Genetics of ovine resistance to gastrointestinal nematodes

by

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DECLARATION

By submitting this dissertation electronically, I declare that the entirety of the work contained therein is my own, original work, that I am the sole author thereof (save to the extent explicitly otherwise stated), that reproduction and publication thereof by Stellenbosch University will not infringe any third-party rights and that I have not previously in its entirety or in part submitted it for obtaining any qualification

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ABSTRACT

This study consists of various papers on the genetic evaluation of sheep for resistance to gastrointestinal nematodes in South Africa using faecal worm egg count (FWEC) as a proxy. Outcomes from the study suggested that Merino lines divergently selected for reproduction at Elsenburg research farm did not differ for log transformed FWEC. Heritability estimates for FWEC at Tygerhoek research farm were low in autumn (0.07 ± 0.05), but moderate in winter (0.13 ± 0.05) and spring (0.19 ± 0.05), suggesting that the best time to sample FWEC for genetic improvement in parasite resistance in Mediterranean South Africa is after the break of season. Genetic and phenotypic parameters for FWEC, live-weight traits, wool traits, subjective traits and testis dimensions were estimated in the Elsenburg Merino flock. The direct heritability estimates of these traits ranged from 0.09 ± 0.04 for FWEC to 0.60 ± 0.03 for clean yield (CY). Genetic correlations of FWEC with the other traits of economic importance were not significant, ranging from -0.24 ± 0.18 with crimps per 25 mm to 0.30 ± 0.23 for weaning weight, suggesting that selection for parasite resistance is unlikely to hamper genetic progress in other trait complexes. Genetic variation of FWEC was estimated in mature reproducing Elsenburg Merino ewes and correlated with number of lambs born and weaned. The heritability of FWEC was low at 0.03 ± 0.03, implying genetic change in FWEC of mature ewes would be difficult. Heritability of number of lams born and weaned was respectively 0.19 ± 0.03 and 0.11 ± 0.03. FWEC and reproduction traits were favourably correlated. An across-flock genetic evaluation of FWEC in South African Merinos at both Elsenburg and Tygerhoek yielded a heritability estimate of 0.11 ± 0.02 for FWEC. The sire x site/season variance ratio was low at <2%, suggesting minimal reranking of sires across flocks. Further studies suggested an overall breed difference for FWEC between Dormer and SA Mutton Merino yearlings and breeding ewes although the results were not consistent across years. Genetic parameters for FWEC and the Famacha© traits were investigated in Merinos at Tygerhoek and Dormers and SA Merinos at Elsenburg. All traits were heritable, suggesting that genetic improvement would be feasible should it be desired. Genetic correlations suggested that selection for lower eye scores would result in a change in FWEC at Elsenburg. Genetic correlations also suggested that animals with anaemic eye scores of 4 would be more likely to have high FWECs at Elsenburg, where haematophageous helminths were more likely because of irrigated pastures. The study provided useful

information on genetic parameters for FWEC as indicator of host resistance to gastrointestinal nematodes and provided the background needed for planning further research on this important input trait.

OPSOMMING

Die studie bestaan uit artikels aangaande die genetiese evaluasie van skape vir weerstand teen inwendige rondewurmparasiete deur wurmeiertellings (WET) as aanduiding te gebruik. Resultate het daarop gedui dat Merinolyne op Elsenburg navorsingsplaas wat uiteenlopend vir reproduksie of geselekteer is nie vir WET verskil het nie. Die oorerflikheid van WET op die Tygerhoek navorsingsplaas was laag in die herfs (0.07 ± 0.05) en matig in die winter (0.13 ± 0.05) en lente (0.19 ± 0.05). Die resultaat dui daarop dat monsterneming vir die bepaling van WET verkieslik na die eerste winterreëns in Meditereense Suid-Afrika gedoen moet word. Genetiese en fenotipiese parameters vir WET, liggaamsgewig-eienskappe, woleienskappe, subjektiewe eienskappe en testiseienskappe is in die Elsenburgkudde beraam. Direkte oorerflikheidsberamings vir die eienskappe het tussen 0.09 ± 0.04 vir WET en 0.60 ± 0.03 vir skoonopbrengs gevarieer. Genetiese korrelasies van WET met die ander ekonomies belangrike eienskappe was nie betekenisvol nie en het tussen -0.24 ± 0.18 vir kartels per 25 mm en 0.30 ± 0.23 vir speengewig gevarieer, wat daarop dui dat seleksie vir parasietweerstand waarskynlik nie genetiese vordering in ander eienskapkomplekse sal benadeel nie. Genetiese variasie in WET in volwasse Elsenburg Merino-ooie sowel as genetiese korrelasies met getal lammers gebore en speen is vervolgens beraam. Die oorerflikhed van WET was laag op 0.03 ± 0.03, aanduidend dat dit moeilik sal wees om WET in volwasse ooie geneties te verander. Die oorerflikhede van getal lammers gebore en gespeen was onderskeidelik 0.19 ± 0.03 en 0.11 ± 0.03. WET en reproduksie-eienskappe was gunstig gekorreleer. 'n Oorkudde genetiese evaluasie vir WET met Merinos van beide Elsenburg en Tygerhoek het 'n oorerflikheidsberaming van 0.11 ± 0.02 vir WET opgelewer. Die vaar x lokaliteit/seisoen variansieproporsie was laag teen <2%, wat daarop dui dat vaars se rangorde redelik konstant oor lokaliteite behoort te wees. Verdere studies het op 'n algemene rasverskil vir WET tussen Dormer- en SA Vleismerino-jongskape sowel as volwasse ooie gedui, alhoewel die rasverskil nie konsekwent oor jare was nie. Genetiese parameters is vir WET en die Famacha©-eienskappe op Tygerhoek en Elsenburg beraam. Alle eienskappe was oorerflik, sodat genetiese vordering haalbaar behoort te wees indien dit verlang sou word. Genetiese korrelasies het daarop gedui dat diere met anemiese oogpunte van 4 op Elsenburg, met 'n groter waarskynlikheid van bloedsuiende parasiete as gevolg van besproeide weidings, waarskynlik ook hoër WETs sou hê. Die studie het nuttige inligting verskaf oor WET as 'n indikator-eienskap vir die weerstand van skape as

gashere teen inwendige parasiete sowel as agtergrond vir verdere navorsing op hierdie belangrike inset-eienskap verskaf.

