trait analyses. Four different forms of single-trait mixed animal models (in matrix notation) that were fitted for all traits were as follows:

$$\text{Model 1 } Y = X\mathbf{b} + Z_1\mathbf{a} + e$$

$$\text{Model 2 } Y = X\mathbf{b} + Z_1\mathbf{a} + Z_2\mathbf{m} + e \text{ \{with cov } (\mathbf{a}, \mathbf{m}) = 0\}}$$

$$\text{Model 3 } Y = X\mathbf{b} + Z_1\mathbf{a} + Z_2\mathbf{m} + Z_3\mathbf{c} + e \text{ \{with cov } (\mathbf{a}, \mathbf{m}) = 0\}}$$

$$\text{Model 4 } Y = X\mathbf{b} + Z_1\mathbf{a} + Z_3\mathbf{c} + e$$

Where Y = vector of observations,

\mathbf{b} = vector of fixed effects influencing traits,

\mathbf{a} = vector of direct additive effects,

\mathbf{m} = vector of random maternal additive (dam) effects,

\mathbf{c} = vector of random permanent maternal environmental effects,

e = randomly distributed vector of residuals;

Where X , Z_1 , Z_2 and Z_3 are considered as the corresponding incidence matrices relating observations to their respective fixed and random effects as well as the vector of residuals.

It was assumed that:

$$V(\mathbf{a}) = \mathbf{A}\sigma_a^2; V(\mathbf{m}) = \mathbf{A}\sigma_m^2; V(\mathbf{c}) = \mathbf{I}\sigma_c^2 \text{ and } V(e) = \mathbf{I}\sigma_e^2$$

Where \mathbf{A} is the numerator relationship matrix among animals in the pedigree file and \mathbf{I} being an identity matrix; σ_a^2 , σ_m^2 , σ_c^2 and σ_e^2 direct genetic variance, maternal genetic variance, maternal permanent environmental variance and the environmental (residual) variance respectively.

7. 4 Results and Discussion

7.4.1 Model selection

Log likelihood values were obtained for single-trait analyses on the respective traits. Inclusion of random factors such as direct additive effects, additive maternal effects, dam permanent environmental effects and the correlation between additive direct genetic and additive direct maternal effects resulted in significant increments in log likelihood values for live weight traits only. The fluctuations in the values are

not reported in this instance because they closely resembled what has already been reported in section 4.4.1. Addition of extra random effects after the additive direct genetic effects to the fitness, reproduction and stayability data did not result in any significant change in the Log likelihood values. It was therefore appropriate to fit additive genetic effects as the only random effects to such data.

7.4.2 Single-trait analyses

The implementation of single-trait analyses using Restricted Maximum Likelihood procedures to the across flock Dorper data set to weaning weight and post-weaning weight resulted in moderate estimates of direct heritability amounting to respectively 0.21 ± 0.01 and 0.27 ± 0.02 , as depicted in Table 7.4.1. These moderate estimates fell within the ranges that were reported in the literature across breeds (Tosh & Kemp, 1994; Mortimer & Atkins, 1995; Fossceco & Notter, 1995; Vaez Torshizi *et al.*, 1996; Nesar *et al.*, 2001; Cloete *et al.*, 2001; Duguma *et al.*, 2002b; Safari *et al.*, 2005b).

Table 7.4.1 REML estimates of variance components and ratios from single-trait analyses live weight traits in the Dorper breed

Parameters	Weaning Weight	Post-weaning weight
Direct additive (σ_a^2)	3.88	5.33
Direct Additive Maternal (σ_m^2)	1.02	0.79
Maternal permanent environment (σ_c^2)	1.48	0.83
Total phenotypic (σ_p^2)	18.64	19.5
Residual (σ_e^2)	12.25	12.5
Direct additive ($h^2 \pm SE$)	0.21 ± 0.01	0.27 ± 0.02
Direct additive maternal ($m^2 \pm SE$)	0.05 ± 0.01	0.04 ± 0.02
Dam permanent environment ($c^2 \pm SE$)	0.08 ± 0.01	0.04 ± 0.02

It was also apparent that there was an increment in additive genetic variation as well as heritability with the progression of age, as reported earlier by Tosh & Kemp (1994), Maniatis & Pollott (2002a), Simm *et al.* (2002) and Zishiri (2009). Safari *et al.* (2005b), in their review of genetic parameter estimates in sheep, also highlighted that weighted means for heritability of growth traits were generally moderate in magnitude and ranged from 0.15 to 0.41 with very low standard errors (range 0.01–0.04). These moderate estimates clearly illustrate that Dorper sheep have the propensity to transmit reasonable genetic variation to their progeny that will result in genetic gains in growth traits with a concomitant improvement in meat production. It can further be reported that the models that were fitted managed to partition the genetic variation further into additive direct maternal effects as well as dam permanent environment.

It was demonstrated that the maternal effects diminish with age because the direct additive maternal effects as well as the dam permanent environmental effects both declined from weaning weight to post-

weaning weight (Table 7.4.1). Direct maternal heritability (m^2) for both weaning weight and post-weaning weight were respectively 0.05 ± 0.01 and 0.04 ± 0.02 . These estimates accorded with other estimates across sheep breeds worldwide (Snyman *et al.*, 1995; Vaez Torshizi *et al.*, 1996; Analla & Serradilla, 1997; Al-Shorepy & Notter, 1996; Cloete *et al.*, 1998; Bromley *et al.*, 2000; Naser *et al.*, 2001; Cloete *et al.*, 2002; Maniatis & Pollot 2002a; Duguma *et al.*, 2002b; Simm *et al.*, 2002).

Similarly dam permanent environment was estimated at 0.08 ± 0.01 and 0.04 ± 0.02 respectively. Despite the low magnitude these findings further endorse that maternal effects need to be considered for early growth traits of sheep, but that it is not as important at later ages. There are several reports that have shown inflated direct heritability (h^2) estimates and consequently inflated breeding values when maternal effects were not included in the model of analysis (Nashom & Danell, 1996; Vaez Torshizi *et al.*, 1996; Maniatis & Pollott, 2002b). The importance of maternal effects in livestock species is well known. Such effects emanate as a result of the ability of the dam to produce milk needed for growth of the offspring as well as maternal behaviour during the post-natal phase. Genetic evaluation schemes therefore attempt to separate direct and maternal effects where appropriate. However, accurate evaluation requires accurate estimates of genetic variances for direct and maternal effects and their correlations. Such estimates may differ according to breed or production systems. Accounting for maternal effects also increases the accuracy of breeding values, and hence for selection (Robinson, 1995).

Apart from live weight traits, the present study also considered reproduction, longevity and survival in the Dorper breed using across flock data with the intention of assessing the genetic basis of such traits. Some Dorper breeders are concerned that their sheep may lose some of their desirable attributes (hardiness, adaptability and an ability to reproduce under adverse conditions) due to the emphasis placed on breed standards and shows because the lack of knowledge of genetic relationships between the desirable attributes and subjective traits. Their production records were thus used to derive genetic parameters for reproduction and fitness in the Dorper breed. With the current economic environment in South Africa, reproduction is by far the most important trait in sheep farming. Net reproduction rate per ewe (defined as total weight of lamb weaned, accumulated over the lifetime of a ewe) can be increased by improving some or all of its components (Olivier, 2002). Single-trait across flock genetic parameter estimates of reproduction and fitness traits are therefore presented in Table 7.4.2.

Significant genetic variation was found for all traits considered. The h^2 for Total Weaning Weight per Ewe Lambing (TWW/L) was estimated at 0.12 ± 0.02 . Our estimate was in line with several literature estimates (Fogarty *et al.*, 1995; Gates & Urioste, 1995; Snyman *et al.*, 1997; Duguma *et al.*, 2002b; Safari *et al.*, 2005b; Olivier & Cloete, 2006). More interestingly our estimate is quite similar to that of Safari *et al.* (2005b) who derived an average h^2 estimate for TWW/EL of 0.11 ± 0.02 from 11 literature estimates. Genetic evaluations for reproduction in sheep have been quite popular especially in South African Merino

sheep because Olivier (2002) reported that under the extensive conditions typical of the South African production environment, optimal net reproduction per flock within the constraints of the environment is important. In years of drought and in arid regions, the environment often cannot support marked increases in litter size.

Table 7.4.2 REML estimates of variance components and ratios from single-trait analyses for reproduction, longevity and lamb survival traits in the Dorper breed

Traits	Parameters			
	Direct additive (σ_a^2)	Residual (σ_e^2)	Total phenotypic (σ_p^2)	Heritability ($h^2 \pm SE$)
TWW/L	12.57	88.30	100.87	0.12±0.02
Lamb survival	0.0013	0.019	0.02	0.07±0.01
Litter Size	0.009	0.12	0.13	0.07±0.02
EPL	0.005	0.09	0.10	0.05±0.01
ILP	15.26	1012.64	1027.9	0.01±0.03
Fertility (TL/LC)	0.0048	0.0184	0.0232	0.21±0.01
Lambing Chances/EL	0.0946	0.3104	0.4050	0.23±0.01
Times Lambed/EL	0.0199	0.1681	0.1880	0.11±0.01
NLB/EL	0.0639	0.5600	0.6239	0.10±0.01
NLW/EL	0.0589	0.6022	0.6610	0.09±0.01
Two Year Lambing	0.36	3.3	3.66	0.10±0.02
STAY2	0.16	3.3	3.46	0.05±0.02
STAY3	0.32	3.3	3.62	0.09±0.03
STAY4	0.42	3.3	3.72	0.11±0.04

In such cases the quality of the lambs produced may become more important than the number of lambs produced by ewes. The outcomes of the current study therefore endorse the former assertions in which not only the quantity of lambs born matters but their fitness as well because the Dorper breed has demonstrated that if TWW/L is strived for during selection, genetic progress pertaining to net reproduction rate is likely to accrue in the long run.

This study also aimed to consider component traits of overall reproduction, as well as longevity and lamb survival in an effort to fully advise Dorper stud breeders on suitable strategies for genetic improvement of overall reproduction rate. The number of lambing events recorded per ewe was demonstrated to be heritable when assessed as the number of lambing chances afforded per ewe lifetime (LC/EL). Although there are no comparable literature estimates, the moderate h^2 estimate of 0.23±0.01 indicates that Dorper

sheep can be bred to ensure a higher number of lambing events during their lifetimes. It can be argued that the number of lambing events per lifetime is an indication of vitality in ewes, implying that such selection is likely to result in ewes of reasonable longevity. The number of times lambled per ewe lifetime (TL/EL) also had a fairly low heritability of 0.11 ± 0.01 . This implies that it is quite feasible to improve the longevity of ewes through selection on the basis of TL/EL although genetic gains are expected to be slow. It is important to stipulate that (as previously alluded) studies on ewe longevity are essential because the costs of ewe replacements can be quite high. Sheep breeding enterprises should endeavour to incorporate ewe longevity in their selection indices because it can significantly affect their profitability. Ideally a prudent sheep breeder would desire to rear sheep that have a combination of high fertility, high fecundity, excellent mothering ability, high lamb survival rate as well as high longevity. Since longevity can only be assessed late in the life of an animal, indirect selection should be considered.

The number of lambs born is a component trait of net reproduction rate. When the number of lambs born per ewe lifetime (NLB/EL) was considered the direct h^2 estimate of 0.10 ± 0.01 indicates that genetic improvement is feasible, while the derived response is likely to be aided by substantial levels of phenotypic variation (a CV of 72%). There are no comparable literature estimates for NLB/EL despite the existence of few estimates of number of lambs born per ewe joined (NLB/EJ). In their preliminary study Olivier & Cloete (2006) derived a h^2 estimate of 0.04 in Dorper sheep by fitting a repeatability model. Snyman *et al.* (1997) derived a moderate h^2 estimate of 0.26 in Afrino sheep. Olivier *et al.* (2001) derived h^2 estimates of 0.23 and 0.19 in the Grootfontein and Carnarvon Merino flocks respectively. Fogarty *et al.* (1994) also derived a moderate heritability estimate of 0.17 ± 0.06 in Hyfer sheep. The same workers then proceeded to derive a moderate heritability estimate of 0.20 ± 0.08 for number of lambs born per ewe lambing (NLB/L) in the first parity. Gates & Urioste (1995) derived low to moderate to high h^2 estimates between the first and fifth parity in Pelt sheep ranging from 0.07 to 0.35. Other workers obtained very low h^2 estimates for NLB/L across parities in various sheep breeds (Al-Shorepy & Notter, 1996; Matos *et al.*, 1997; Davis *et al.*, 1998; de Vries *et al.*, 1998; Okut *et al.*, 1999; Yazdi *et al.*, 1997; Ingham, 2003). The number of lambs born alive per ewe lambing (NLBA/L) were estimated to have a low heritability by Okut *et al.* (1999). In a review of genetic parameter estimates, Safari *et al.* (2005b) derived mean heritability estimates for number of lambs born per ewe joined, number of lambs born alive per lambing and number of lambs born per lambing of 0.10 ± 0.01 , 0.10 ± 0.05 and 0.13 ± 0.01 respectively. In a nutshell, it seems like there is a consensus in literature that the heritability estimates for number of lambs born per given opportunity or from repeated records over a long period of time is low. The current study progressed deeper to assess fertility in Dorper ewes by evaluating the propensity of ewes to lamb when they are two years old as a binary trait. It was apparent that the direct h^2 estimate of 0.10 ± 0.02 indicated that selecting ewes on the basis of whether they have the potential to lamb on or before they are two years old can result in genetic improvement. This study also confirmed that there was no genetic basis for inter-lambing period (ILP). This should not be surprising in flocks with a fixed breeding season because ILP is

determined by managerial decisions. ILP can therefore be improved by sound management. Breeders should therefore endeavour to select precocious ewes because they will have the maximum production time in the breeding flocks which will in turn result in higher profit margins.

Our study went on to derive a trait that takes into cognizance fertility, lamb survival, growth rate, rearing ability and longevity of Dorper ewes. The number of lambs weaned per ewe lifetime (NLW/EL) was estimated to have a low heritability of 0.09 ± 0.01 . It can thus be declared that genetic improvement of Dorper sheep for NLW/EL is quite feasible although it takes time to garner significant momentum. There are a few literature estimates to compare our findings. Similarly, the number of lambs weaned per ewe joined (NLW/EJ) have been estimated to be lowly to moderately heritable by some workers (Fogarty *et al.*, 1994; Snyman *et al.*, 1997; Olivier *et al.*, 2001; Ingham, 2003; Olivier & Cloete, 2006).

The lamb survival to weaning of Dorper sheep warranted to be investigated because there have been several anecdotal reports that Dorpers are well adapted to harsh environments and that they have a good survival rate. Our study revealed that lamb survival to weaning has a low additive genetic variance component amounting to 0.0013 and a direct h^2 estimate of 0.07 ± 0.01 . There is concordance between our estimate with literature. Direct heritability of survival in Merino sheep, or lamb viability, has been reported to be very low (Piper & Bindon, 1977) with low estimates reported in other breeds (Barwick *et al.*, 1990; Gama *et al.*, 1991; Lopez-Villalobos & Garrick, 1999; Morris *et al.*, 2000; Safari *et al.*, 2005b; Riggio *et al.*, 2008). In the current study lamb survival to weaning was derived as the proportion of the total number of lambs weaned over the total number of lambs born. The definition implies that the ability of ewes to rear progeny (ewe rearing ability) was assessed. The low estimate derived in the current study is also consistent with estimates for ewe rearing ability found in literature (Fogarty *et al.*, 1994; Ingham, 2003). Our study failed to partition the variation further into maternal effects and their components. This could have resulted in an inflated direct heritability estimate. Most reports of the maternal component of survival, or ewe rearing ability, suggest that it may be greater than the direct genetic effect (Lopez-Villalobos & Garrick, 1999; Morris *et al.*, 2000; Riggio *et al.*, 2008), but not all concur (Barwick *et al.*, 1990; Burfening, 1993) due to differences in analytical techniques and models. More recently it has been suggested that genetic variation in lamb viability is influenced by lamb age with estimates declining with time after birth (Southey *et al.*, 2001; Sawalha *et al.*, 2007; Riggio *et al.*, 2008).

Cloete *et al.* (2009) reported that studies on the potential genetic improvement of lamb survival have found limited genetic variation (Olivier *et al.*, 1998; Snyman *et al.*, 1998b; Lopez-Villalobos & Garrick, 1999). The lack of genetic variation has led to recommendations that the improvement of lamb survival should rather be based on modification of the environment to create conditions suitable for survival of lambs (Morris *et al.*, 2000; Everett-Hincks *et al.*, 2005). However, contrary to that, Cloete *et al.* (2009) noted that some previous studies suggested differences between lines within breeds that were brought

about by selective breeding (Haughey, 1983; Knight *et al.*, 1988). Gudex *et al.* (2005) more recently reported significant variation in survival of the progeny of respective sires. Other scholars have also postulated that it would be fruitless to study lamb mortality without considering lamb birth weight (Morris *et al.*, 2000; Gudex *et al.* 2005). Taking into cognizance all the facts and findings that have been highlighted, it can thus be recommended to incorporate lamb survival to weaning in Dorper selection decisions as both a trait of the lamb and the ewe.