DEDICATION

I'd be a reckless breeder if I didn't think of my future offspring when I was writing this dissertation. To the fruit of my womb, my cubs, my babies, here's to a better life filled with the abundance of God's blessings, cheers.

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RESEARCH OUTPUTS FROM THIS STUDY

Publications in peer reviewed scientific journals:

Cloete, S.W.P., Mpetile Z. & Dzama, K. 2016. Genetic parameters involving subjective FAMACHA© scores and faecal worm egg counts on two farms in the Mediterranean region of South Africa. Small. Rumin. Res. 145, 33 – 43.

Mpetile, Z., Dzama, K. & Cloete, S.W.P. 2017. Genetic variation in and relationships among faecal worm eggs recorded in different seasons of the year at the Tygerhoek farm in South Africa. J. S. Afr. Vet. Assoc. 88, a1484. https://doi.org/10.4102/jsava.v88i0.1484.

Mpetile, Z., Kruger, A.C.M., Dzama, K., & Cloete, S.W.P. 2015. Environmental and genetic factors affecting faecal worm egg counts in Merinos divergently selected for reproduction. S. Afr. J. Anim. Sci**.** 45, 510-519.

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Mpetile Z., Cloete, S.W.P. & Dzama, K. 2017. Genetic co-variation of faecal worm egg counts and reproduction in Merinos. 50th SASAS congress, Port Elizabeth, 18 -21st September.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

CHAPTER 1: INTRODUCTION

1.1 General introduction

Infestation with gastrointestinal nematodes is a major health problem in ruminants world-wide (Over *et al.*, 1992; Perry *et al.*, 2002; Wolf *et al.*, 2008). It results in economic and production losses. The major species found in sheep include the genera *Trichostrongylus spp, Teladorsargia (Osterstargia)*, *Haemonchus*, and *Nematodirus*. The prevalence of these parasite species result in substantial losses in sheep production through reduced growth rates (Kelly *et al.*, 2010), poor production performance (meat, milk and wool) (Johnstone *et al.*, 1979; Kelly *et al.*, 2010; van Houtert & Sykes, 2010), reduced reproductive efficiency (Chiezey *et al.*, 2008), reduced overall production efficiency stemming from high costs of anthelmintic drenches used for prevention and treatment (Pathak &Tiwari, 2013), and, in severe cases, death of infested animals (Barger & Cox, 1984).

Efforts to eradicate the nematode infestations and improve the economic and production gains using chemical control have been implemented (Dash, 1986; Kenyon *et al.*, 2009; Kelly *et al.*, 2010). However, resistance of gastrointestinal nematodes to the chemicals used for treatment has become very common (Waller, 1994, 1997 a, b; McLeod, 1995; Kenyon *et al.*, 2009; Molento *et al.*, 2011). Thus, it would be unwise to continue relying on drenching with chemicals as the only treatment strategy for controlling gastrointestinal nematode infestations. Additionally, the use of excessive drugs in meat production can result in chemical residues in meat products if proper withdrawal times are not observed which can negatively impact human health. Against this background, breeding for parasite resistance promises a sustainable alternative to control parasitism.

Infestation by gastrointestinal nematodes is reflected by faecal worm egg counts (**FWEC**). Prior research has reported moderate to high heritability estimates (ranging from ~0.15 to 0.50) for faecal worm egg count (Bissett *et al.*, 1992; Eady *et al.*, 1996; Bouix *et al.*, 1998; Baker *et al.*, 1999; Wolf *et al.*, 2008; Matebesi-Ranthimo *et al.*, 2014), with FWEC also being a highly variable trait with the number of worm eggs per gram of wet faeces ranging between 0 and 32,700 in Merinos of the same contemporary group (Matebesi-Ranthimo *et al.*, 2014). The heritability estimates reported vary between different breeds (Baker *et al.*, 1999, 2002;

1

Gruner *et al.*, 2003; Nimbkar *et al.*, 2003) and within breeds (Morris *et al.*, 2000; Woolaston & Windon, 2001) when considering different nematode species.

Studies in Australia (Woolaston & Piper, 1996; Karlsson & Greeff, 2006) and New Zealand (Morris *et al.*, 2005) have reported realized gains for selection for reduced FWEC and no comparable studies on selection for parasite resistance have been published for research conducted in South Africa. Although FWEC is also heritable in South African sheep (Cloete *et al.*, 2007; Matebesi-Ranthimo *et al.*, 2014), it has not been studied in more than a few flocks, while no across-flock analyses has been reported so far. The study of FWEC in the local small stock resource thus needs to be expanded to more flocks to ensure that results are robust across environments. Also, across-flock analyses need to be done, to determine whether FWEC is subject to genotype x environmental interactions, as is commonly found in other traits of economic importance (McGuirk, 2009).

1.2 General objectives

i) To determine the effect of divergent selection for number of lambs weaned on FWEC and estimate the heritability of FWEC

ii) To investigate the genetic variation and relationships among expressions of FWEC recorded in different seasons

iii) To estimate the heritabilies, as well as genetic and phenotypic correlations of FWEC with live-weight traits, wool traits, subjective traits and testis dimensions in South African Merinos

iv) To estimate genetic variation of FWEC in mature reproducing ewes in relation to number of lambs born and number of lambs weaned

v) To do a first local across-flock analysis for FWEC to estimate the genotype x environment interaction for FWEC

vi) To evaluate the breed difference in parasite load between Dormers and SA. Mutton Merino

vii) To investigate co-variance components for subjective FAMACHA© scores and FWEC under South African Mediterranean conditions

1.3 Thesis organization

This thesis is organized into 10 chapters. Chapter 1 (the current chapter) provides background information, establishing a context for the following chapters. Chapter 2 is the literature review describing the impact of gastrointestinal nematodes (GIN) in small stock production and the control measures of GIN. Chapter 3 addresses the environmental and genetic sources of variation in the FWEC data of the Elsenburg Merino flock that was divergently selected for the ability of ewes to rear multiple offspring. In this chapter, phenotypic and genetic trends in FWEC of the divergently selected lines were also inspected for possible divergence indicative of correlated responses to the divergent selection regime. Chapter 4 evaluates the genetic variation of FWEC in different seasons of the year. Also, the genetic and phenotypic correlations between FWEC in different seasons were derived. Chapter 5 is focused on evaluating the genetic variation of faecal worm egg counts and its relationship with live weight, wool, conformation and testis dimension traits in the Elsenburg Merino flock. In Chapter 6, the estimation of genetic parameters for FWEC and reproduction traits in mature ewes from the Elsenburg Merino flock will be discussed. Chapter 7 will evaluate the across flock genetic evaluations for parasite resistance in South African Merino sheep at Tygerhoek and Elsenburg research farms. Chapter 8 will cover the genetic differences in gastrointestinal nematode resistance between Dormer and South African Mutton Merino sheep. Chapter 9 is focused on evaluating the co-variance components for subjective FAMACHE© scores and faecal worm egg counts on two research farms in the Western Cape Province. Finally, in Chapter 10, the conclusions from the research will be presented with recommendations for further research.

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CAPTER 2: LITERATURE REVIEW

2.1 Introduction

A global increase in human population, rapid urbanization, and improved lifestyle has resulted in an increase in demand of meat products and other high quality protein sources (Delgado *et al.*, 1999; Thornton, 2010). In the year 2010, the small stock industry contributed 8 to 10% of the gross animal domestic product to the South African Agricultural economy (Cloete & Olivier, 2010). However, this contribution is small compared to some other livestock sectors. To improve the overall production efficiency and profitability, it is important to deal with factors that directly or indirectly affect the economic gains.

Infestations of gastrointestinal nematodes (**GINs**) impose serious constraints in small stock production. They result in economic and production losses. The most common method to control parasitism is the use of anthelmintics. However, their use in sheep production is not sustainable. Anthelmintics are expensive and can result in anthelmintic resistance by the nematodes (McLeod, 1995; Kaplan, 2004; Molento *et al.*, 2011). Moreover, the consumers are concerned about food safety and therefore, demand high quality products free from chemicals (Tackie *et al.*, 2012; Chamhuri & Batt, 2015). As a result, other alternatives such as selection for parasite resistance have been seen as the part of the long term strategy for controlling gastrointestinal nematode infestations (Gray & Gill, 1993; Woolaston & Piper, 1996; Karlsson & Greeff, 2006).

FWEC remains the principal trait to indirectly measure parasite resistance (Karlsson & Greeff, 2006; Kemper *et al.*, 2010). Its use in small stock production following artificial or natural challenge has been reported extensively (Gray 1991; Mandonnet *et al.*, 2001; Matebesi-Ranthimo *et al.*, 2014). In this review, the impact of gastrointestinal nematodes and control measures to parasitism will be discussed into detail.

2.2 Impact of gastrointestinal nematodes in small stock industry

It is universally accepted that the infestations with gastrointestinal nematodes affect the economic and production gains markedly (Over *et al.*, 1992; Nieuwhof & Bishop, 2005). The economic problems associated with GIN's include the direct annual cost of chemical drenches for treating and controlling parasite infestations, reduced production efficiency i.e. meat, milk, wool and skins (Johnstone *et al.*, 1979; Kelly *et al.*, 2010; Van Houtert & Sykes, 2010), and in severe cases, death of infected animals (Barger & Cox, 1984; Gulland, 1992). The economic

studies estimating the financial cost of gastrointestinal nematodes in production losses or the costs and benefits of strategic measures are scarce. In fact, it is not easy to estimate the precise figures incurred on production from infections or diseases. Possible reasons are i) The production diseases/ infections are multicausal in nature i.e. they can result from the interaction of the host with nutritional or environmental strains, management strategies, coexisting diseases, genetic inclinations, or other factors; ii) Insufficient information on the extent in which the production is affected by infections and iii) a greater variation on the significance of productivity between farms and across countries. Periodic reports on the impact of gastrointestinal nematodes in livestock industry from governmental agencies range to several millions of US dollars per year, worldwide (Beck *et al.*, 1985; Gibbs & Herd, 1986; McLeod, 1995). In South Africa alone, the estimated cost for treating *Haemonchus contortus* is 46 million U.S. dollars/yr (Peter & Chandrawathani, 2005). Animals that were overburdened with GIN's have been shown to have a 16% reduction in wool growth (Johnstone *et al.*, 1979), had a 40% decline in weight gain, decreased food digestibility (Coop & Holmes, 1996), reduced feed intake in lambs up to 30% (Poppi *et al.*, 1990), reduced milk yield by 15% (Sykes, 1982), and had poor reproductive performance (Hussain & Usmani, 2006). These effects have been previously connected with the severity of infection, with higher parasite load resulting in impaired growth rate and a reduction in appetite (Coop *et al.*, 1982). The most common clinical signs of GIN's include weight loss, anorexia, emaciation, weakness, scouring, a rough coat, and anaemia (Idris *et al.*, 2012). Sometimes, production losses may result without any clinical signs of infestation.

2.3 The life cycle of gastrointestinal nematodes

In order to understand the best ways to control or prevent parasitism, it is important to understand the life cycle of GIN's common in sheep. The cycle consists of an egg stage followed by four larval stages and an adult stage. Gastrointestinal nematode life cycle can be divided into two parts i.e. the animal and pasture phases (see Figure 2.1). Adult worms in the abomasum and intestines of the host produce a large number of eggs that are expelled out of the host onto pastures through faeces of the host (Soulsby, 1965).

This begins the pasture phase of the life cycle. Once the faeces are excreted on the pasture, under favourable environmental conditions the eggs hatch and develop into larvae which then molts into the various larval stages. The first 2 stages of larval development (L1 and L2) are known as inactive stages because of the inability of larvae in these stages to infect the host.

8

Larvae in the L1 and L2 stages feed on faecal microorganisms and bacteria for their survival (Zajac, 2006). Moisture and temperature are the two driving factors that control larval development at these stages (O'Connor *et al.*, 2006). This explains why infections are more prevalent in moist environments when compared to dry environments. In addition, it also accounts for the seasonal occurrences of nematode infestations. The third larval stage (L3), on the other hand, is known as an active stage because of the ability of L3 larvae to infect the host. Larvae in the L3 stage have limited ability to migrate from faecal pellets onto pasture plants where they can be ingested by sheep. Therefore, it requires rains to disintegrate manure in order to contaminate grasses with L3 larvae. Animals that graze closer to the ground are likely to ingest a greater concentration of L3, leading to higher incidences of parasitism and greater parasitic loads (Hasheider, 2014).