Litter size was elucidated to have a low h^2 estimate of 0.07 ± 0.02 . It should nevertheless be noted that there are conflicting reports in literature on the heritability of litter size probably because of the effect of parity. Several scholars have derived low estimates for litter size (Al-Shorepy & Notter; 1996; Matos *et al.*, 1997; Davies *et al.*, 1998; de Vries *et al.*, 1998; Okut *et al.*, 1999; Ingham, 2003). Contrary to the low estimates, some workers derived moderate to high estimates for litter size (Fogarty *et al.*, 1994; Gates & Urioste, 1995). It can thus be concluded that genetic improvement in litter size is quite feasible, if it is considered that the trait has a CV of 31%. Furthermore, litter size at birth is directly related to ovulation rate, though selection for this trait would not be sufficient to increase lamb production since it does not include lamb survival and weight at weaning. Litter size at weaning includes the number of lambs present at weaning but not weight (Snyman *et al.*, 1997).

Studies on stayability and longevity are scarce in sheep breeding literature because the life expectancy of most ewes exceeds the period required to keep them in the flock to be economically viable. This is particularly true in flocks lambing annually, as there is sufficient time between lambings to build up reserves again. Stayability is an economically relevant trait due to its direct relationship with profitability of the production system. Increased stayability is associated with a reduction in annual cost of the replacement of ewes, increased flock production, increase in voluntary culling and an increase in generation interval. This study assessed ewe stayability as a binary trait at two, three and four years of age using the binomial logit transformation and demonstrated that there is a possibility of genetically improving it. Ewe Production Life (EPL) or longevity was assessed as a continuous trait and it was also elucidated to exhibit some genetic variation. Low heritability estimates amounting to 0.05 ± 0.02 , 0.09 ± 0.03 , 0.11 ± 0.04 and 0.05 ± 0.01 were derived for STAY2, STAY3, STAY4 and EPL respectively in the Dorper breed. To our knowledge there is only one study that has been conducted in sheep that had the theme of estimating genetic parameters for ewe stayability. The findings of Borg *et al.* (2009) are in harmony with our findings. Heritability estimates for stayability in Targhee sheep ranged from 0.00 to 0.09 in single-trait evaluations with significant genetic variation only expressed for stayability up to 5 and 6 years, given that ewes were present at 2 years of age (STAY 5|2, STAY 6|2), stayability up 5 years given that ewes were present at 4 years of age (STAY 5|4), and stayability up to 6 years given that ewes were present at 5 years of age (STAY 6|5). In conclusion Borg *et al.* (2009) suggested that genetic variation in stayability implies that breeding objectives could incorporate selection for ewes that stay in the flock for a

longer period of time. Their conclusions and our findings can only lead us to recommend Dorper breeders to incorporate stayability and longevity in their selection decisions initially by recording the ages at which animals are removed from their flocks and the reasons for their removal because improvements in these traits will result in efficiency of production as a consequence of reduced ewe replacement costs.

7.4.3 Relationships between growth, reproduction, fitness and longevity in Dorper sheep

Across flock genetic and environmental correlations in the Dorper breed are presented in Table 7.4.3. Both weaning weight and post-weaning weight exhibited high and positive genetic correlations (r_g) with net reproduction rate defined as TWW/L in the magnitude of 0.80 ± 0.10 and 0.72 ± 0.14 respectively. The correlations were in agreement with those cited in literature (Safari *et al.*, 2005b). Although their definition of total weight of lamb weaned was slightly different from that used in the current study, Snyman *et al.* (1998a, b) reported high (0.69-0.89) genetic and moderate (0.13-0.32) phenotypic correlations between total weight of lamb weaned and various lamb weights. The environmental correlations between live-weights and TWW/L were also positive implying that an environment that is conducive to improvement live weight traits will have a concurrent improvement in TWW/L. The positive genetic correlations which were in agreement with those in the review by Safari *et al.* (2005b) between live weight traits and NLB/EL and NLW/EL were expected because the former traits are components of net reproduction rate.

Both weaning weight and post-weaning weight were positively correlated with fitness which was defined as lamb survival to weaning (0.36 ± 0.05 and 0.24 ± 0.03) respectively. These findings are similar to those of Matika *et al.* (2001). Selection for live weight in Dorper sheep will therefore improve survival to a moderate extent. The positive environmental correlations between lamb survival to weaning and live weights also indicate that environments that promote improvements in live weights are beneficial to lamb survival to weaning. The low but positive genetic and environmental correlations between live weight and stayability at 2 and 4 years of age imply that direct selection for live weight traits will not improve longevity to a great extent but will have some beneficial effects. The current findings are quite novel because only the work of by Borg *et al.* (2009), in which stayability showed a trend for a positive genetic correlation with lamb body weights, has been reported in literature. Correlations between live weights and Ewe Productive Life were inconclusive because they ranged from negative to positive. However, fertility was positively correlated with live-weights regardless of whether it was assessed as times lambed per ewe lifetime, lambing chances per ewe lifetime or a ratio of the two.

Genetic and environmental correlations among TWW/L, NLB/EL and NLW/EL ranged from moderate to high. The r_g between TWW/L and NLW/EL (0.60 ± 0.07) implies that selecting ewes that wean many lambs with significant weight will culminate in an increment in ewe longevity. There are no comparable literature estimates, however high relationships between Total Weaning Weight per Ewe Joined (TWW/EJ), Number of Lambs Born per Ewe Joined (NLB/EJ) and Number of Lambs Weaned per Ewe Joined

(NLW/EJ) have been reported by several scholars. Safari *et al.* (2005b) reviewed genetic parameter estimates in sheep and reported that the 95 % confidence interval for the r_g between TWW/EJ and NLW/EL lies between -0.34 and 0.99. Other scholars derived very high genetic and environmental correlations for the same trait combinations (Fogarty *et al.*, 1994; Snyman *et al.*, 1998a; Cloete *et al.*, 2004).

The Dorper, like other meat breeds, is well positioned with regards to reproductive efficiency because Olivier (2002) reported that with the current economic environment in South Africa, reproduction is by far the most important trait in sheep farming. This statement is articulated at this instance bearing in mind that this study as well as the preliminary study by Olivier & Cloete (2006) demonstrated that it is feasible to breed Dorper sheep with the overall objective of improving reproductive capacity. The current positive correlations between net reproductive rate and other traits of economic importance as well as the high coefficients of variation also endorse the notion that if reproduction and live-weight traits are incorporated into selection criteria, improvements in reproduction capacity will be realized with the passage of time. Net reproduction rate per ewe (defined as total weight of lamb weaned, accumulated over the lifetime of a ewe) can be increased by improving some or all of its components. Safari *et al.* (2005b) also reported that the 95 % confidence interval for the r_g between TWW/EJ and NLB/EL lies between 0.00 and 0.89.

It was noted that although the genetic correlations of TWW/L with NLB/EL and NLW/EL was positive, the correlation between NLB/EL and NLW/EL was higher (0.85 ± 0.03). There are no comparable literature estimates that also include the per ewe life time component despite several authors having reported high positive genetic correlations between NLB/EJ and NLW/EJ (Brash *et al.*, 1994; Fogarty *et al.*, 1994; Snyman *et al.*, 1998a; Cloete *et al.*, 2004; Safari *et al.*, 2005b). TWW/L was lowly but positively (0.22 ± 0.12) correlated with Ewe Productive Life (EPL). This attribute implies that selecting ewes on the basis of net reproductive rate does not compromise ewe longevity. However, the selection response in terms of improved longevity would take a significant amount of time to accomplish due to the low genetic correlation. There was no environmental correlation (-0.01 ± 0.01) between TWW/L and EPL.

It is difficult to debate our finding because there is a literature dearth on estimates of correlations between TWW/L and longevity. However, Brash *et al.* (1994) reported a negative to positive genetic correlation (-0.11 ± 0.44) between NLW/EJ and longevity. There is thus much to be gained in terms of an increased accuracy of this correlation by future researchers. A low genetic correlation (0.22 ± 0.12) between TWW/L and lamb survival to weaning implies that selecting ewes on the basis of net reproductive rate does not have an adverse effect on lamb survival although substantial improvements in survival would probably not accrue very soon. The moderate environmental correlation (0.40 ± 0.01) implies that an environment conducive to a high TWW/L will also likely sustain a high survival rate. To our knowledge, there currently no literature estimates of such relationships in literature to warrant comparisons with our results or

findings. As anticipated, the r_g between TWW/L and Litter Size (0.61 ± 0.09) was high. This finding lends further support to the high correlations that were derived for the relationship between TWW/L and NLB in the literature that has been cited previously. The genetic correlation of lamb survival to weaning with litter size was unfavourable (-0.41 ± 0.15). This attribute implies that if ewes bear too many progeny during one lambing, their lamb rearing ability is compromised. On the other hand, correlations between litter size at weaning and TWW/L are favourable in direction, and approaching a level of double the corresponding standard error. Inconclusive correlations were derived for the relationships between TWW/L and fertility. Fertility was negatively or not correlated with reproduction and longevity. Stayability was lowly correlated with TWW/L. This implies that selecting ewes that rear many lambs with high weaning weights does not directly imply that the ewes will stay longer in the flocks.

Ewe Productive Life (EPL) was lowly to moderately genetically correlated with stayability up to two and four years of age (0.38 ± 0.11 and 0.23 ± 0.16 respectively). The environmental correlations were also positive. This implies that selecting animals on the basis of EPL will likely result in a correlated response in stayability, particularly at two years of age. There was an inconclusive genetic correlation between litter size and STAY2 (0.14 ± 0.13). There was also an inconclusive genetic correlation between litter size and STAY4 (-0.19 ± 0.19). These correlations were almost the same magnitude as their standard errors, different in direction and therefore not very accurate. The correlations can be refined by future researchers when more balanced data on ewe stayability becomes available. However at this juncture we can only hint that if future research confirms the sign of the correlation it would imply that very fecund ewes may experience a slight reduction in longevity. This also means that a high reproductive rate does not necessarily imply that the costs of ewe replacement will be reduced.

Our study also demonstrated that selection of ewes on the basis of lamb survival to weaning will have a correlated response in improvement in longevity because a moderate (0.48 ± 0.18) genetic correlation with STAY 4 was derived. There were low positive genetic correlations between STAY2 and NLB/EL and NLW/EL (0.16 ± 0.09 and 0.19 ± 0.09 respectively). However, STAY4 was moderately genetically correlated with NLW/EL. This means that selecting Dorper ewes for reproduction component traits will result in improvements in stayability despite genetic progress taking a long time to attain due to the low additive genetic variances associated with reproduction and stayability. In other words, selection for NLW/EL will not compromise stayability. Our findings are quite novel because there is a dearth in the sheep literature on longevity studies for comparison. Genetic variation in stayability implies that breeding objectives could incorporate selection pressure for ewes that exhibit distinctive maternal performance or an indirect selection for ewes stay in the flock for a longer period of time should be considered.

Table 7.4.3 REML estimates (SE in brackets) of genetic (above diagonal), and environmental (below diagonal) correlations between growth, reproduction, fitness and longevity traits in the Dorper sheep breed using multi-trait analyses

	TWW/L	Survival	Litter	EPL	Fertility	LC/EL	TL/EL	NLB/EL	NLW/EL	STAY2	STAY4	WW	PWW
TWW/L	-	0.22±0.12	0.61±0.09	0.22±0.12	-0.04±0.07	0.13±0.07	0.26±0.11	0.44±0.09	0.60±0.07	0.08±0.11	0.07±0.15	0.80±0.10	0.72±0.14
Survival	0.40±0.01	-	-0.41±0.15	0.21±0.14	0.10±0.11	0.09±0.11	0.27±0.17	0.04±0.16	0.29±0.15	-0.07±0.12	0.48±0.18	0.36±0.05	0.24±0.03
Litter	0.62±0.01	-0.16±0.01	-	0.15±0.15	-0.05±0.09	0.04±0.08	0.05±0.12	0.48±0.09	0.38±0.11	0.14±0.13	-0.19±0.19	0.20±0.08	0.16±0.07
EPL	-0.01±0.01	-0.06±0.01	0.01±0.01	-	0.09±0.07	0.07±0.07	0.34±0.10	0.38±0.11	0.51±0.11	0.38±0.11	0.23±0.16	-0.10±0.40	-0.18±0.42
Fertility	-0.06±0.01	-0.09±0.01	-0.01±0.01	0.09±0.01	-	-0.79±0.02	0.04±0.06	-0.06±0.06	-0.07±0.07	0.09±0.06	-0.07±0.09	0.15±0.03	0.10±0.02
LC/EL	0.03±0.01	0.04±0.01	0.01±0.01	0.14±0.01	-0.54±0.01	-	0.46±0.05	0.38±0.06	0.38±0.06	-0.02±0.06	0.18±0.09	0.48±0.10	0.35±0.08
TL/EL	-0.01±0.01	-0.05±0.01	-0.01±0.01	0.27±0.01	0.44±0.01	0.34±0.01	-	0.81±0.04	0.76±0.06	0.14±0.08	0.18±0.13	0.33±0.12	0.29±0.10
NLB/EL	0.32±0.01	-0.06±0.01	0.64±0.01	0.17±0.01	0.29±0.01	0.24±0.01	0.66±0.01	-	0.85±0.03	0.16±0.09	-0.01±0.14	0.60±0.05	0.35±0.02
NLW/EL	0.62±0.01	0.47±0.01	0.50±0.01	0.11±0.01	0.17±0.01	0.22±0.01	0.49±0.01	0.75±0.01	-	0.19±0.09	0.31±0.15	0.30±0.02	0.23±0.01
STAY2	-0.01±0.01	-0.05±0.01	0.01±0.01	0.31±0.01	0.04±0.01	0.09±0.01	0.14±0.01	0.09±0.01	0.07±0.01	-	-0.16±0.13	0.18±0.03	0.15±0.01
STAY4	-0.01±0.01	0.04±0.01	-0.01±0.01	0.22±0.01	0.01±0.01	0.03±0.01	0.05±0.01	0.03±0.01	0.01±0.01	-0.19±0.01	-	0.16±0.01	0.09±0.02
WW	0.20±0.04	0.28±0.03	0.18±0.01	0.06±0.10	-0.04±0.01	0.10±0.02	0.19±0.03	0.34±0.08	0.30±0.05	0.20±0.02	0.06±0.01	-	0.74±0.02
PWW	0.25±0.03	0.22±0.01	0.15±0.01	0.03±0.05	-0.02±0.01	0.08±0.01	0.11±0.01	0.20±0.04	0.20±0.07	0.02±0.01	0.05±0.01	0.56±0.01	-

However, the genetic relationships between stayability and other production traits are unclear and currently do not provide a good indication for early life traits suitable for indirect selection for stayability. Further studies with more detailed information regarding time and reason for flock removal are needed to properly address genetic and environmental effects on early growth and ewe productivity to account for their influence on ewe stayability.

7.5 Conclusions

There is a fine balance between the various production, reproduction, fitness and longevity functions that should be considered when constructing and implementing a breeding plan for Dorper sheep. The holistic approach of this study, where all traits that have an impact on ewe reproduction and fitness were evaluated provided very useful information that can assist in modifying Dorper breeding plans. The most important result of this study is that reproductive performance, defined as total weight of lamb weaned per ewe lambing (TWW/L), can be improved genetically through either direct or indirect selection. The estimated positive genetic and environmental correlations indicate that direct selection for TWW/L would be a suitable selection criterion to improve reproductive and fitness performance. This is because weaning weight alone although positively correlated with many component traits of reproduction might not be sufficient to improve reproduction and fitness.

Reproduction rate (TWW/L) was demonstrated to exhibit high coefficients of variation (CV %). This attribute, as well as a higher additive genetic variance than weaning weight (Table 7.4.1 and Table 7.4.2), implies that there is likely to be some reasonable selection response if this composite trait is incorporated in selection decisions. This is an important consideration in flocks where the lambing and weaning percentages are already high and an increase in the number of lambs may be undesirable. It is evident that WW should be recorded, as it is necessary for the calculation of total weight of lamb weaned, which is the trait that has the largest influence on the income in sheep production enterprises. This study demonstrated that it is possible to genetically improve reproduction and fitness of Dorper sheep through selection. However, selection response of reproduction and fitness traits will take time to accomplish due to the low additive genetic variances and heritabilities that are characteristic of these traits. The studies on longevity and stayability demonstrated that it would be beneficial to breeders if they incorporate these traits in their selection indices because they have a direct impact on profitability.