The animal phase of the gastrointestinal nematode life cycle begins once L3 larvae are ingested. Once L3 larvae gained access to the digestive tract, they either go into hypobiosis, an inhibition stage that prevents larval development, or proceed with larval stage of growth (L4) and eventually molt into adults (O'Connor *et al.*, 2006). Larvae in the stomach, or intestines, can cause damage to the stomach glands (Yakoob *et al.*, 1983; McKellar, 1993), a reduction in appetite (Greer *et al.*, 2008), and competition for protein (Houdijk *et al.*, 2001). Tissue damage is caused by migration of worms through the various tissues (Yakoob *et al.*, 1983; Houdijk *et al.*, 2001). *Haemonchus contortus* begins to suck blood, resulting in anemia, when in the L4 larval stage. When molting is complete, adults begin to lay eggs to start a new generation of parasites. *Haemonchus contortus* requires at least 18 days to commence egglaying while *Nematodirus*, *Trichostronglyus spp,* and *Teladorsargia* require 28 days after being ingested by the host to start laying eggs. Fecundity of adult females varies by species and is about 50 eggs/day for *Ostertargia*, about 260 eggs/day for *Trichostrongylus spp*, and about 40 eggs/day for *Nematodirus* and can range from 5000 to 10,000 eggs/day for *Haemonchus contortus* (Coyne *et al.*, 1991; Sutherland & Scott, 2010).

It is not clear what triggers the induction of hypobiosis but differences in genetic make-up of the host and environmental conditions (i.e. extreme temperatures and insufficient moisture levels) could be major causes (Captini *et al.*, 1990). Hypobiosis can last 3 to 4 months and the animal may not show any clinical signs of a host response to hypobiotic larvae. Some dewormers may not be effective against hypobiotic larvae. Once hypobiosis is over, the larvae

develop into fully-grown adults and lay eggs which are expelled through faeces and the cycle continues.

The host's response to parasitism can be explained by resilience and resistance. Resilience, is described as "the productivity of an animal in the face of infestation" (Bishop, 2012). Animals that are able to maintain health and production performance under a high parasite load are regarded as resilient animals (Bisset *et al.*, 1994; Baker *et al.*, 2003). In a study by Albers *et al.* (1987), resilience was measured by comparing the performance, specifically live weight gain, of nematode infested animals. Albers *et al.* (1987) estimated resilience to be lowly heritable (0.09 ± 0.07) which means that resilience would be difficult to improve through selection. In addition, resilience is influenced by environmental factors such as the abundance and quality of feed and the intensity of infective larval challenge (Bisset *et al.*, 2001; Knox *et al.*, 2006).

Bishop (2012) on the other hand, defined resistance as "the ability for the host animal to exert control over parasite or pathogen". Therefore, resistant animals are able to suppress the establishment of parasites and/or remove the parasitic load. Faecal worm egg counts (**FWEC**), following exposure to natural or artificial challenge has been used in most breeding studies as a measure of nematode burden (Gray, 1991; Mandonnet *et al.*, 2001; Cloete *et al.*, 2007; Mathebesi-Ranthimo *et al.*, 2014). Animals with low FWEC are considered to be resistant to parasitism and are desirable in livestock production.

 The merits of selecting for parasite resistance are a reduction in pasture contamination which also results in a decrease in infestation challenge and a reduction in production costs by eliminating the need for expensive anthelmintic treatments. The consequences of selecting for parasite resistance depend of the direction and magnitude of genetic relationships between FWEC and other production traits in the breeding system.

2.4 Phenotypic traits associated with parasite resistance

FWEC, FAMACHA© score and hematocrit count are the most commonly used traits to measure parasite resistance. These traits are often used to measure the degree and rate of parasite infection. Below each of these traits will be discussed into detail.

2.4.1 Faecal worm egg count

Faecal wom egg count is an indicator trait for parasite status in sheep. It is influenced by several factors including the type of species infecting the host, level of larval challenge,

parasite burden, nutritional composition of the pastures (especially protein load) and grazing habits of the host. FWEC is commonly calculated using the McMaster Technique. This technique expresses worm eggs relative to grams of wet faeces. It also helps producers identifying animals that need to be drenched. The limitations to the use of FWEC in livestock industry are that; it is expensive and labour intensive to measure, samples can only be stored for a short period of time and it requires animals to be challenged (naturally or artificially) with nematodes for it to be effective. This practice may become unethical if not properly monitored and controlled as it may impair animals' welfare and, in severe cases, result in the death of animals being challenged. Outside of that, animals that are challenged could spread the worm eggs to the paddocks, forcing the poducers to pay additional attention to pasture management strategies.

2.4.2 FAMACHA©

To gain control of *Haemonchus contortus*, the FAMACHA© system was developed in South Africa. The objective of this system was to allow producers to score the mucosal colour and rank the level of anaemia in an individual animal in order to determine which animals need to be drenched (Bath *et al.*, 1996; Kaplan *et al.*, 2004). The score ranges from 1 to 5 where scores of 1 and 2 indicate that an animal is normal while a score of 4 or 5 indicates that an animal is anaemic and needs to be treated. Using the FAMACHA© system reduces the need to deworm all animals in the flock by identifying the animals that are more susceptible to gastrointestinal nematode infection (Burke *et al.*, 2007). Treating only the animals that cannot cope with infection improves the risk of pasture contamination, reduces anthelmintic resistance and reducess the overall cost of anthelmintic treatments. The limitations of the FAMACHA© system are i) Over-reliance on anaemia: *H. contortus* is not the only cause of anaemia, hookworms, liver fluke, nutritional deficiencies and other parasites could also result in anaemia, and ii) challenging the animals could result in production losses. A study by Riley & Van Wyk (2009) in Merino lambs reported the heritability estimates for FAMACHA score ranging from 0.06 to 0.24, with the highest estimate obtained at the peak of the challenge. Snyman (2007) on the other hand, reported moderate heritability estimates for FAMACHA at 0.17. Higher heritability estimates for FAMACHA scores in Merinos were reported by Van Wyk & Bath (2002), suggesting that this trait can be used for genetic improvement.