7.6 References

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CHAPTER 8

AN EVALUATION OF RELATIONSHIPS BETWEEN REPRODUCTION AND FITNESS TRAITS IN THE DORPER BREED USING BAYESIAN METHODS

8.1 Abstract

Across flock genetic parameter estimates for reproduction and fitness traits were derived for the Dorper breed by using Bayesian inference. Data were retrieved from the NSIS database from breeders that were constantly submitting performance data for a period spanning 30 years (1980 to 2009). It was quite evident from the studies that reproduction traits are characterized by low additive genetic variation which culminated in the point estimates of direct heritability (h^2) being higher and than those obtained using residual maximum likelihood (REML). The favourable genetic and environmental correlations indicate that direct selection for Total Weaning Weight per Ewe Lambing (TWW/L) would be a suitable selection criterion to improve net reproduction rate, fitness and robustness in Dorper sheep. Number of Lambs Born per Ewe Lifetime (NLB/EL) and Number of Lambs Weaned per Ewe Lifetime (NLW/EL) were also demonstrated to exhibit low genetic variation. There are low and negative genetic and environmental correlations between lamb survival to weaning and the NLB/EL in the magnitude of -0.11 ± 0.04 to -0.14 ± 0.01 , suggesting that breeding lambs that have a propensity to survive up to weaning might have very little or no effect on birth rate as a trait of the ewe. It was demonstrated that improvements in NLW/EL will result in improvements in fertility, EPL and TWW/L because favourable genetic and environmental correlations were derived using Markov Chain Monte Carlo (MCMC) methods. The point heritability estimates of STAY2 on the underlying liability scale were quite high ranging from 0.47 ± 0.16 to 0.48 ± 0.18 . These estimates were significantly different from the low heritability estimate that amounted to 0.05 ± 0.02 derived using REML methods. The direct heritability estimates for STAY3 (ranging from 0.22 ± 0.10 to 0.29 ± 0.08) and STAY4 (ranging from 0.08 ± 0.06 to 0.10 ± 0.06) could have been less accurate because in some cases the 95% confidence intervals for the Highest Posterior Densities (HPD) fluctuated from negative through zero to positive. It was recommended that further research on the effect of intensive reproduction on longevity should be conducted when more balanced data on ewe stayability and longevity becomes available. It has been demonstrated that Bayesian methods are useful for estimating genetic parameters for both linear and threshold traits. This study derived traits of reproduction and based on the variation in these traits, it was concluded that it is feasible to improve net reproduction rate, fitness and robustness in Dorper sheep.

Keywords: Gibbs, threshold, posterior density, stayability, reproduction, heritability, longevity, genetic, correlation, lamb survival, fertility

8.2 Introduction

Improved ewe productivity is a major objective in the local sheep industry. This could be achieved in part by increasing the number of lambs weaned and weight of lambs weaned per ewe per year. These traits are important since most sheep are raised for meat production (Duguma *et al.*, 2002a). A fact that is

accepted by animal breeders is that reproduction rate and survival rate are universally important traits in sheep, because these traits determine the efficiency of lamb production (Snyman *et al.*, 1997). In the past great emphasis has been placed on the individual component traits of reproduction such as fertility, litter size, lamb survival rate and the number of lambs born per ewe joined. However, ewe productivity, defined as the number or total weight of lamb weaned per ewe joined, which comprises of several component traits (Fogarty *et al.*, 1982), has received much less attention (Fogarty, 1995) and only a few genetic parameter estimates are available. Furthermore, despite the discrete and threshold nature of reproductive and fitness traits, linear methods have mainly been implemented to derive genetic parameters for them.

It is now commonly accepted by animal breeders and producers that total weight of lamb weaned per year is the best single measure of a flock's productivity (Snyman *et al.*, 1997). This is particularly true in woolled sheep, where less emphasis is placed upon early lamb growth traits, like weaning weight, and the likelihood of double counting is reduced. Total weight of lamb weaned per ewe per year is a function of the number of lambs born, their survival and the individual lamb weight at weaning. According to Snyman *et al.* (1997), there is 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 (Olivier *et al.*, 2001). The ability of the ewe to rear her litter to weaning is determined by the successful execution of several processes. These processes are driven by genetics, management, and the environment (Everret-Hinks & Cullen, 2009). 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, lamb survival to weaning and the growth potential of the lamb (Snyman *et al.*, 1997).

Reproduction, survival rate, fertility and stayability are by definition threshold traits. In these cases, the phenotype is expressed in two or more distinct, mutually exclusive and exhaustive categories. If a polygenic mode of inheritance is assumed for these traits, it is evident that the threshold concept should apply (Gianola & Foulley, 1982). Despite the existence of a plethora of genetic parameters for reproduction and fitness traits in sheep, the same has not been reported for the Dorper breed apart a preliminary study by Olivier & Cloete (2006). Furthermore, genetic parameters for reproduction and fitness traits in a diversity of sheep breeds have been estimated using mainly REML procedures by several workers.

In recent years there has been a renewed interest by quantitative geneticists to derive genetic parameters for various traits using various techniques because of the advent of alternative statistical methods and the software associated with it (Misztal *et al.*, 2002; Misztal *et al.*, 2008). Against this background, this study

aimed to add value to the (co) variance components and ratios obtained using REML procedures by applying Bayesian methodologies to estimate (co)variance components, posterior standard deviations (PSD), 95 % Highest Posterior Density (HPD) confidence intervals, variance ratios as well as genetic and environmental relationships of reproduction, fitness and longevity traits in the Dorper breed.

8.3 Materials and Methods

The origins of the reproduction data and descriptive statistics of the data were given in section 3.3 and Table 7.3.1 respectively. Furthermore, apart from the editing process that was described in section 7.3.1, the reproductive traits were further categorized as depicted in Table 8.3.1. Ewe productivity was defined as the Total Weight of Lamb Weaned per Ewe Lambing (TWW/L) after correction for age and sex. The actual number of lambing chances afforded to ewe and the actual times a ewe lambed per ewe lifetime (LC/EL and TL/EL respectively) were assessed as traits indicative of reproduction and longevity. Number of Lambs Born/ Weaned per Ewe Lifetime (NLB/EL and NLW/EL respectively) were taken as component traits of ewe productivity and as indicators of longevity.

Table 8.3.1 Categorical traits of reproduction and fitness that were analysed in conjunction with linear traits of reproduction

Trait	Number of Categories
Lambing Chances per Ewe Lifetime (LC/EL)	7
Times Lambed per Ewe Lifetime (TL/EL)	4
Number of Lambs Born per Ewe Lifetime (NLB/EL)	6
Number of Lambs Weaned per Ewe Lifetime (NLW/EL)	6
Two Year Lambing (TYL)	2
Stayability at 2 years of age (STAY2)	2
Stayability at 3 years of age (STAY3)	2
Stayability at 4 years of age (STAY4)	2

Fertility and precociousness were also computed as a binary trait by assessing whether a ewe lambed at 2 years of age or not (Two-Year Lambing). Fitness was derived through the computation of lamb survival to weaning as a proportion of the number of lambs weaned over the number of lambs born alive expressed as a trait of the ewe. The trait also indicated the ability of a ewe to rear a lamb up to weaning. Ewe Productive Life was derived from the age of the ewe at last lambing and was indicative of longevity for ewes born on or before the year 2005.

Stayability at 2, 3 and 4 years of age for ewes born on or before the year 2005 was assessed as binary traits also indicative of longevity. The categorical traits were further edited in such a way that seven or more Lambing Chances per Ewe Lifetime (LC/EL) were pooled together because of the low incidence of LC/EL greater than 7. Four or more Times Lamed per Ewe Lifetime (TL/EL) were pooled together and six or more lambs born or weaned per ewe life time were also pooled together. The other major change involved the statistical analysis.

8.3.1 Statistical analysis

The data were analyzed using two-trait linear-threshold animal models. The fixed effects that were fitted were year of birth (29 levels), age of dam (7 levels), and birth type (2 levels), contemporary group (1772 levels, consisting of flock-year-season combinations) and breeder (120 levels). The contemporary groups were compiled from the flocks that were reared in similar environments and management. Furthermore, a number of covariates were fitted depending on the trait that was being evaluated such as the number of production years as a covariate to NLB/EL, NLW/EL and TWW/L. These fixed effects had been proven to be significant ($P < 0.05$) using ASREML (Gilmour *et al.*, 2002), as described in section 7.3.2. The model included only the random direct animal additive genetic effect. The equation for the two-trait animal model was the following:

$$\mathbf{y}_{ijk} = \mathbf{f}_{ij} + \mathbf{a}_{ik} + \mathbf{e}_{ijk}$$

In this model, \mathbf{y} was a vector of observations for underlying values for i 'th trait; \mathbf{f}_{ij} was the fixed effect j for the i 'th trait; \mathbf{a}_{ik} was the additive genetic effect of the k 'th animal for the i 'th trait; and \mathbf{e}_{ijk} was the vector of randomly distributed residual effects.

The software used was THRGIBBSF90 (Misztal *et al.*, 2002). This software was reported by Lee *et al.* (2002) to be suitable for the estimation of variance components and genetic parameters in threshold animal mixed models for any combination of categorical and continuous traits. The software is robust enough to handle multiple-trait analyses efficiently regardless of the presence of missing observations. The program POSTGIBBSF90 was used for post-Gibbs analysis (Misztal *et al.*, 2002). The use of such software has been applied in the estimation of genetic parameters for lamb survival in South African Merino sheep by Cloete *et al.* (2009). Our study generated single chains of 1 000 000 samples with the first 250 000 samples being discarded as the burn-in period. For all analyses, convergence was assessed using methodology presented by Raftery & Lewis (1992). Convergence of the analyses was confirmed the attainment of a stationary stage by graphical through graphical inspection after plotting the post Gibbs sample values against the iterations. Every 10th sample was stored after 250 000 iterations, giving a total of 75 000 samples for the computation of posterior means and posterior Standard

Deviations (PSD), as well as 95% Highest Posterior Density (HPD) confidence intervals. Based on results from the analysis, 95% HPD confidence intervals were also computed for the (co)variance components when applicable. Point estimates were calculated as the posterior mean of the specific variance component, using the results from the final 75 000 samples as set out above. Direct genetic, maternal, dam permanent environmental and environmental (residual) correlations were derived from these analyses.

8.4 Results and Discussion

Histograms depicting posterior density distributions for the additive genetic variances from the two-trait analyses are presented in Figures 8.4.1 to 8.4.6. The genetic variance components were significant for all the traits analysed, as reflected by the 95% confidence limits for the HPD. However, it was confirmed through the implementation of Gibbs sampling that generally reproduction and fitness traits are characterized by low additive genetic variation.

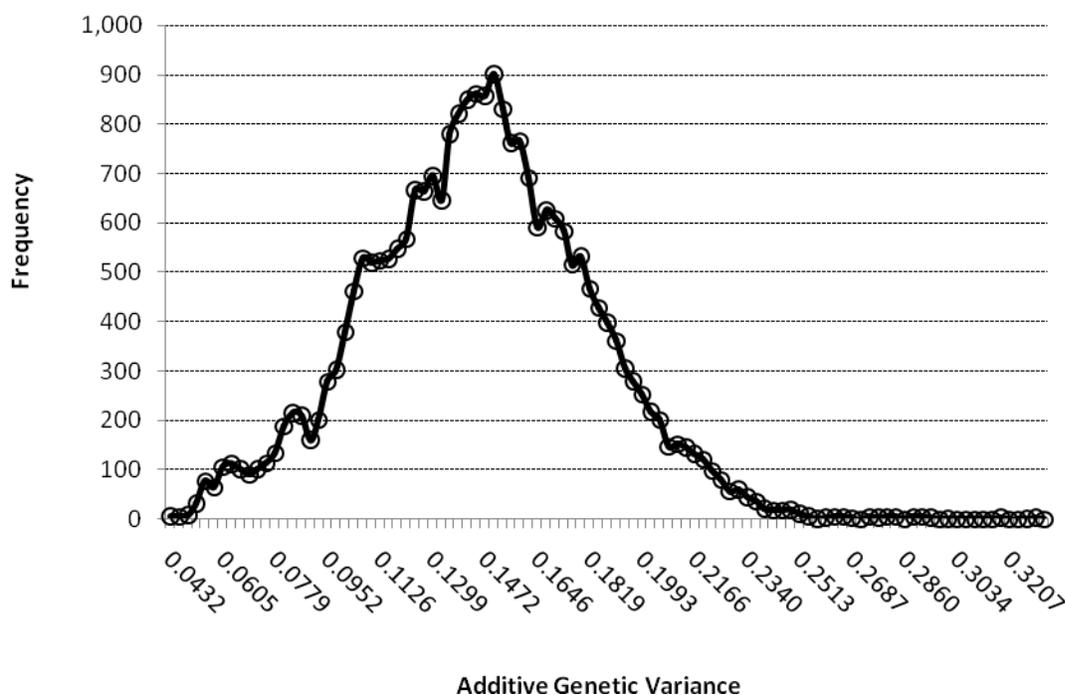


Figure 8.4.1 Posterior density distributions for the additive genetic variance of Number of Lambs Weaned per Ewe Life time (NLW/EL)

The sample histogram in Figure 8.4.1 suggested that NLW/EL was approaching a normal distribution. The distribution demonstrates that linear methods (REML) can also be utilized to estimate co (variance) components and ratios for this trait. Threshold methods were applied in the current study due to the

categorical nature of the NLW/EL as depicted in Table 8.3.1. In particular Figure 8.4.1 established that the point estimate that was derived using REML procedures for the additive genetic variance (0.0589) (see Table 7.4.2) was within the 95% HPD confidence interval of NLW/EL. It should however be noted that the implementation of MCMC methods resulted in NLW/EL exhibiting more additive genetic variance than that which was observed through the implementation of REML procedures.

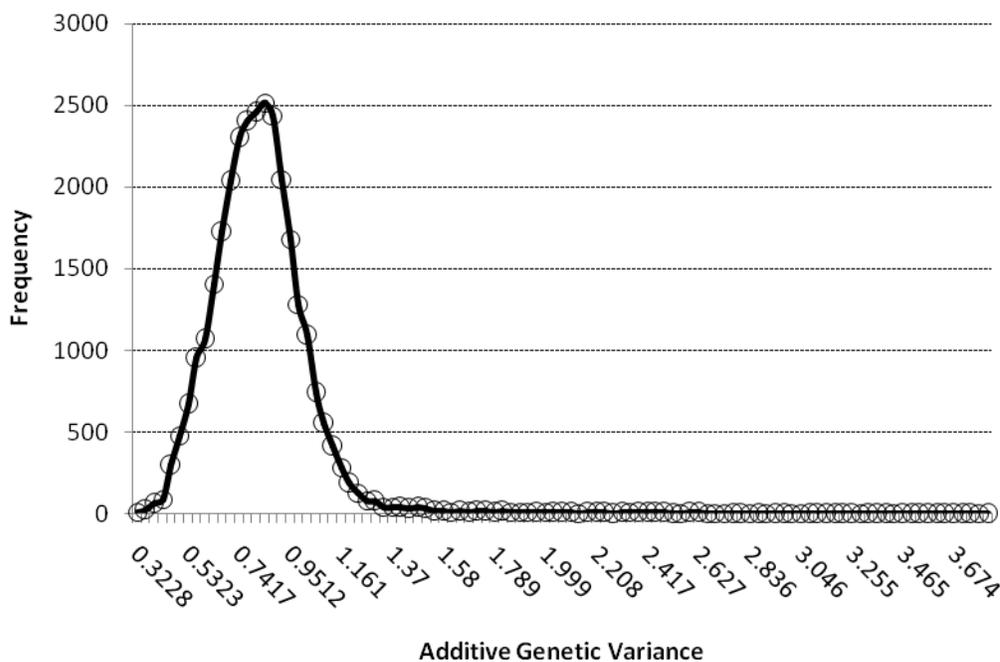


Figure 8.4.2 Posterior density distributions for the additive genetic variance of Two Year Lambing (TYL)

The 95 % HPD depicted in Figure 8.4.2 established that TYL was indeed a binary trait that exhibits the appropriate distribution. It was demonstrated that the point estimate of the additive genetic variance (0.36) that was computed with the utilization of linear methods (Table 7.4.2) was within the range of the current histogram. However, threshold methods resulted in higher additive genetic variance being derived. It can be deduced that Bayesian methods have unique statistical properties that can be used for the estimation of (co) variance components and ratios for binary traits. This argument is supported by the assertions of Gianola and Foulley (1982) in which they reported that fertility is a threshold trait because its phenotype is expressed in two or more distinct, mutually exclusive and exhaustive categories. It was appropriate to implement Bayesian inference for TYL because Pretorius and Van der Merwe (2000) reported that such methods have several practical advantages over the classical REML inference. One of the advantages is that the variance estimates from Bayesian inference are always within the allowed parameter space whereas estimates that result from the implementation of REML procedures can be outside the parameter space due to their asymptotic distributions.