2.4.3. Hematocrit

Hematocrit, also known as packed cell volume (PCV) is the ratio of the volume of red blood

cells to the total volume of blood expressed as a percentage. Since, *Haemonchus contortus* is a hemophatogous nematode, its existence in the host results in the depletion of red blod cells. With that in mind, the hematocrit represents the level of infestation of the host with lower scores suggesting greater level of infestation. In a stuy by Vanimisetti *et al.* (2004) in ewes that were 50% Dorset, 25% Rambouillet, and 25% Finnsheep, the heritability estimates for hematocrit were 0.15, suggesting that selection for this trait can be feasible. Gauly *et al.* (2002) on the other hand, reported higher heritability estimates for hematocrit in Merino Landsheep ranging from 0.51 ± 0.27 to 0.56 ± 0.20.

2.5 Strategic measures to control the impact of nematode infection

A variety of ways to control gastrointestinal infections include the use of effective anthelmintic drenches (Overend *et al.*, 1994), improved grazing management techniques (Barger, 1996), nutritional manipulation (Knox & Steel, 1996), vaccination against GIN's (Knox & Smith, 2001) and selection for genetic resistance in the host (Karlsson *et al.*, 1991). Below, each of the above-mentioned strategic methods to control GIN infections will be discussed into detail.

2.5.1 Use of anthelmintic drenches

For many years, control of GIN's has relied on the use of anthelmintic drugs to prevent and treat disease incidences. Anthelmintic drenches have been broadly categorized as suppressive, strategic, tactical, and curative (Kelly *et al.*, 2010). Suppressive programs rely on regular administration of anthelmintic drenches to suppress worm burdens. In a suppressive program, three or more anthelmintic drenches are administered over an interval of 6 weeks (Bath, 2014). In strategic programs, the application of anthelmintic depends on epidemiology of the nematodes and is often seasonal. Some farmers administer anthelmintic two or more times a year, often at the beginning of the grazing season and at the end of summer. Additionally, some farmers drench their animals before rotating them to different paddocks. Once treated, animals get moved to clean, or safe, pastures to prevent re-infestation.

Tactical control of GIN infections relies on the strategic evaluation of environmental or parasite load and requires treatment only when a predetermined threshold has been reached (Kelly *et al.*, 2010). Tactical programs work best when chemical and nonchemical approaches are utilized to reduce pasture contamination. Non-chemical approaches include understanding of meteorology and the epidemiology of the worm infestation. Curative programs require

12

treatment about 1 or 2 months after the expected peak infection of the host (Besier & Love, 2003). Therefore, in curative programs, the anthelmintic drenches are administered after clear clinical signs of infection have appeared.

Although an increase in frequency of anthelmintic intervention has been successful in treating parasitism and maximizing production efficiency (Johnstone *et al.*, 1979), misuse and overuse of chemicals is a problem in livestock production (McLeod, 1995; Sangster, 1999; Kaplan, 2004). Major concerns with the use of anthelmintic treatments for GIN infection control are the possibility of drug residues in tissues that could have a negative effect on human health, potential negative environmental impacts; direct costs of anthelmintic treatments can be unaffordable for small scale farmers, and the development of resistance to chemicals by parasites (Mwamachi *et al.*, 1995; Waller, 1997; Besier & Love, 2003).

2.5.2 Anthelmintic resistance

Anthelmintic resistance is basically the ability of some nematodes to survive a standard recommended dose of anthelmintic treatments which would normally be effective. It is heritable and, therefore, can be passed on to offspring. Misuse and overuse of anthelmintic treatments is a major cause of anthelmintic resistance (Waller, 1997; Kaplan, 2004). Anthelmintic resistance is a world-wide problem and resistance can occur in a short period of time, ranging from 3 to 9 yr (Kaplan, 2004).The first case of anthelmintic resistance to avermectin drugs was reported in South Africa over 2 decades ago (Van Wyk & Malan, 1988) and has become common since then (O'Brien *et al.*, 1994; Sangster, 1999; Leathwick *et al.*, 2001). Although proper management practices can slow down the development of anthelmintic resistance (Geary *et al.*, 1999), the control of drug resistance, particularly resistance to multiple chemical drenches, is important to the sustainability of livestock production (O'Brien *et al.*, 1994). Moreover, the consumers demand high quality meat free from chemicals thus, forcing producers to consider other means to control parasitism.

2.5.3 Drench on demand anthelmintic programs

Drench on demand anthelmintic programs requires selective treatment of animals. Selective treatments target certain groups of animals that are more susceptible to infection for application of anthelmintic drenches. The anthelmintic treatment is then applied only to selected individuals showing clinical signs of GIN infection. Some animals have greater drenching requirements than others (Bisset *et al.*, 1994). Selective drenching reduces the

potential for anthelmintic resistance if applied properly (Van Wyk, 2001). Population modelling by Bisset *et al.* (1994) showed that dose on demand is likely to slow down the development of chemical resistance by the nematodes.

2.5.4 Grazing management

Literature has reported a variety of ways on how to manage grazing systems (Barger 1996, 1998; Waller, 1997). In general, the goal is to reduce pasture contamination and to make pasture and animal management a key component in breaking the gastrointestinal nematode life cycle. Waller (1997) and Barger (1998) classified strategies for grazing management as preventive, evasive, and dilutive. The preventive strategy aims at raising worm-free animals on clean pastures. The evasive strategy involves the removal of moderately existing parasites using anthelmintic drenches combined with the movement of treated animals to safe pastures. The dilutive strategy requires the mixing of susceptible parasites with resistant prasites to dilute the magnitude of infective larvae from the faecal pellets of the susceptible group. The two groups are identified by the use of FWEC, with low FWEC representing resistant animals. The dilutive strategy can also involve the mixing of different animal species on the same pasture (Waller, 1997; Barger, 1998). However, there is an overlap of parasites that infect sheep and goats; therefore, mixed grazing of goats and sheep is not recommended.

Clean, or safe, pastures fall under several classifications. Pastures which are harvested for hay and/or silage are considered safe. Pastures which have been grazed by different species are also considered safe due to minimal cross-species parasitic infections. However, there is an overlap of parasites between sheep and goats so consideration must be made if the pasture was previously grazed by goats. Land that has not been grazed for a long time is also considered safe. Proper application of grazing strategies into safe pastures requires a large piece of land which can be subdivided into paddocks to allow for rotational grazing by sheep. Rotations should be scheduled in such a manner that pastures have sufficient time to allow for new growth and to stop nematode depositions. Fleming *et al.* (2006) recommended that the pastures should be rested for 6 months during cold weather conditions and 3 months during hot dry weather.