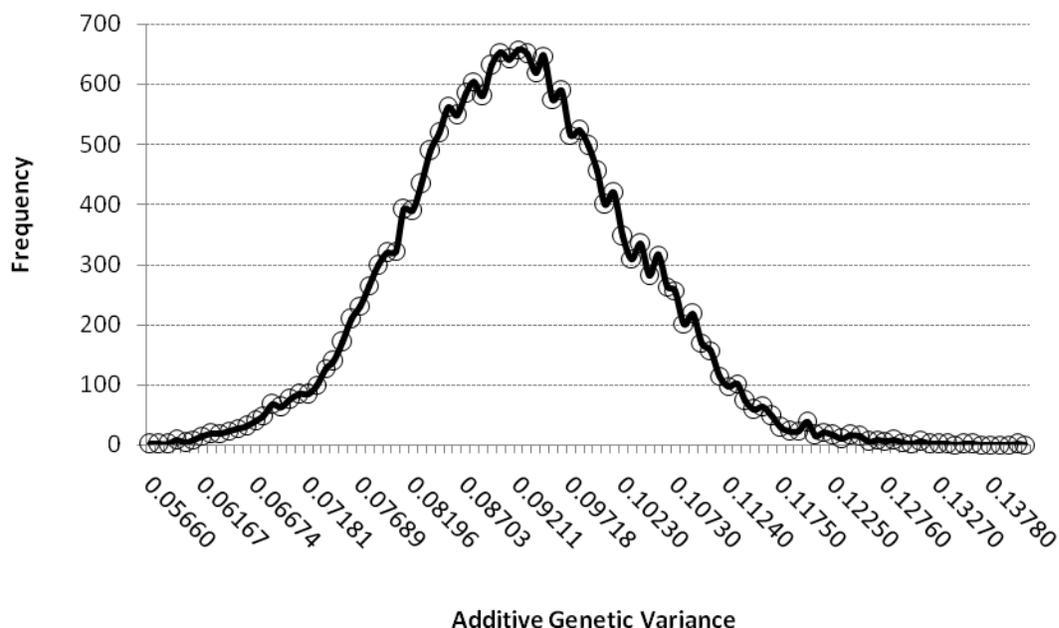


Figure 8.4.3 Posterior density distributions for the additive genetic variance of Number of Lambs Born per Ewe Lifetime (NLB/EL)

It was evident from the histogram presented in Figure 8.4.3 that the NLB/EL exhibited a distribution that approached an almost perfect normal distribution. The feature was also prevalent in NLW/EL. This finding is not a deviation from our expectations because REML procedures derived a high positive genetic correlation (0.85 ± 0.03) between the two traits as reported in Table 7.4.3. Linear methods can thus be utilized to compute variance components for such traits. However, the implementation of Gibbs sampling results in higher estimates of additive genetic variance as depicted in the 95 % HPD confidence interval for NLB/EL in Figure 8.4.3.

Stayability is a binary trait whose distribution allows the estimations of (co) variance components and ratios to be implemented more accurately via Bayesian methods. Figure 8.4.4 and Figure 8.4.5 depict the 95 % HPD confidence intervals for stayability at three years of age (STAY3) and at two years of age (STAY2) respectively. It is apparent that both histograms were skewed demonstrating the binary nature of the traits. Variance ratios and components for various measures of stayability had previously been estimated using generalized linear mixed models in REML using the logit transformation. In such analyses the residual variation was fixed at 3.3. The estimates derived using that method were low. Such attributes motivated the current study in which the application of Bayesian inference was used to evaluate if there will be any change the variance components and ratios.

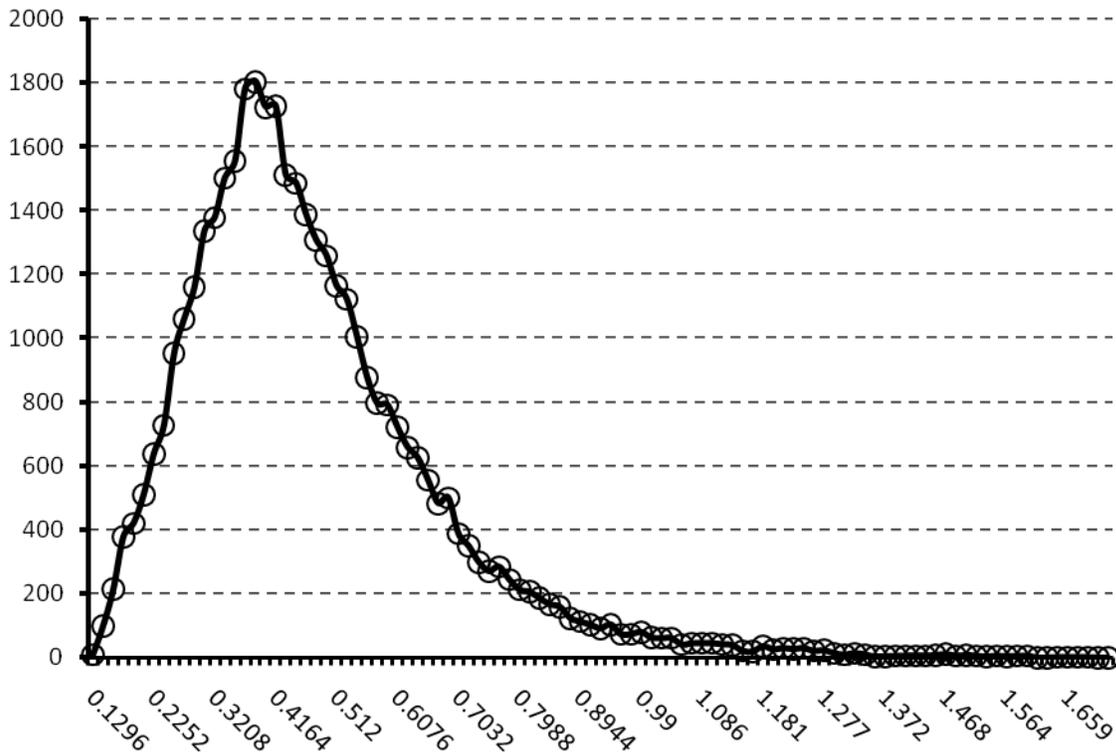


Figure 8.4.4 Posterior density distributions for the additive genetic variance of Stayability at 3 years (STAY3)

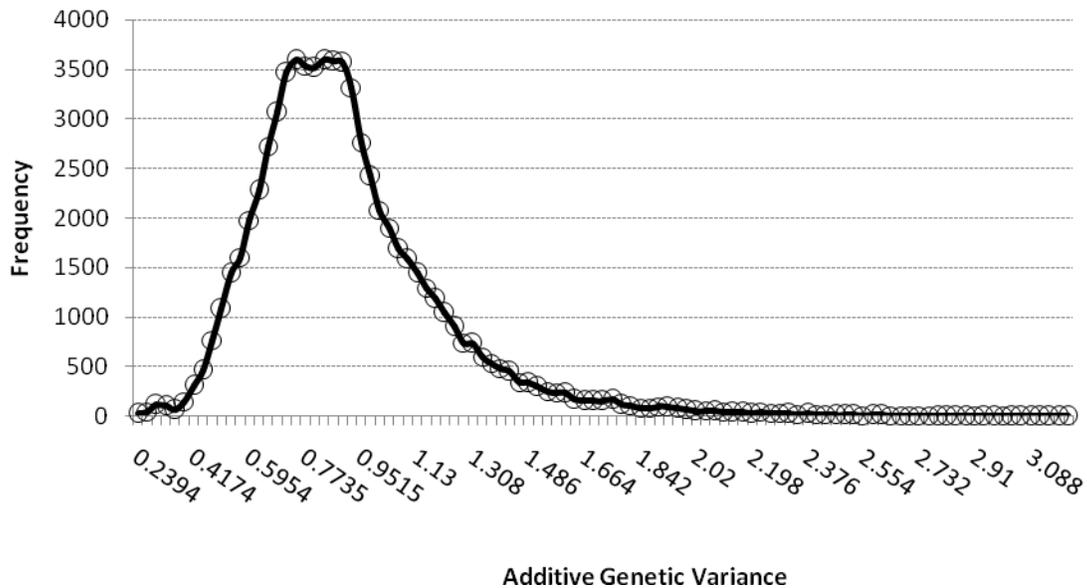


Figure 8.4.5 Posterior density distributions for the additive genetic variance of Stayability at 2 years (STAY2)

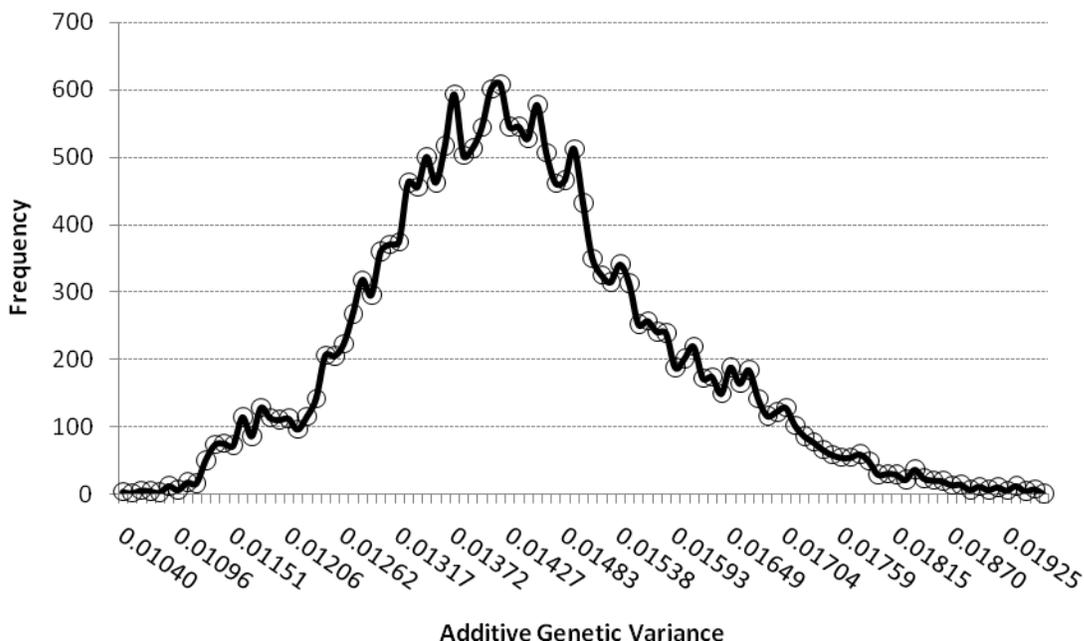


Figure 8.4.6 Posterior density distributions for the additive genetic variance of Times Lambded per Ewe life time (TL/EL)

The distribution of the additive genetic variance for TL/EL approximated a normal distribution (Figure 8.4.6). This was similar to the previously discussed traits of reproduction (NLB/EL and NLW/EL) in which there were several categories and thresholds. The approximation of the normal distribution in these traits justified the earlier analyses in which linear (REML) methods were applied. The application of Bayesian methods in the estimation of variance components and ratios resulted in more effective separation of different sources of variation for threshold traits as compared to linear methods, as demonstrated in the current study.

Table 8.4.1 shows that the HPD for NLB/EL ranged from 0.06795 to 0.11850. This interval excluded the variance component of 0.00639 that was derived through the implementation of REML procedures. It should be noted that the scale of the threshold analyses differed from the REML analyses because the residual variance for the threshold trait in the threshold analyses was set to a value of 1.0, whereas the linear model allows the residual variance to be whatever it is in all probability lower than 1.0. It was however, noted that despite the low genetic variation exhibited by the trait, it was moderately heritable (0.16 ± 0.04) and should therefore respond to selection. The heritability estimated computed through REML (0.10 ± 0.01) was somewhat lower than the one derived using Markov Chain Monte Carlo (MCMC) procedures on the underlying liability scale.

The NLW/EL exhibited low additive genetic variance whose 95% confidence interval for PSD ranged from a minimum of 0.07172 to a maximum of 0.278 (insert Table 8.4.1). The point estimate for additive genetic variance that was computed using REML (0.0589) was below the lower limit derived using Gibbs sampling. Despite the differences in magnitude of the point heritability estimates derived using two-trait analyses (0.10 ± 0.05 to 0.14 ± 0.06), it can be concluded that it is feasible to achieve genetic improvement in both reproduction and longevity by selecting animals on the basis of NLW/EL. It should be noted that studies on genetic evaluation of stayability in ovine species are quite novel because to our knowledge only the ground breaking work by Borg *et al.* (2009) has been published. Our study confirmed and supported the findings of the former researchers because it was quite evident that the additive genetic variation associated with stayability was higher than that which is expressed by some reproduction traits. The 95% confidence interval of the HPD for STAY2 ranged from a minimum of 0.25080 to a maximum of 1.577. Consequently the point heritability estimates of STAY2 were quite high ranging from 0.47 ± 0.15 to 0.48 ± 0.18 on the underlying liability scale. These estimates are different from the low (0.05 ± 0.02) heritability estimates that were derived using REML methods. The 95% confidence intervals of the HPD for STAY3 and STAY4 ranged from -0.00397 to 0.73640 and -0.07020 to 0.27930 respectively (Table 8.4.1). However, it was noted that the direct heritability estimates for STAY3 (ranging from 0.22 ± 0.10 to 0.29 ± 0.10) and STAY4 (ranging from 0.08 ± 0.06 to 0.10 ± 0.06) could have been biased because in some cases the 95% confidence intervals for the PSD fluctuated from negative through zero to positive. In an effort to obtain more robust estimates, the number of Gibbs samples was increased to 1 500 000 with a burn in period of 500 000 in order to ensure that the analysis fully converges. Despite that measure the results did not change much. It is however, noteworthy to state that this impediment is a common feature when running Gibbs samples for binary traits that are not evenly distributed between the two categories, as reported by Cloete *et al.* (2009).

NLB/EL was positively genetically (0.28 ± 0.05) and environmentally (0.18 ± 0.01) correlated with Ewe Productive Life. It is essential to reiterate that both traits are indicative of ewe longevity therefore, it can thus be said it is feasible to genetically improve Dorper ewes to achieve better longevity through selection. Selection is likely to be aided by a CV of 68% for EPL. The current findings endorse the revelations that resulted from REML procedures although the magnitude of the estimates differed. These findings are unique because there are no literature estimates to compare the present results to. The current study demonstrated that there is a very low and negative genetic and environmental correlation between lamb survival to weaning and (NLB/EL) in the magnitude of -0.11 ± 0.04 and -0.14 ± 0.01 respectively as presented in Table 8.4.2. These correlations are in agreement with the ones computed using REML procedures regardless of the differences in magnitude. The low and negative relationships suggest that selecting ewes to bear lambs that have a propensity to survive up to weaning has very little adverse effect on reproduction and longevity because NLB/EL is an indirect measurement of ewe longevity (Insert Table 8.4.2).