Animal management is another important component of grazing management since animals are the source of contamination. Having many animals graze in a small paddock can increase the likelihood of having a higher concentration of infective larvae in a grazing area. Therefore, it is important to reduce the number of animals in a grazing area while also taking into

consideration two grazing habits that make sheep more susceptible to GIN infections. Sheep tend to graze pastures closer to the ground and higher concentrations of infective larvae are in the lower parts of the pasture grasses, resulting in an increase in the consumption of infective larvae. Moreover, sheep also like to be clustered in groups when grazing and tend to graze selected areas of the pastures very closely, even when there is abundant pasture space. As a result, they are likely to ingest a large number of infective larvae due to the concentration of faecal material in small areas. To remedy this problem, a recommendation of incorporating anthelmintic treatment into a rotational grazing program was made by Barger (1997) to lower the parasite burden. However, misuse and overuse of anthelmintic treatments can lead to anthelmintic resistance by the nematodes. As a result, Bath (2014) suggested short durations of high pressure grazing in order to maximally utilize feed within a short space of time. By shortening the duration that sheep graze a pasture, it can reduce the chance of consuming infective larvae because it can take a week to several months for larvae to develop from the first to the third stage of growth where it becomes infective.

2.5.5 Nutritional manipulation of the host to control gastrointestinal nematode infection

Nutritional manipulation of the host is one of the important strategies used to control parasitism in small stock production. The primary effects of gastrointestinal nematode infestations, apart from high mortality rate in severe outbreaks, are reduced feed intake and feed efficiency, resulting in an increased protein requirement to maintain production levels. The reason for the reduction in appetite is not clear; however, feed intake may be reduced by up to 20% as compared to non-parasitized animals (Symons, 1985; Holmes, 1987). Sykes & Greer (2003) evaluated the effects of parasitism on the nutrient balance of sheep. In their study, a reduction in appetite of up to 50% was observed in parasitized sheep and the reduction in appetite showed a marked impact on the protein balance of the host by reducing the total nutrients available for anabolic processes. In addition to appetite reduction, parasitism also results in malabsorption and redirection of nutrients from production purposes to maintaining homeostasis (Roy *et al.*, 2003).

Reduced protein metabolism as a result of parasitism leads to reduced growth rates and reduced wool and milk production (Coop & Kyriazakis, 1999). Therefore, it is clear that supplementary feeding, especially that of protein, can minimize the effect of parasitism on the production of small ruminants. Other scientists also believe that supplementing animals with

protein would maintain the production efficiency and improve the immune response of the host (MacRae, 1993; Coop & Kyriazakis, 1999; Greer *et al.*, 2009). A study by Knox *et al.* (2006) has shown that supplementing small ruminants with protein improved host resilience and resistance. In small stock production, periparturient ewes that were supplemented with protein eliminated the periparturient rise in FWEC and, as a result, reduced pasture contamination at the beginning of the grazing season (Donaldson *et al.*, 2001; Kahn, 2003 a; 2003b). In a study on dairy goats, goats that were supplemented with protein showed an improved production performance compared to non-supplemented goats (Etter *et al.*, 2000; Chartier *et al.*, 2000). An improved diet can reduce the negative impact of parasitism and maximize returns. However, the problem with supplementary feeding is that it is expensive and may not be affordable to resource-poor farmers.

2.5.6 Use of vaccines to prevent parasite infestation

One way to prevent the losses due to nematode infestations is through the use of vaccines. Research to produce a vaccine against *Haemonchus contortus* have been conducted (Newton & Meusen, 2003; Smith & Zarlenga, 2006). A new commercially available vaccine for *Haemonchus contortus* (Barbervax®) was developed and released in 2014. The invention of this vaccine offers a strong protection of the animals with no issues of chemical residues. This vaccine gets imported to South Africa but, although that is the case, it has not gained popularity yet. Most people, especially small scale farmers, therefore do not know about it.

2.5.7 Selecting for parasite resistance

Selecting for low FWEC has been seen as an alternative strategy to control parasitism (Karlsson & Greeff, 2006), supported by a large body of literature that reported moderate to high heritability estimates for FWEC, ranging from 0.15 to 0.50 (Bissett *et al.*, 1992; Eady *et al.*, 1996; Bouix *et al.*, 1998; Baker *et al.*, 1999; Cloete *et al.*, 2007; Wolf *et al.*, 2008), with FWEC being a highly variable trait with the number of worm eggs per gram of wet faeces ranging between 0 and 32,700 in the same contemporary group (Matebesi-Ranthimo *et al.*, 2014). The genetic variation of FWEC reported in literature vary between different breeds (Baker *et al.*, 1999, 2002; Gruner *et al.*, 2003; Nimbkar *et al.*, 2003) and within breeds (Morris *et al.*, 2000; Woolaston & Windon, 2001) when considering different nematode species. It is no surprise that realized gains due to selection for GIN's have been reported in New Zealand (Morris *et al.*, 2005) and Australia (Woolaston & Piper, 1996; Karlsson & Greeff, 2006). In contrast, no comparable results have been published in South African sheep. However, the

16

heritability estimates obtained in South Africa are moderate, suggesting that genetic gains can be realised should selection for parasite resistance be desired (Cloete *et al.*, 2000, 2007; Matebesi-Ranthimo *et al.*, 2014). Selection for host resistance to gastrointestinal nematodes can reduce the need for anthelmintic treatments due to the greater host control of the nematode burdens. However, commercial sheep breeding operations are expected to include the only economically important traits in their selection objectives. Therefore, in order to design a sound breeding program to select against GIN's, the heritability estimates for FWEC as a measure of parasite resistance, the heritability of individual production traits and their genetic relationships with FWEC are required. In a study by Bishop *et al.* (1996), the genetic correlations between FWEC and body weight ranged from -0.63 to -1.00, suggesting that selection for low FWEC could increase body weight in lambs.