Table 8.4.1 Mean (co)variance components, posterior Standard Deviation (PSD), 95% highest posterior density (HPD) confidence intervals and variance ratios of reproduction and fitness traits in the Dorper breed using a series of two-trait analyses

		Categorical traits							
Linear trait	Item	NLB/EL	NLW/EL	TYL	STAY2	STAY3	STAY4	LC/EL	TL/EL
Lamb survival to weaning	PSD	0.01077	0.03740	0.21400	0.29730	0.13610	0.06941	0.00130	0.00145
	Lower HPD	0.07063	0.11700	0.38820	0.31550	0.02250	-0.0505	0.01107	0.01142
	Upper HPD	0.11280	0.26370	1.22700	1.48100	0.55590	0.22160	0.01615	0.01751
	σ_a^2	0.09173	0.19030	0.80760	0.89820	0.28920	0.08555	0.01361	0.01440
	σ_e^2	0.49390	1.20600	1.00000	1.00000	1.00000	1.00000	0.13444	0.13370
	σ_p^2	0.58563	1.39630	1.80760	1.89820	1.28920	1.08555	0.14805	0.14810
	$h^2 \pm SE$	0.16 \pm 0.04	0.14 \pm 0.06	0.45 \pm 0.12	0.47 \pm 0.16	0.22 \pm 0.10	0.08 \pm 0.06	0.09 \pm 0.02	0.10 \pm 0.02
TWW/L	PSD	0.01291	0.04330	0.24930	0.33820	0.18890	0.08920	0.00130	0.00145
	Lower HPD	0.06795	0.09860	0.35600	0.25080	-0.00397	-0.07020	0.01112	0.01150
	Upper HPD	0.11850	0.26860	1.33330	1.57700	0.73640	0.27930	0.01621	0.01720
	σ_a^2	0.09325	0.18350	0.84470	0.91380	0.36620	0.10460	0.01360	0.01440
	σ_e^2	0.48580	0.71680	1.00000	1.00000	1.00000	1.00000	0.13444	0.13370
	σ_p^2	0.5791	1.45420	1.84470	1.91380	1.36620	1.10460	0.14804	0.14810
	$h^2 \pm SE$	0.16 \pm 0.04	0.13 \pm 0.06	0.46 \pm 0.14	0.48 \pm 0.18	0.27 \pm 0.14	0.09 \pm 0.08	0.09 \pm 0.02	0.10 \pm 0.02
EPL	PSD	0.10291	0.04210	0.21850	0.27980	0.10920	0.07204	0.00128	0.00130
	Lower HPD	0.06795	0.11280	0.38340	0.34310	0.19800	-0.02874	0.01116	0.01107
	Upper HPD	0.11850	0.27800	1.24000	1.44000	0.62620	0.25360	0.01628	0.01615
	σ_a^2	0.09325	0.19540	0.81180	0.89160	0.41210	0.11240	0.01362	0.01361
	σ_e^2	0.48580	1.25000	1.00000	1.00000	1.00000	1.00000	0.13444	0.13440
	σ_p^2	0.57910	1.44540	1.81180	1.89160	1.41210	1.11240	0.14806	0.14801
	$h^2 \pm SE$	0.16 \pm 0.04	0.14 \pm 0.06	0.45 \pm 0.12	0.47 \pm 0.15	0.29 \pm 0.08	0.10 \pm 0.06	0.09 \pm 0.02	0.09 \pm 0.02

Table 8.4.2 Genetic and environmental correlations between reproduction and fitness traits in a Dorper breed using two-trait analyses

		Categorical traits							
Linear trait	Correlation	NLB/EL	NLW/EL	TYL	STAY2	STAY3	STAY4	LC/EL	TL/EL
Lamb survival	Genetic	-0.11±0.04	0.21±0.04	0.37±0.03	0.25±0.13	0.05±0.02	-0.39±0.08	0.14±0.02	0.38±0.09
	Environmental	-0.14±0.01	0.40±0.10	-0.03±0.02	0.07±0.01	0.37±0.10	0.02±0.01	0.37±0.12	0.19±0.06
TWW/L	Genetic	0.58±0.06	0.43±0.05	0.40±0.22	0.16±0.06	0.40±0.07	-0.41±0.08	0.25±0.04	0.24±0.01
	Environmental	0.40±0.02	0.73±0.03	-0.04±0.02	-0.12±0.01	-0.09±0.01	0.02±0.01	0.08±0.02	-0.02±0.01
EPL	Genetic	0.28±0.05	0.26±0.03	0.04±0.04	0.45±0.10	0.40±0.06	0.35±0.10	0.21±0.04	0.33±0.06
	Environmental	0.18±0.01	0.06±0.01	0.01±0.03	0.24±0.02	0.18±0.02	0.14±0.01	0.18±0.01	0.25±0.01

Furthermore, an environment that is conducive to a higher lamb rearing capacity does not necessarily mean that there will be an improvement in the NLB/EL and longevity. There is a dearth in published literature estimates for comparison with our findings. However, the only report that may have a resemblance to our work was the genetic correlation between the number of lambs born per ewe joined (NLB/EJ) and longevity (-0.15 ± 0.43), as derived by Brash *et al.* (1994d) in Dorset sheep. The same workers also derived positive genetic correlations between number of lambs born per ewe joined (NLB/EJ) and ewe rearing ability in the magnitude of 1.00 ± 0.77 in Dorset sheep and 1.00 ± 0.54 in Corriedale sheep respectively.

Genetic improvement in NLW/EL will result in improvements in fertility, EPL and TWW/EL because positive genetic and environmental correlations were derived using MCMC methods (Table 8.4.2). NLW/EL was demonstrated to be positively correlated with lamb survival to weaning (0.21 ± 0.04). There are not many published literature estimates that are comparable to the current one. However, it was demonstrated that the genetic correlation between number of lambs weaned per ewe joined (NLW/EJ) and ewe rearing ability exhibited a 95 % confidence interval reported by which ranged from -0.60 to 0.97 (Safari *et al.*, 2005b). This interval varied from moderate negative to high positive, thus encompassing a wide range of all possible options.

TWW/L was positively genetically correlated with both NLB/EL and NLW/EL to the magnitude of 0.58 ± 0.06 and 0.43 ± 0.05 respectively (Table 8.4.2). Bromley *et al.* (2001) derived very high positive genetic correlations between Weight of Lamb Weaned per Ewe Lambing (WW/EL) and Number of Lambs Weaned per Ewe Lambing (NLW/EL). Safari *et al.* (2005b) highlighted that there are positive genetic correlations between WW/EL and NLB/EL and NLW/EL in the magnitude of -0.19 to 1.00 and -0.48 to 0.98 respectively, thus encompassing a wide range of all possible options. The former authors also concluded that NLB/EL and NLW/EL are indeed genetically similar traits. The current study further demonstrated that TWW/EL is positively correlated with Lambing Chances per Ewe Lifetime (LC/EL) and the actual Times Lamed per Ewe Lifetime (TL/EL) in the magnitude of 0.25 ± 0.04 and 0.24 ± 0.01 respectively. However, the direct heritability estimate for LC/EL was lower than the estimate derived in REML (0.09 ± 0.02 vs. 0.23 ± 0.01). Furthermore, threshold and linear estimates for direct heritability were quite similar (0.10 ± 0.02 vs. 0.11 ± 0.01) (Table 8.4.1). It was therefore concluded that selecting Dorper ewes on the basis of TWW/L will result in a correlated response in the number of lambing opportunities that can potentially be achieved in a lifetime as well as ewe longevity. The current findings are consistent with the direction of the correlations that were derived using REML procedures although the correlations differ in magnitude.

The current study also elucidated that there was a moderate and positive genetic correlation between lamb survival to weaning (as a trait of the ewe) and Two Year Lambing (TYL) in the magnitude of

0.37±0.03 (Table 8.4.2). This result suggests that breeding ewes being more fertile and precocious at 2 years of age will likely to have a good lamb rearing ability. However, it should be considered that the low additive genetic variance ratios associated with both lamb survival to weaning and TYL might hamper genetic improvement, although both traits exhibit fairly high levels of phenotypic variation (CV's of respectively 31% and 50%). TYL was also demonstrated to be positively correlated (0.40±0.22) with TWW/EL. The positive correlation imply that selecting fertile and precocious Dorper ewes at 2 years of age will result in ewes that wean more and heavier lambs per lambing in subsequent years. TYL did not exhibit any significant genetic or environmental correlation with Ewe Productive Life (EPL). Therefore, breeding precocious ewes is not a guarantee for improved ewe longevity. There are no literature estimates to compare the present results to.

The current study derived a low positive genetic correlation between lamb survival to weaning and STAY2 (0.25±0.13) (Table 8.4.2). However there was a very low positive correlation between lamb survival to weaning and STAY3 (0.05±0.02). There was an antagonistic genetic correlation (-0.39±0.08) between lamb survival to weaning and STAY4. TWW/L also had positive genetic correlations with both STAY2 and STAY4 but an antagonistic relationship with STAY4. There is no published literature to compare the current findings to. The implementation of MCMC procedures derived positive genetic and environmental correlations between Ewe Productive Life and several reproduction traits and stayability (Table 8.4.2). It should be noted that EPL is a direct measurement of ewe longevity. The only limitation that is associated with EPL is that it was lowly heritable. However, selection is likely to be aided by a CV of 68% for the trait.

8.5 Conclusions

It has been demonstrated that Bayesian methods are useful for estimating genetic parameters for both linear and threshold traits. This study derived traits of reproduction and based on the variation in these traits, it was concluded that it is feasible to improve net reproduction rate, fitness and robustness in Dorper sheep. Furthermore, it was also apparent that the variation may have a genetic basis and would, therefore, be expected to respond to selection in the Dorper breed. The estimated mostly favourable genetic and environmental correlations led to the conclusion that direct selection for TWW/L would be an appropriate selection criterion to improve net reproduction rate, fitness and robustness in Dorper sheep. It has also been confirmed that efficiency of lamb production in the Dorper breed can be achieved by selection programs that target reproduction and survival rate (Snyman *et al.*, 1997). Our study endorsed reports by Falconer & Mackay (1996) who postulated that several components influence ewe productivity and that each of these components can be used as a selection criterion, as each has a direct impact on total ewe productivity. It was demonstrated that it is quite feasible to improve the robustness or fitness of Dorper sheep by indirectly selecting in favour of Ewe Productive Life and other component traits of

reproduction such as NLB/EL and NLW/EL. Further research on the effect of intensive reproduction on longevity should be conducted when more balanced data becomes available in future.

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CHAPTER 9

AN ASSESSMENT OF GENETIC PROGRESS IN REPRODUCTION AND FITNESS TRAITS IN THE SOUTH AFRICAN DORPER SHEEP BREED

9.1 Abstract

Genetic trends were constructed to assess the genetic change in reproduction and fitness traits in the Dorper sheep breed, as based upon single-trait analyses on animals from the NSIS database over a period of 11 years from 1998 to 2008. Genetic trends were calculated as the regression of averaged annual predicted breeding value on year of birth using standard regression techniques. The traits that were assessed were Total Weaning Weight per Ewe Lambing (TWW/L), Number of Lambs Born per Ewe Lifetime (NLB/EL), Number of Lambs Weaned per Ewe Lifetime (NLW/EL), lamb survival to weaning (survival), litter size (LS), Lambing Chances per Ewe Lifetime (LC/EL), Times Lambed per Ewe Lifetime (TL/EL), Ewe Productive Life (EPL) and weaning weight (WW). Most reproduction traits exhibited a slight decrease or no response to selection. This aspect demonstrated a lack of directed selection for reproduction and fitness traits in the breed. Despite low additive genetic variation and heritability in reproduction and fitness traits, it was highlighted that responses to selection could be achieved as a consequence of either direct selection for reproductive traits or through correlations with any of the component traits. The slight negative genetic trends were also attributed to the possible over-emphasis of subjectively assessed traits such as Conformation, Type and Size at the expense of incorporating selection on the BLUP of breeding values for objectively measured traits such as weaning weight and total weaning weight per ewe joined.

Keywords: correlated, regression, selection response, EBV, trend, progress

9.2 Introduction

The sheep industry has gone through a period of major change in recent years. In particular, a significant shift in the relative prices of wool and meat has led to the adoption of different types of commercial enterprises. In addition, the amount of genetic information available to breeders has increased, from a new genetic evaluation system that has been implemented by the National Small Stock Improvement Scheme (NSIS). The NSIS has for some time not only been recording live weight traits but has made significant strides in recording traits related to reproduction and fitness in various sheep breeds. The evaluation of livestock in South Africa has developed steadily from simple ratios of performance in similar environments through selection indices based upon own and close relatives' performance to BLUP of breeding values (Schoeman *et al.*, 2010). Recent advances in the processing power of computers and developments in BLUP computing strategies have led to the widespread acceptance of the concept of evaluating individual animals for genetic merit rather than just one portion of the population, traditionally the sires (Robinson & Chesnais, 1988). Selection based on estimated breeding values (EBV) has been effective in making continuous genetic improvement in production traits (Wang *et al.*, 2005).

It has been reported that reproduction is a complex composite trait influenced by numerous components including age at puberty, ovulation rate, estrus, fertilization, embryo implantation, pregnancy, parturition, lactation, and mothering ability (Snowder, 2007). The genetic effect on each component of reproduction has been demonstrated to vary in ovine species (Safari *et al.*, 2005b). Although component traits of reproduction are under the influence of many genes, a limited number of major genes associated with separate components of reproduction have been reported in sheep (Piper & Bindon, 1982; Bradford *et al.*, 1986; Davis *et al.*, 1991). Expressions of the genetic effects on reproduction are influenced by numerous environmental parameters such as season, climatic conditions, management, health, nutrition, ram to ewe breeding ratio, age of ewe, and ram libido and fertility. Because genetic and environmental factors interact, genetic improvement of reproduction is challenging (Snowder, 2007).

Selection for a single component of reproduction such as ovulation rate, litter size at birth or number of lambs weaned has been traditionally practiced. However, selection for a single component of a composite trait does not always result in an overall improvement of a complex trait such as reproduction (Snowder, 2007). Improvement in a component trait may be offset by an antagonistic correlated response or a lack of response in a supporting trait such as a failure to increase lactation for larger litter sizes or faster growing lambs (Snowder, 2007). The phenotypic variation of a composite trait is influenced by the level of variability among its component traits and their interactions. Within a production or management system, variation in litter weight weaned among ewes is useful to estimate a ewe's overall reproductive success and her adaptation to that system. Reproduction and survival rate are the most important factors determining the efficiency of lamb production (Snyman *et al.*, 1997).

Falconer & Mackay (1996) demonstrated that several components influence ewe productivity and that each of these components can be used as a selection criterion, as each has a direct impact on total ewe productivity. One of the main objectives in the South African sheep industry is improved ewe productivity. This could be accomplished in part by increasing the number of lambs weaned and weight of lamb weaned per ewe per year (Cloete *et al.*, 2002). Until recently emphasis has mostly been placed on the individual component traits of reproduction such as fertility, litter size, lamb survival rate and the number of lambs born and weaned per ewe joined. Ewe productivity, defined as the number or total weight of lamb weaned per ewe joined, which comprises of several component traits has received much less attention (Fogarty, 1995) and only a few genetic parameter estimates are available.

The NSIS has accumulated data on a variety of reproductive traits in diverse sheep breeds. Genetic parameters for several growth and some reproductive traits have been estimated as a result of the accumulation of these data (Van Wyk *et al.*, 1993b; Snyman *et al.*, 1997; Cloete *et al.*, 1998a; Olivier *et al.*, 2001; Cloete *et al.*, 2001; Cloete *et al.*, 2002; Cloete *et al.*, 2006; Olivier & Cloete, 2006; Cloete *et al.*,

2009). Apart from a significant amount of genetic parameters having been estimated for South African sheep breeds, substantial effort has also been directed at assessing genetic progress that has been achieved over the years. Genetic trends have thus been reported for a variety of sheep breeds under a variety of South African production systems (Van Wyk *et al.*, 1993c; Olivier *et al.*, 1995; Naser *et al.*, 1995; Gray *et al.*, 1999; Cloete *et al.*, 2004; Swanepoel, 2006; Olivier & Cloete, 2006; Cloete *et al.*, 2009; Zishiri, 2009; Zishiri *et al.*, 2010). It is very critical to compute genetic trends because it is only through them that breeders have the opportunity to assess their breeding evaluation schemes and thereafter make changes to their selection criteria so as to achieve maximum genetic progress.

Genetic improvement of reproduction has typically focused on selection for the ability of ewes to rear multiples (Atkins, 1980; Cloete & Scholtz, 1998a; Cloete *et al.*, 2004). However, improvements in lamb survival are unlikely if litter size is increased through selection without any regard to whether the additional lambs born can be successfully reared (Lindsay, 1982) as multiple-born lambs are more likely to die than singles (Hatcher *et al.*, 2009). Genetic improvement in lifetime production efficiency is dependent upon selection for traits with which lifetime production efficiency is genetically correlated. Many early life traits have been suggested and are being used as selection criteria (Saoud & Hohenboken, 1984). In recent years sheep breeders in South Africa have acknowledged the relevance of breeding robust sheep. However, efforts to genetically improve sheep for reproduction and fitness have been hampered by the unavailability or limited performance records for traits related to reproduction and fitness.

Apart from contributing a significant 25% to the South African national sheep population, the Dorper sheep breed has made a marked contribution to the meat industry not only in terms of meat output and revenue accrued but also by contributing germplasm for crossbreeding with the intention of achieving prime lamb production. Despite the popularity of the Dorper breed, there is very little information about its growth, reproduction and fitness. Furthermore, there have been very limited genetic evaluation studies that have been carried out to generate genetic parameters. Explicit genetic trends for reproduction and fitness traits in the Dorper have not been estimated besides a preliminary study conducted by Olivier & Cloete (2006).

It is important to have knowledge of genetic trends in the Dorper breed to assess present selection strategies. In the past decades there has been a major emphasis on selecting Dorper rams and ewes on the basis of subjectively assessed traits in the show ring, possibly at the expense of performance recording. It was against this background that the current study was initiated to assess if the selection of Dorper ewes and rams resulted in the desired genetic responses on an industry basis.

9.3 Materials and Methods

Data were retrieved from the NSIS database from breeders that were constantly submitting performance data for a period spanning 11 years (1998 to 2008). All the progeny were descended from a pedigree spanning 15 generations out of 4 064 sires and 76 952 dams. Furthermore, the progeny emanated from 713 great grand sires and 16 613 great grand dams. The descriptive statistics for the traits considered were given in Table 7.3.1. Reproduction and fitness traits that were assessed for genetic improvement were weaning weight (WW), Number of Lambs Born per Ewe Lifetime (NLB/EL), Number of Lambs Weaned per Ewe Lifetime (NLW/EL), Total Weaning Weight per Ewe Lambing (TWW/L), Litter size (LS), Lamb survival to weaning (Survival), Lambing Chances per Ewe Lifetime (LC/EL), Times Lambled per Ewe Lifetime (TL/EL) and Ewe Productive Life (EPL).

Direct breeding values were derived for each trait by using the data from the most appropriate single-trait animal models in ASREML (Gilmour *et al.*, 2002). Genetic trends were calculated as the regression of average predicted breeding value on year of birth using Proc Reg (REG) in the Statistical Analysis System (SAS, 2004). Regression coefficients and their standard errors ($b \pm SE$), correlations (r), intercepts and R^2 values were also derived as part of the procedure. The genetic change per annum was derived by expressing the regression coefficient (b) of the particular trait as a percentage of the phenotypic mean for that particular trait.

9.4 Results and Discussion

Genetic trends for reproduction and fitness traits for the period 1998 to 2008 are presented in Table 9.4. It was apparent from the genetic evaluations that were carried out that there was generally negligible genetic progress, or a lack of any genetic progress in reproduction and fitness traits in the Dorper sheep breed. WW was characterised by very low Estimated Breeding Values (EBVs) between 1998 and 2008 (Figure 9.4.1), resulting in minimal or no accumulated genetic progress in WW. The EBVs were lower relative the ones derived by Zishiri *et al.* (2010) in Dorper and Ile de France sheep. The EBVs of WW declined approximately from 250 grams to about 150 grams between 1998 and 2001. In the following seven years up to 2008 the EBVs rose to a maximum of 300 grams. The relatively low breeding values for WW are alarming because it had been established that weaning weight is moderately heritable (0.21 ± 0.01). An annual increment in WW of 0.003% (9.27 grams per year) is thus exceptionally low. This is particularly true if it is considered that the genetic trend for WW in the flock studied in Chapter 6 increased from ~ 0 kg to >3 kg over the period from 1993 to 2003 (see Figure 6.4.1).

Table 9.4 Regression coefficients (b), standard errors (SE), regression correlations (r), intercepts, goodness of fit (R²), Least Square Means (LSM) and annual genetic change % for production, reproduction and fitness traits in the Dorper breed

Trait	b±SE	Intercept	r	R ²	LSM	Annual change (%)
WW	0.001±0.0004	0.204	0.12	0.013	30.9	0.003
TWW/L	-0.026±0.004	0.159	-0.90	0.82	31.9	-0.08
NLB/EL	0.0004±0.0001	0.001	0.34	0.11	2.14	0.02
NLW/EL	-0.003±0.001	0.022	-0.88	0.78	1.83	-0.16
Survival	-0.0007±0.0001	0.003	-0.96	0.82	0.93	-0.08
LS	0.0004±0.0001	-0.002	0.86	0.80	1.2	0.03
LC/EL	-0.005±0.0002	0.174	-0.37	0.14	2.45	-0.20
TL/EL	-0.0003±0.0001	-0.001	-0.10	0.009	1.73	-0.02
EPL	-0.0006±0.0001	-0.006	-0.87	0.76	2.2	-0.03

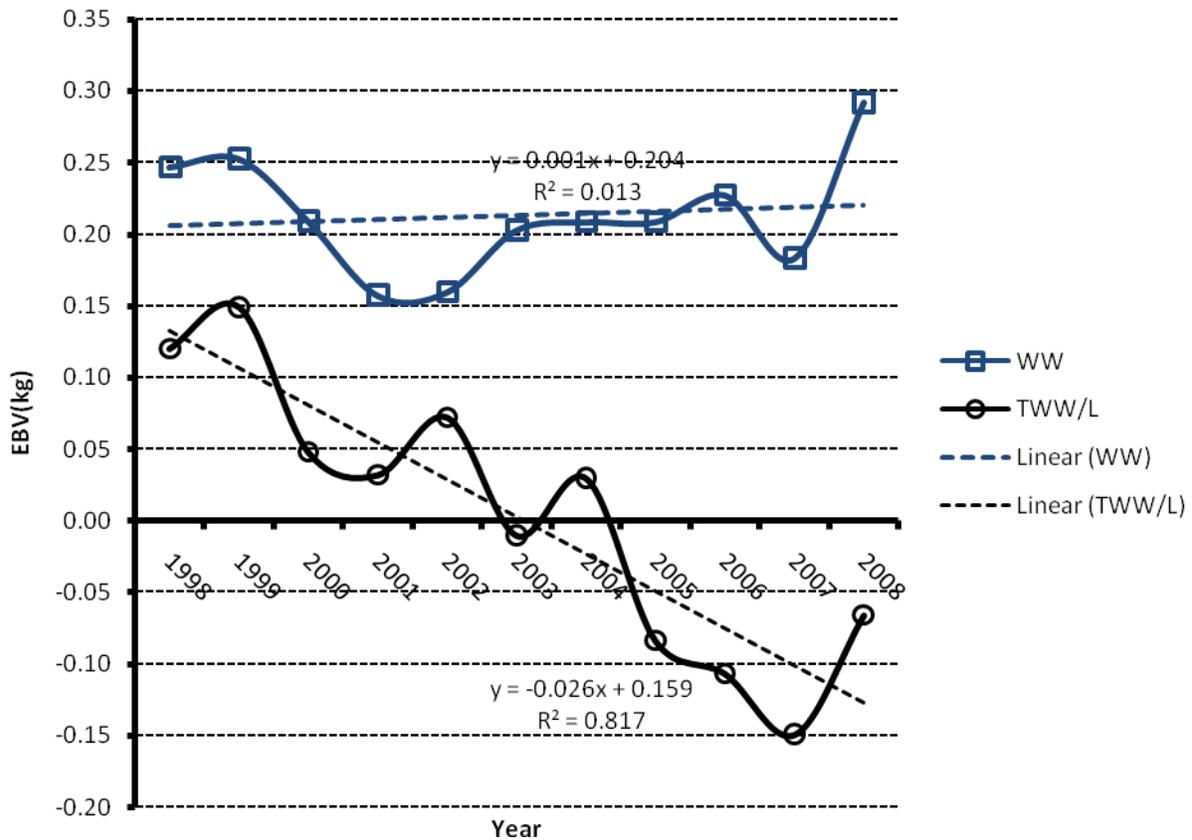


Figure 9.4.1 Direct genetic trends for Weaning Weight and TWW/L in the Dorper breed

The current finding as pertaining to WW is consistent with the very low response to selection of 0.009 ± 0.006 kg per annum that was reported by Olivier & Cloete (2006). The lack of substantial response to selection ($r=0.12$) of Dorper sheep is difficult to explain because positive and favourable genetic correlations between WW and subjectively assessed traits were obtained. However, the response to selection on subjectively assessed traits would be slow due to the modest heritability estimates that were derived. The only possible reason for the lack of genetic progress is that there was no directed selection for objectively measured traits. If breeders had used BLUP breeding values based on actual performance records WW would have been expected to respond positively to such selection. This statement is articulated on the basis of the fact that it was demonstrated that over time it is possible to attain a selection response that exceeds 1% per annum in meat sheep if thorough selection based on breeding values is adhered to (Zishiri *et al.*, 2010). Higher breeding values than the current ones for WW have also been derived in a selected Dorper population (Neser *et al.*, 1995). It is also important to consider that the lack of selection response to WW also has negative implications on reproduction, because it has been reported in the current and other studies that the relationship between WW and reproduction is favourable (Safari *et al.*, 2005b). Weaning weight is a component of net reproduction rate when it is assessed as Total Weaning Weight per Ewe Lambing (TWW/L).

The present across-flock genetic evaluation has shown that TWW/L in the Dorper breed has actually declined with time (Figure 9.4.1 and Table 9.4). The annual decline of -0.07% ($r=-0.90$) in TWW/L EBVs can possibly be ascribed to an over-emphasis of type scores at the expense of using actual performance records. It was reported by Olivier & Cloete (2006) that there is a high and negative correlation amounting to -0.51 ± 0.28 between TWW and Conformation. Furthermore, a generally negative genetic correlation (-0.21 ± 0.28) between Type and TWW was also derived by Olivier & Cloete (2006). It should be noted that genetic progress depends on selection pressure, heritability of the trait, the amount of phenotypic variation the trait exhibits as well as genetic correlations with other traits of interest. No selection pressure was applied to improve net reproduction rate in the Dorper breed, therefore, no genetic progress was realized. It would therefore be prudent and also in the best interests of sheep breeders to concentrate upon selection based on BLUP of breeding values for objectively measured reproduction traits.

Since reproduction is a complex trait, genetic trends for component traits of reproduction were also constructed in order to assess if there was any link between them (Figure 9.4.2). A concise assessment of the trends lead to the inference that there was negligible change in NLB/EL during the 11 years of evaluation which resulted in a slight increment of 0.02% per annum ($r=0.34$). Given that the mean NLB/EL was a very low at 2.14 lambs per ewe lifetime, it leads to the conclusion that there was no genetic progress in reproduction in the Dorper breed. This anomaly could also have been a result of lack of submission of the appropriate data. Based on these results, it seems that Dorper sheep have not yet achieved the levels of fitness that would be required for effective production. There is no published

literature on genetic trends for NLB/EL in the Dorper breed to compare our estimates. The lack of genetic progress in this composite trait of reproduction that is also indicative of longevity implies that there was a lack of genetic improvement in the breed with regards to longevity as well.

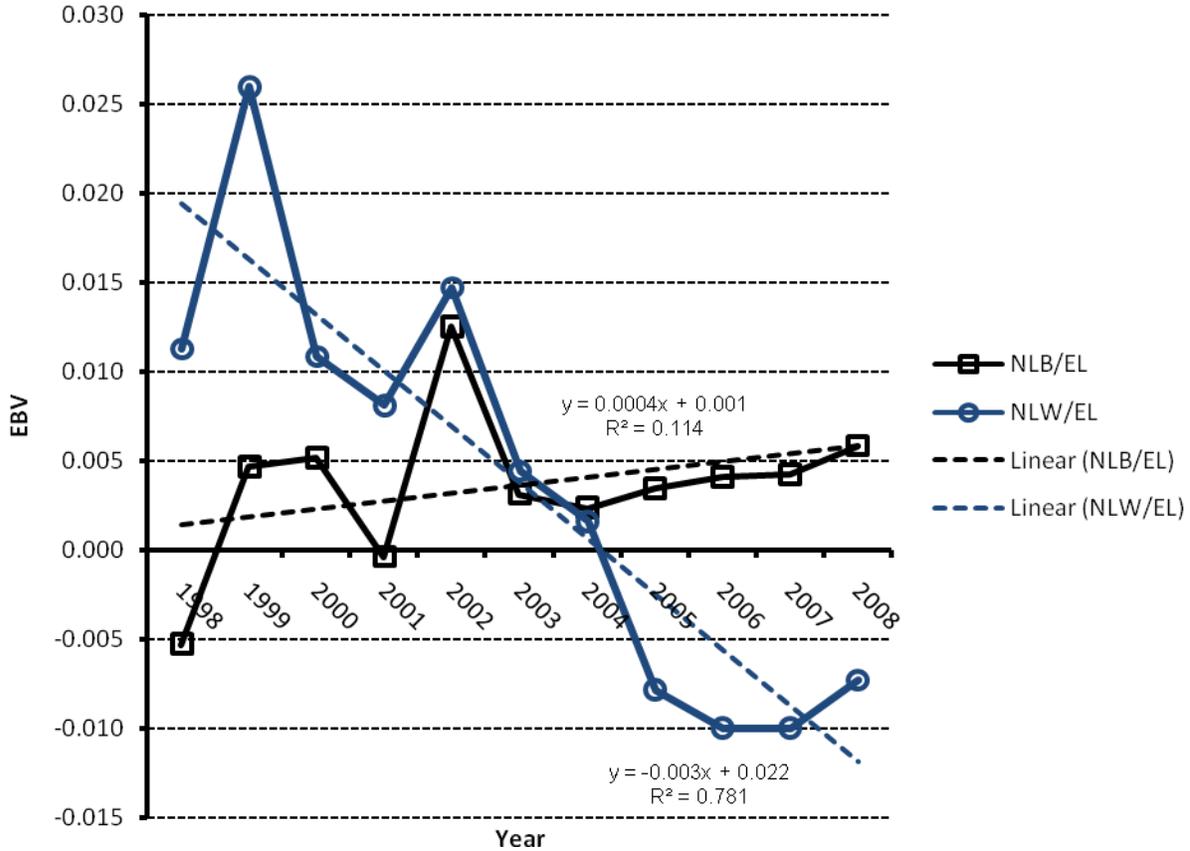


Figure 9.4.2 Direct genetic trends for NLB/EL and NLW/EL in the Dorper breed

It is universally acceptable that ideally prudent sheep producers would desire ewes that bear as many progeny as possible during their lifetimes. According to the data that was analysed, it was clear that this attribute lags behind in the Dorper breed. This lack of genetic improvement in the desired direction in the breed could possibly be attributed to an over-emphasis of breed standards, as both Conformation and Type have both been demonstrated to have antagonistic relationships with reproduction (Olivier & Cloete, 2006). Our study furthermore indicated that NLW/EL decreased at an annual rate of -0.16% ($r=-0.88$) in the Dorper breed. This negative trend confirms that the ability of Dorper ewes to rear their lambs to weaning deteriorated in the recent past. In their review of production parameters for Dorpers from the literature, Cloete *et al.* (2000) reported generally acceptable levels of reproduction in the breed. In view of the lack of genetic progress for NLW/EL in Dorpers, it was appropriate to monitor the number of

Lambing Chances afforded per Ewe Lifetime (LC/EL) and the actual number of times ewes lambed in their lifetimes (TL/EL). These traits can be indicative of vitality and longevity, and appropriate genetic trends are presented in Figure 9.4.3

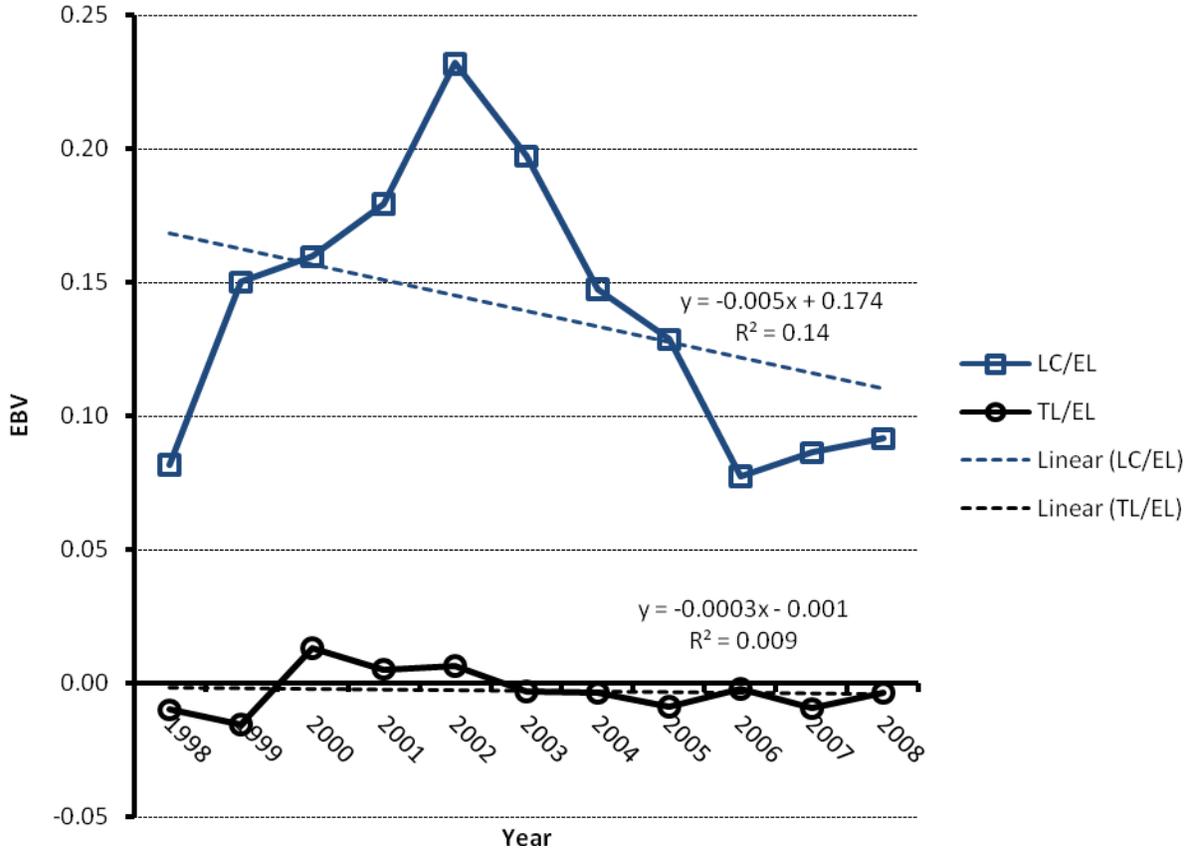


Figure 9.4.3 Direct genetic trends for LC/EL and TL/EL in the Dorper breed

There was a modest decline in the number of lambing chances afforded to a ewe per lifetime at an annual rate of -0.20% ($r=-0.37$). A decline in the LC/EL could also have been partly responsible for lack of selection response with regard to reproduction rate and longevity in Dorper ewes because positive genetic and environmental correlations between LC/EL and other reproduction and fitness traits were evident (see Table 7.4.3). It is also feasible to ascribe the decline in the lambing chances to early embryonic mortality rates or poor conception rates. A critical examination of the low mean associated with the trait (2.45) does not depict a decent image on reproduction and longevity in the breed. In an accelerated lambing system, the objective will be to achieve three lambings in 2 years. The Dorper breed is still to achieve that target probably when selection pressure is applied in future basing on BLUP of

breeding values for objectively measured traits. It was therefore worth assessing the genetic trend for the actual number of times lambled per ewe lifetime.