2.5.8 Genomic selection for parasite resistance: A bright hope for tomorrow

Meuwissen *et al.* (2001) was the first to introduce the concept of Genomic selection (GS) as a strategy to be used in traits that are hard to measure, like parasite resistance. The basic principle of GS is that, a greater number of markers can be used to calculate genomic breeding values without having a precise knowledge of the location of specific genes affecting a trait of interest in the genome. The prediction of genomic breeding values for any trait depends on the genotyping of DNA samples. With hundreds of thousands of Single Nucleotide Polymorphisms (SNPs) well chosen to represent the entire genome, it is expected that i) at least one SNP will always be close to the gene of interest, ii) at least one or more SNP are in linkage disequilibrium with the gene of interest and iii) some mutations may have a large effect and could account for significant genetic variation in a trait of interest (Meuwissen *et al.*, 2001; Meuwissen & Goddard, 2010). With dense SNP arrays, comparable performance can be accounted for in the absence of parental relationships. The use of SNPs in a breeding program therefore allows breeders to get information from the genotype before its expression; thus, providing an opportunity for producers to be able to select at an early stage (Schaeffer, 2006).

The first step in applying genomic selection is the establishment of a reference population, also known as a training population or a predictor population, with links to the the population prediction needed from a large database. The phenotypes for the traits of economic importance should be accurately measured and animals with extended phenotypes should also be genotyped. Both phenotypes and genotypes in a reference population are used to derive the prediction equation which predicts genomic breeding values. GS captures a larger

portion of genetic variance throughout the genome in comparison to pedigree information by accounting for the Mendelian sampling effect (Meuwissen *et al.*, 2001). About 49 000 SNPs have been validated in 75 traits of economic importance in sheep (Kijas *et al.*, 2009). The predictive ability of GS has been shown to be increased compared to traditional breeding strategies (Schaeffer 2006). In a study by Pryce *et al.* (2010) the estimated genetic gain was ~50% higher with application of GS compared to a traditional breeding program. Factors affecting the reliability of genomic breeding values have been clearly demonstrated in literature (Meuwissen *et al.*, 2001; Habier *et al.*, 2007; Goddard, 2008; Hayes & Goddard, 2010; Hayes *et al.*, 2011). Genomic selection increases the rate of genetic gains and also reduces the costs associated with progeny testing (Schaeffer 2006; Van Raden 2008). Therefore, its use in sheep production could result in economic gains. Al Kalaldeh *et al.* (2018) imputed high density (HD) SNP-data to whole genome sequences in regions found to be related to FWEC. A genomic relationship matrix (GRM) including selected SNP genotypes from the imputed data were subsequently fitted along a GRM based on 50K SNP-data. This resulted in an improved accuracy from 13% when using only 50K SNP-data to 26% when additional information imputed to whole genome sequences was added. The authors related this improvement to rare variants in linkage disequilibrium with FWEC phenotypes being captured in the latter analysis. From these results it seems that additional genomic information may play a role during the selection of animals for a hard-to-measure trait such as FWEC. It is expected that further genomic research will unlock additional possibilities for selection for a lower FWEC.

2.6 Scouring Management

Scouring could be caused by various factors, including bacterial infections resulting from ingestion of *Trichostronglyid* larvae (Larsen *et al.,* 1994). Two types of scouring due to gastrointestinal nematodes were identified, i.e. high FWEC scouring as a result of a high adult worm burden and low FWEC scouring due to ingestion of infective *Trichostronglyid* larvae (Larsen *et al.*, 1994; 1995). High FWEC scouring is associated with low immune response and is very common in weaners. Although that is the case, some animals may also be affected at hogget stage. Selection for low FWEC would also lower this type of scouring. Low FWEC scouring on the other hand is mostly expressed in hoggets. So, selection for low FWEC could potentially increase low FWEC scouring. Karlsson *et al.* (1995) indicated that selection for low FWEC may result in an unfavourable response to scouring, with a suggestion for animals that

were selected for low FWEC to show a higher incidence of scouring compared to the control line. In another study by Karlsson & Greeff (1996), the genetic correlation between FWEC and scouring was -0.67 at weaning but, it reduced to -0.12 in Merino sheep at hogget age, suggesting that selection for FWEC at a younger age could increase the risk of scouring later in life.

2.7 Conclusion

GIN affects economic and production gains in small stock industry worldwide. The use of chemical drenches to treat, prevent and control the nematode infestations is not sustainable. Their use in livestock industry can result in resistance by the nematodes. Literature has reported an overwhelming evidence of genetic variation in FWEC between and across breeds. Selection for parasite resistance can therefore be possible.