Assessment of the EBVs of TL/EL confirms earlier findings that there was decline in selection response to reproduction in the Dorper. TL/EL declined ($r=-0.10$) at a minute annual rate of -0.02% . It is now apparent that claims by some breeders that Dorper sheep are robust are anecdotal and are yet to be proven when sufficient data becomes available after selection pressure has been applied to fitness traits to assess fitness. If the breeders had selected their ewes basing on actual performance records the genetic trends for reproduction could have shown at least some favourable response to selection because it has also been demonstrated by several workers that selection for weaning weight results in a concomitant increment in net reproductive rate and ewe productivity (Snyman *et al.*, 1997; Olivier *et al.*, 2001; Duguma *et al.*, 2002b). It was essential to construct genetic trends for lamb survival to weaning since it is a component trait of net reproduction rate (Figure 9.4.4).

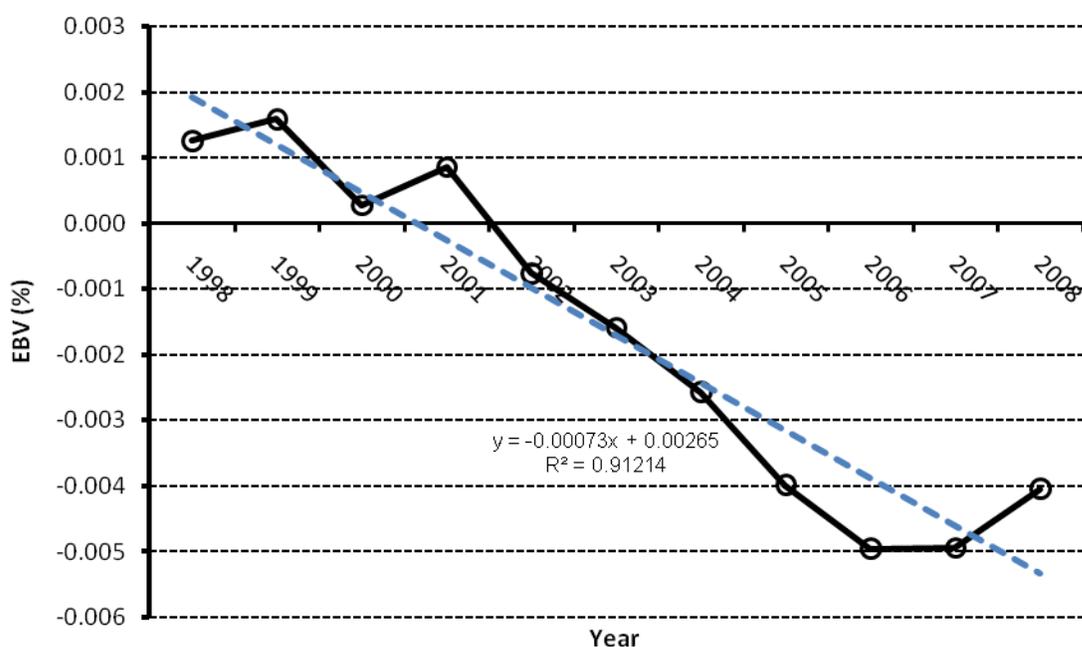


Figure 9.4.4 Direct genetic trends for Lamb survival to weaning in the Dorper breed

Lamb survival to weaning declined at an annual rate of -0.08% ($r=-0.96$). The decline in the genetic capacity of lamb survival to weaning contributed to the decline in TWW/L and NLW/EL presented earlier. It has, however, been established by Cloete *et al.* (2009) that it is feasible to achieve genetic improvement in lamb survival under certain conditions. Haughey (1983) established significant differences in lamb survival of the progeny of lambled ewes that were selected from a larger population to have a good or a poor rearing record. Donnelly (1982) and Knight *et al.* (1988) accordingly reported

differences in lamb survival between populations where selection was directed at lamb survival or ewe rearing ability.

There is a paucity of genetic trends for lamb survival in literature. Cloete *et al.* (2009) computed an increment of 1.3% per annum in direct breeding values for lamb survival from docking to weaning in Merino sheep selected for their ability to rear multiples. Their findings debunked earlier contentions in the literature that such progress in sheep flocks is unlikely. In summary, it can be postulated that if well informed selection decisions in the Dorper breed had been based on the BLUP of breeding values of an objective assessed trait like TWW/L or NLW/EL, progress in lamb survival to weaning could have been favourable due to the positive genetic correlations that were computed between component traits of reproduction. Our study also computed a negligible increment (0.03 % per annum) in the genetic propensity of Dorper ewes to improve litter size depicted by the genetic trend for litter size in Figure 9.4.5.

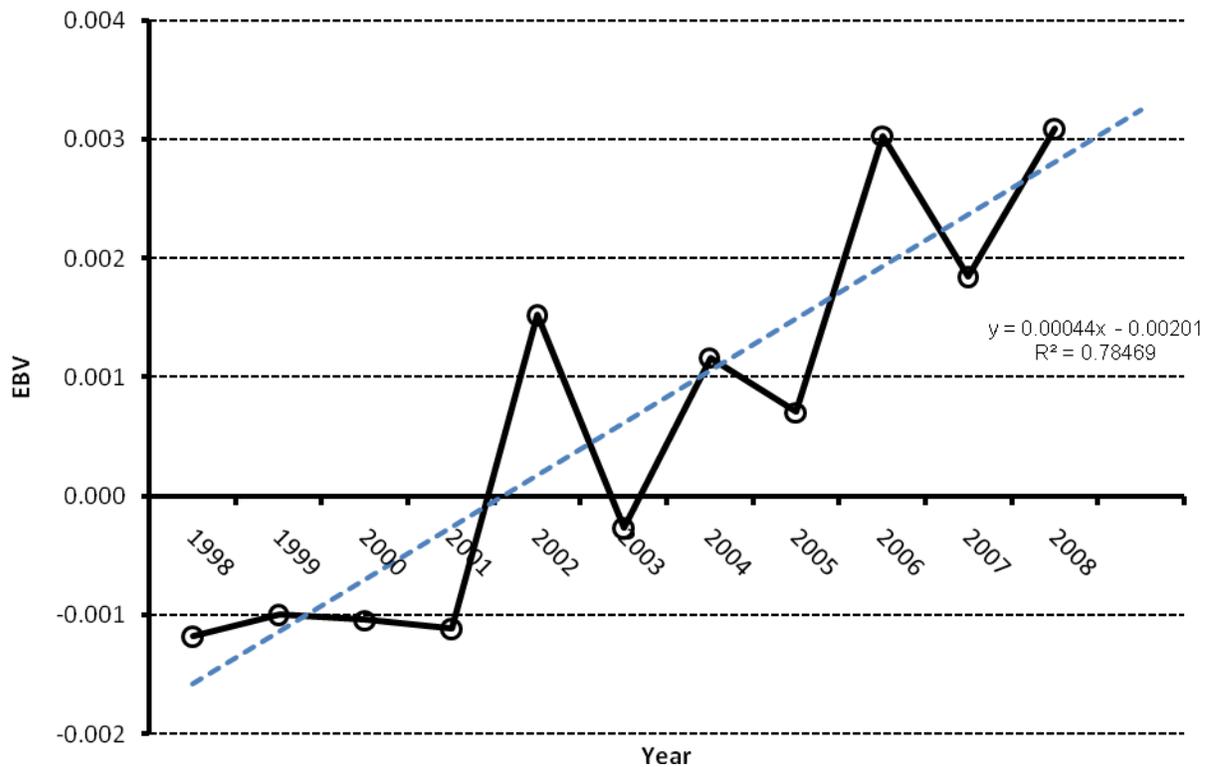


Figure 9.4.5 Direct genetic trends for Litter Size in the Dorper breed

The very low genetic improvement in litter size in can be explained by the fact that litter size was demonstrated to be characterized by a very low additive genetic variation as well as a low heritability amounting to 0.0013 and 0.07±0.01 respectively. It was also reported by Snyman *et al.* (1997) that litter size at birth is directly related to ovulation rate, though selection for this trait would not be sufficient to

increase lamb production since it does not include lamb survival and lamb weaning weight. Hanford *et al.* (2006) computed positive genetic trends in litter size at birth in the magnitude of 0.3 lambs between 1977 and 1998 in Polypay sheep. It was also interesting to note that Cloete *et al.* (1998a) computed a positive annual genetic trend of 1.3% in a Merino flock selected for multiple rearing ability. Their findings render some form of consolation because if well informed selection procedures are implemented in the Dorper breed based on breeding values derived from performance records then it will be feasible to attain genetic progress in litter size although significant magnitudes would obviously take some time to attain due to low genetic variation. Finally, our study computed the genetic trends of Ewe Productive Life (EPL) which is indicative of longevity (Figure 9.4.6).

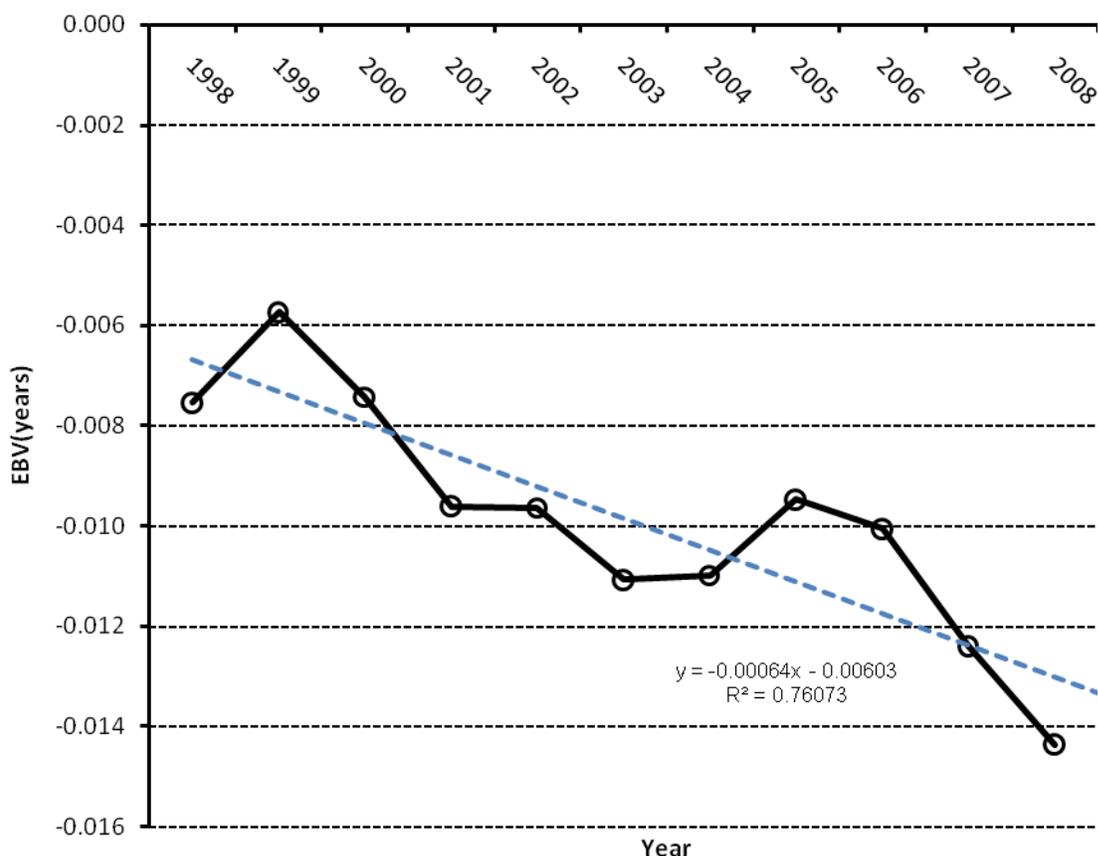


Figure 9.4.6 Direct genetic trends for Ewe Productive Life in the Dorper breed

Figure 9.4.6 indicates a very low or negligible decline in the propensity of Dorper ewes to remain in the flock for an extended period, amounting to -0.03% per annum ($r=0.87$). This finding is quite novel because to our knowledge there are no published estimates of genetic trends for any trait that is related to longevity in South African sheep literature. The negative genetic trend can also be explained by the fact that Dorper ewes were not directly selected for the trait. Furthermore, there could have been a

possibility of the trait having responded to selection as a correlated trait because early analyses led to the inference that EPL was positively correlated with reproduction and fitness traits using both linear methods and Bayesian inference (Table 7.4.3 and Table 8.4.2). However, correlations between EPL and live weights were inconclusive because they varied from negative to positive (Table 7.4.3). The low additive genetic variance ratio associated with the EPL could be offset by high levels of phenotypic variation (a CV of 68%). However, the present study seems to demonstrate a lack of directed selection pressure as well.

9.5 Conclusions

Improved reproduction efficiency is a prerequisite for economic success because meat production contributes markedly to income in all sheep enterprises. Results from this suggested that no significant genetic gains were realized in the Dorper breed for important traits like TWW/L, NLW/EL and lamb survival. To the contrary, all these traits appeared to deteriorate with time. Based upon the heritability estimates and the phenotypic variation of the traits in question, genetic gains should have been possible for all the traits considered if selection pressure had been applied. Generally the lack of genetic progress in reproduction and fitness traits prevalent in this study could be reversed if breeders select their animals on the basis of BLUP of breeding values of the traits because it has been demonstrated by other workers that favourable responses can be achieved in most traits (Cloete *et al.*, 1998a; Cloete *et al.*, 2009). It was therefore speculated that the performance of Dorper sheep in the show ring in an effort to satisfy breed standards does not guarantee improved reproduction and fitness capacity in the flocks. Anecdotal claims by breed societies on the good performance of Dorper sheep in the semi-arid and harsh environmental conditions of South Africa seem to be over-optimistic and are yet to be proven when sufficient data becomes available after applying selection pressure basing on breeding values of objectively measured traits.

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CHAPTER 10

GENERAL DISCUSSION, CONCLUSIONS AND RECOMMENDATIONS

The purpose of this chapter is to summarise the general conclusions of individual chapters from the studies that were undertaken and to make some recommendations based on the outcomes of the studies. In a nutshell, the objectives of this study were to estimate genetic parameters and relationships between objectively measured and subjectively assessed traits as well as to assess genetic progress in the Dorper sheep breed. The first aspect that was addressed by the current study was to assess and describe the quality of the Dorper data that were submitted to the National Small Stock Improvement Scheme (NSIS). Secondly, the genetic parameters that were estimated for subjectively assessed and objectively measured traits using a single flock as well as across flock data sets are summarized and their implications are discussed. The implications of the genetic trends that were constructed in the various studies are discussed and some recommendations are made. Finally some suggestions for future research are given.

Description of the of the Dorper Sheep Breeders' Society data

This study has demonstrated that it is essential to organize and edit animal breeding data in a cognitive manner so that anomalies will be identified and rectified before robust statistical machinery and analytical tools are used for analyses. It was apparent from the description of the data that was given prior to the analyses that the Dorper sheep breeders' society was slow in implementing performance testing for objective traits of economic importance. Submission of Dorper performance data to the National Small Stock Improvement Scheme (NSIS) only improved as from 1994 despite the fact that performance recording for the wool sheep breeds had commenced in the 1950s. The quality of the data was demonstrated to have an impact on the inferences that were drawn. Random entrance and exit of flocks from the performance recording schemes culminates in the loss of genetic links that further complicate the partitioning of variation during the estimation of variance components and ratios and also reducing the accuracy of genetic trends that were constructed to monitor genetic change.

It was demonstrated in the studies that it is necessary to explore the data and implement summary statistics to observe the distributions in the data prior to any analyses being implemented. Such distribution analyses will assist analysts in making decisions on the type of statistical tests to implement on the data. Live weight traits were recorded at various age ranges. As a result of that prior to the analyses, the data was rigorously edited. The importance of assigning animals to contemporary groups was emphasised in the studies. Statistical inference demonstrated that the nature of the distribution of

binary data has got an influence on the 95 % confidence intervals that were derived for the Highest Posterior Densities (HPD) for variance components.

The present study noted that some claims by breeders that Dorper sheep have an outstanding reproduction rate, excellent survival rate as well as very high longevity should be thoroughly verified because it was demonstrated that approximately 43 % of the ewes in the study data that was submitted gave birth to only one lamb in their entire lifetimes, while 24 % of ewes produced only 2 lambs. Furthermore, 7 % of the ewes in the study data did not wean a lamb in their entire lifetimes and 45 % weaned only 1 lamb in their lifetimes. The study indicated that 1.6 % of the 64 835 ewe records indicated that no lambing chance was afforded to the ewes. More than one third (36 %) of the ewes were afforded only one lambing opportunity in their entire lifetimes. A positive genetic correlation was computed between number of lambing chances and stayability up to 4 years. It was evident from the data that approximately 40 % of the ewes stayed in the flocks until 2 years whereas 22 and 12 % stayed up to 3 and 4 years respectively. The absence of 60 % of the ewes from the flocks at only 2 years could have resulted from inconsistent submission of data to the NSIS or that other considerations, like conformation and likability also contributed to decisions to use ewes for breeding.

The study was successful in defining traits indicative of reproduction and fitness. Longevity in the Dorper sheep breed was assessed through a number of traits such as Number of Lambs Born Alive per Ewe Lifetime (NLB/EL) and Number of Lambs Weaned per Ewe Lifetime (NLW/EL). Furthermore traits indicative of longevity were extrapolated and described from the data that were submitted. Stayability was derived for ewes that remained in the flock for up to two, three and four years of age given that they had been granted the opportunity to stay in the flocks up to that stage. Ewe Productive Life (EPL) was extracted from the age at last lambing for animals that were afforded sufficient opportunities to lamb and remain in the flocks. Net reproduction rate was extracted from the data by deriving the Total Weight of Lamb Weaned per Ewe Lambing (TWW/L) across parities. Fitness was also assessed by deriving lamb survival to weaning on a per ewe basis. The trait was similar to ewe lamb rearing ability. It can be concluded that the traits that were derived can be used describing reproduction and fitness in the Dorper sheep breed. A trait indicative of fertility and precociousness was derived from the submitted data and was defined as a binary trait assessing whether a ewe lambed at two years of age or not.

Finally, the study extracted data from a breeder who was scoring sheep for breed standards (subjective traits) and concurrently taking objective measurements in order to estimate relationships between subjectively assessed and objectively measured traits since it was part of the theme of these studies. The subjective traits were subjected to distribution analyses as well as correlation analyses. It was observed that all the five subjective scores observed a normal distribution hence the use of linear methods to estimate genetic parameters for such traits were justified. It was established through the implementation

of Pearson's correlations that the subjectively assessed traits were positively correlated to each other. The study concluded that Dorper sheep breeders desist from over-emphasizing on breed standards but should exert more effort on accumulating animal performance data with the overall objective of selecting their animals on the basis of BLUP of breeding values. After editing and organizing the data, the study was successful in estimating genetic parameters for subjectively assessed and objectively measured traits in a well recorded Dorper flock.

Estimation of genetic parameters and relationships between objectively measured and subjectively assessed traits in a Dorper flock

The implementation of Residual Maximum Likelihood (REML) procedures derived accurate genetic parameters for live weight and growth traits in the Dorper sheep breed using both single-trait and multi-trait analyses. The estimates that were derived using Bayesian methods for the same traits were quite similar. It is noteworthy to state that Bayesian methods derived higher estimates of variance components for categorical (threshold) traits. The current study demonstrated that live weight and growth traits are heritable and can be genetically improved through selection. The genetic parameters that were derived for live weight and growth traits were consistent with literature cited. It was also demonstrated that genetic parameters that are obtained in genetic evaluation exercises are dependent on the models that are implemented. The current study was successful in partitioning variation into direct additive genetic effects, additive maternal effects and dam permanent environmental effects using both linear and Bayesian methods. The structure of the live weight and growth data probably resulted in biased estimates of the correlation between direct additive and maternal effects. It was attempted to fit additional random effects with terms such as the sire X year interaction to possibly counteract such effects, but such models were discarded as they did not lead to a better fit. The study established that live weight and growth traits are positively genetically correlated with each other. That finding was in agreement with literature cited. The Dorper sheep breed was thus demonstrated to exhibit significant genetic variation for live weight and growth traits. It was concluded that Dorper sheep breeders should continue recording live weight and growth traits, to select their breeding stock basing on their BLUP breeding values. It can be recommended that when more data on repeated measurements over time becomes available on live weights and growth traits random regression models can be implemented to derive better variance components and ratios as well as breeding values.

It is generally accepted that breed improvement in the Dorper sheep breed is currently based on subjectively assessed traits as determined by show standards. It has been reported by Olivier (1993) that breed standards and characteristics were the major focal points of most of the sheep breeders in South Africa during the previous decades. The main aim was thus to breed national champions and/or rams that would fetch record prices at auctions. Buyers from communal production systems compared their animals

against these big and well-managed animals and were willing to purchase these animals. Some breeders are concerned that the breeds may lose some of their desirable attributes (hardiness, adaptability and reproductive ability under adverse conditions) due to the emphasis placed on breed standards and shows. Our study therefore addressed these concerns by unraveling the relationships between subjectively assessed and objectively measured traits in the Dorper sheep breed. It was established through the implementation of linear and Bayesian methods that subjective traits are characterized by relatively low additive genetic variance ratios. Furthermore, it was established that the implementation of Bayesian methods emanated in higher point heritability estimates than linear methods for traits without normal distributions. It is critical to perceive that subjective traits can be biased at times although breeders insist that only well trained and experienced judges are allowed to carry out the routine exercise. This conflict of scoring obviously has an impact on the quality and reliability of the data that is generated. It needs to be stated that such inconsistencies will be substantially reduced when sires are, for example, evaluated over a number of progeny.

Currently, the main selection criteria for Dorper sheep are Conformation and Type (Olivier & Cloete, 2006). Our study demonstrated that selecting Dorper rams and ewes on the basis of BLUP breeding values of objectively measured traits will yield better and more desirable genetic progress than selection based on subjectively assessed traits. Genetic parameters that were computed for subjective traits using both the Frequentists' and Bayesian approaches established that low additive genetic variance is associated with these traits. Our study derived moderate to high genetic and environmental correlations between Conformation and Type with live weight and average daily weight gains. However, negative genetic correlations with reproduction have been derived by Olivier & Cloete (2006) for Conformation and Type, which is considered as important conformation traits.

The genetic correlations between Fat distribution and the objectively measured live weight and average daily weight gain traits were positive and varied from moderate to high. The positive correlations led to the inference that selecting Dorper sheep on the basis of the Fat distribution scores does not have a negative impact on growth. Alternatively one would also infer that selecting animals that have good live weights and fast growth will result in animals that have a reasonable fat distribution according to the scoring system utilised. It was highlighted that Fat distribution scores should be treated with caution as too fat animals could be undesirable, although they may have desirable growth patterns. Fat distribution was moderately to highly genetically correlated with Conformation and Type.

The relationships between Colour and some live weight traits such as Yearling weight were unfavourable. It is essential for Dorper breeders to accept that too much emphasis on breed standards such as Colour will not yield better genetic progress than putting selection pressure on objectively measured live weight and growth traits. A ram or ewe might be appealing visually yet in production terms its performance may

be sub-standard. It was therefore recommended that Dorper stud breeders aim to maintain the existing standards for Colour during selection, since the desired phenotype of a black head and a white body has been established in the breed. More focus should be placed on objective measurements of production and reproduction traits with the ultimate goal of deriving BLUP breeding values and selecting animals on that basis.

Genetic parameters and relationships between reproduction and fitness traits in the Dorper sheep breed

Fitness traits are critical in all livestock species. Fitness characteristics are difficult to measure in practice because they encompass all phenotypic expressions that influence an individual's ability to contribute offspring to the next generation. It was reported by Falconer and MacKay (1996) that the component traits that may influence the overall fitness of an individual with the primary characteristics included survival, reproduction, and the maternal ability of the breeding female. Any differences in fitness that are associated with genetic variation in the component traits of fitness are therefore influenced by selection. In commercial Dorper production systems, the importance of fitness relates to the attrition of both lambs and breeding ewes. Therefore, components of fitness that were assessed in the Dorper breed included reproductive traits such as fertility, lamb survival to weaning as a trait of the ewe (rearing ability), litter size, and Number of Lambs Born and Weaned per Ewe Lifetime (NLB/EL and NLW/EL respectively), Total Weaning Weight per Ewe Lambing (TWW/L) and indicator traits of longevity such as Ewe Productive Life (EPL) and stayability. Differences in breeding ewe fitness are expressed by early removal from the flock for reasons such as illness, injury, or death, or for producer imposed reasons that include reproductive failure, poor milking ability, or unthrifty body weight characteristics that may lead to culling prior to the next lamb crop (Borg *et al.*, 2009). Personal preference may also play a role.

Heritability estimates that were derived for NLB/EL and NLW/EL were low and in agreement with literature. It was also demonstrated that the former traits are positively genetically correlated with components traits of reproduction and fitness such as litter size lamb survival to weaning, stayability at two and four years of age and EPL. Weaning and post weaning weights were also positively genetically correlated with NLB/EL and NLW/EL. It is therefore possible to improve the reproduction and fitness of Dorper sheep by either exerting sufficient selection pressure on these traits or their components. The current studies also established through the implementation of REML and Gibbs sampling that TWW/L or litter weight weaned is a composite trait that can be used as a biological index for selection to improve overall reproductive rate in Dorper sheep breed. Although the heritability of litter weight weaned was established to be low, its large phenotypic variance when coupled with intense selection can result in favourable selection responses in the Dorper breed. Long-term selection for TWW/L should result in a balanced biological system within the environment and production system selected upon. TWW/L is

recommended as a major trait to select for an increased overall reproductive rate. Increasing reproduction rate is an important component of the improvement of specialised lines for dual-purpose and meat enterprises in the longer term. Dorper ram breeders may therefore have to increase the emphasis on reproduction in their breeding objectives. The potential to improve reproduction rate has been limited in the past by low levels of recording in the Dorper breed.

The studies that were conducted were successful in estimating genetic parameters for reproduction and fitness traits using both linear and Bayesian methods. It was demonstrated using both methods that reproduction and fitness traits are characterized by low additive genetic variance ratios, although levels of phenotypic variation was relatively high with CV's of 31% to 74%. Traits indicative of reproduction, longevity and fitness were defined in the present studies. The genetic basis of the number of lambing chances afforded to a ewe per lifetime (LC/EL) was estimated. Although there were no comparable literature estimates, it was reported with certainty that it is feasible to breed Dorper sheep with the aim of improving LC/EL because a moderate h^2 estimate of 0.23 was computed. It was highlighted that the number of lambing chances per lifetime afforded is an indication of vitality in ewes, although it may also indicate the preferences of specific breeders. That implies that selection of ewes on the basis of the genetic merit of lambing chances per ewe lifetime will most likely result in ewes of reasonable longevity. The number of times ewes lambed per ewe lifetime was also estimated to be lowly heritable at 0.11. That implied that it is quite feasible to improve the longevity of ewes through selection on the basis of number of times lambed per ewe lifetime, particularly since a high CV of 67% was computed. The fitness of Dorper sheep warranted to be investigated because there have been several reports that Dorpers are well adapted to harsh environments and that they have a good survival rate. Our study revealed that lamb survival to weaning, expressed as a trait of the ewe, has a low additive genetic variance amounting to 0.0013 and a direct h^2 estimate of 0.07 ± 0.01 , which was consistent with the literature. Lamb survival to weaning was negatively correlated with litter size. It was therefore concluded from the study that genetic improvement with the sole intention to increase litter size might hamper the ability of ewes to rear the extra lambs to weaning.

Assessment of genetic progress in Dorper sheep

The study was successful in demonstrating that significant genetic progress can be achieved if selection pressure is applied to live weight and growth traits. Despite the fact that genetic progress with regard to live weight traits in the Dorper breed was positive and in the desired direction, however, it was slower compared to what can be achieved in meat sheep breeds when sufficient selection pressure is applied (Zishiri *et al.*, 2010). It can be recommended that breeders should endeavour to record live weight traits, particularly weaning weight at approximately 100 days of age because correlated improvements in reproduction and fitness traits will be achieved. The studies demonstrated that there was very little or

negligible genetic progress in some subjective traits such as Conformation and Type amounting to 0.12 % per annum and 0.09 % per annum respectively. The two subjective traits that were also demonstrated to be positively genetically correlated with live weight traits did exhibit some genetic progress. Other subjective traits such as Colour and Fat distribution did not significantly change over the evaluation period. It is therefore feasible to achieve genetic progress in Conformation and Type through selection, although the gains will be slow. More focus should therefore be exerted on live weight and growth traits that can potentially benefit from thorough selection pressure to attain reasonable genetic progress.

One of the consequences of long term selection on production traits in other species has been a decline in fitness traits such as reproduction, offspring survival, longevity, and disease resistance (Van der Waaij, 2004). The South African sheep industry relies heavily on maintaining breeding ewes in the flock for a number of years and so. As rates of genetic gain begin to accelerate, it is relevant to question what effect the selection indexes may have on fitness. One example which has received recent attention is an unfavourable genetic relationship between fleece weight and reproduction (Safari *et al.*, 2007b). Furthermore, Van der Waaij (2004) used a resource allocation model to demonstrate how fitness traits may decline when finite resources are diverted to production traits. To overcome this limitation it becomes critical to include the important fitness traits as selection criteria in the breeding objectives for South African Dorper sheep.

It was also demonstrated through the computation of genetic trends that the propensity of lambs to survive up to weaning declined by -0.08% per annum between 1998 and 2008. This decrease was anticipated because declines in the net reproduction rate (TWW/L) as well as the component trait of reproduction (NLW/EL) were evident during the same period. Construction of genetic trends for Ewe Productive Life established that the annual mean breeding values for the trait deteriorated between 1998 and 2008. Based on the studies pertaining to traits indicative of longevity, it was recommended that sheep breeding enterprises should endeavour to incorporate some measure of ewe longevity in their selection indices because it can significantly affect their profitability.

There is a general perception in the sheep industry that because heritabilities of reproductive traits are low and selection is likely to be difficult, only slow response can be achieved. However, response to selection is dependent on a function of heritability, phenotypic variation, and selection intensity. Whereas the heritabilities of reproductive traits are generally lower than other production traits such as growth, carcass and wool production, and quality, there is much greater phenotypic variation to compensate (Safari *et al.*, 2005b). A major limitation in direct selection for reproduction is that males need to be mainly selected on the performance of their female relatives and females do not express lamb rearing traits until at least 1.5 or 2.5 yr of age. However, repeated records of lambing performance with the level of

repeatability will approximately double the accuracy of selection or heritability with the use of 3 lambing records, although phenotypic variation may be reduced slightly (Fogarty *et al.*, 1994).

Suggestions for future research

In as much as this study has endeavoured to estimate genetic parameters and trends for objectively measured and subjectively assessed traits in the Dorper sheep breed, there is still much work to be conducted in future research. Since the Dorper is a meat breed, meat and carcass traits play a very essential role in selection decisions. There is a need to record carcass traits such as fat depth, eye muscle area, meat to bone ratio, cooking loss, meat tenderness and many others. When such traits are recorded it will be important to estimate genetic parameters and relationships between them with reproduction and fitness traits. Carcass traits can be measured by non invasive methods such as video image analysis, ultra sound scanning and X-ray computer tomography. Genetic parameters for disease resistance in the Dorper breed need to be estimated and their relationships with live weight, reproduction, fitness and carcass traits need to be derived. Data needs to be collected on traits such as faecal egg worm counts to estimate resistance to internal parasites. Finally genetic parameters for individual fatty acids as well as other blood metabolites need to be elucidated in the Dorper sheep breed, as this may play an important role in consumer preferences.

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