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21

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27

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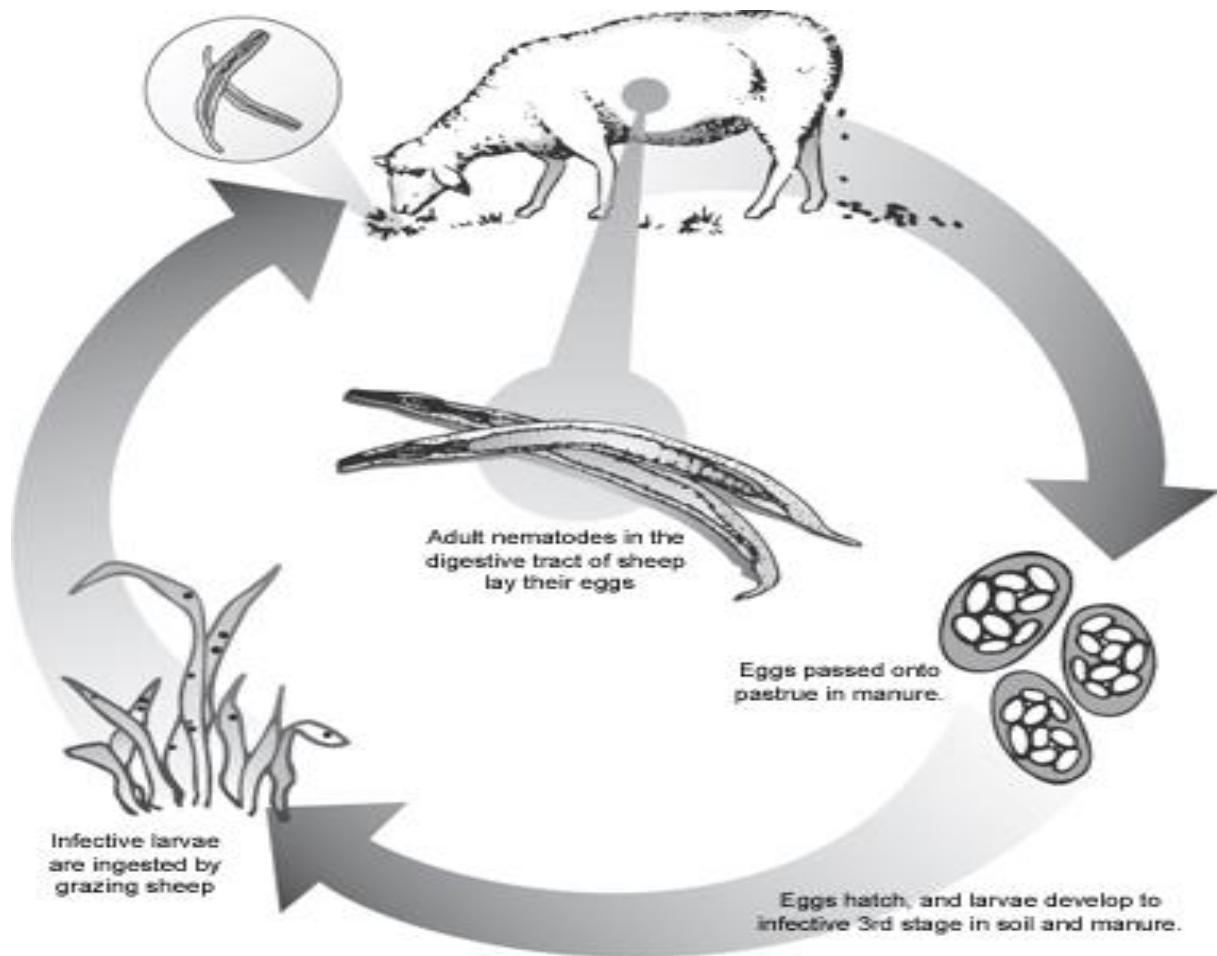
Figure 2. 1 Lifecycle of Tichostrongyle parasites, like *Haemonchus contortus* (Whittier *et al.*, 2009)

CHAPTER 3: ENVIRONMENTAL AND GENETIC FACTORS AFFECTING FAECAL WORM EGG COUNTS IN MERINOS DIVERGENTLY SELECTED FOR REPRODUCTION

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3.1 Abstract

Infestation with gastrointestinal nematodes is arguably among the most pervasive problems in small-stock production worldwide. Faecal worm egg count (FWEC) has been reported as a traditional measure of gastrointestinal nematodes. Environmental and genetic factors of FWEC were assessed, using data from Merino sheep that was divergently selected for reproductive performance at Elsenburg Research farm. Data consisted of animals born in 1995-1996; 1999 and 2001-2013. Two data sets were considered: 1869 FWEC records of animals born in birth years provided above, and 851 records of the divergently selected lines and the reciprocal cross between them born from 2003-2008. Rectal faecal sample grabs were obtained from individual animals after drenching had been withheld for approximately 6 to 10 weeks, generally in April. Nematode eggs in these samples were counted using the McMaster technique, with a sensitivity of 100 eggs /g wet faeces. The fixed effect of the birth year x sex interaction was significant ($P < 0.05$) with rams showing higher mean values for FWEC than ewes in most years, but these results were not consistent. FWEC was significantly but lowly heritable, estimates ranging from 0.06 ± 0.03 for untransformed data to 0.10 ± 0.04 for log transformed data, suggesting that selection progress for FWEC can be slow. There was no evidence of heterosis on either line, suggesting that resistance to roundworms are unlikely to benefit from crossbreeding. This experiment was limited to a data set that was collected during autumn; therefore the results of this study cannot be directly applied to a situation where faecal samples were collected in other seasons. Future work to determine the effect of season on the heritability of parasite resistance in South Africa is needed.

Keywords: Gastrointestinal nematodes, genetic parameters, resistance, faecal worm egg count

3.2 Introduction

Infestation with gastrointestinal nematodes is arguably among the most pervasive problems in small-stock production worldwide. Higher level of gastrointestinal infestations results in substantial losses through reduced growth rates, poor production performance and reduced reproductive efficiency (Chiezey *et al.*, 2008; Kelly *et al.*, 2010; van Houtert & Sykes, 2010). There is thus reduced overall production efficiency stemming from high costs of anthelmintic drenches used for prevention and treatment (Pathak & Tiwari, 2013), and in severe cases, death of infested animals (Barger & Cox, 1984).

For decades, gastrointestinal nematodes were controlled by using chemical drenches to treat infestation and/or prevent production losses associated with infestation; hence to improve overall production efficiency (Dash, 1986). However, resistance of gastrointestinal nematodes to the chemicals used for treatment has become very common (McLeod, 1995; Kenyon *et al.*, 2009; Molento *et al.*, 2011). Thus, relying on drenching with chemicals as the only treatment strategy for controlling gastrointestinal nematode infestations may not be sustainable. Alternative strategies of parasite control, such as, breeding for parasite resistance offer a sustainable solution.

The basic principle of animal breeding and genetics is to improve livestock profitability through selection. Its application in a breeding program would result in cumulative and permanent gains in desired traits. However, for breeding to be implemented, genetic variation of a trait of interest should be present. Literature has reported an existing variation in parasite resistance, indirectly measured by faecal worm egg count (FWEC), ranging from 0.00 to 0.51 (Greeff *et al.*, 1995; Cloete *et al.*, 2007; Matebesi-Ranthimo *et al.*, 2014). Selection of animas with lowest FWEC would thus improve parasite resistance in sheep production.

Gray (1991) identified FWEC as a viable means to indirectly measure parasite resistance. As a result, FWEC has been widely used to measure parasite resistance, following artificial or natural infestation (Mandonnet *et al.*, 2001; Cloete *et al.*, 2007; Matebesi-Ranthimo *et al.*, 2014). Previous studies have reviewed genetic factors affecting FWEC at an international level (Khusro *et al.*, 2004; Safari *et al.*, 2005; Morris, 2011; Pickering *et al.*, 2012). However, in South Africa, the genetic factors affecting FWEC have been limited to the work of Nieuwoudt *et al.* (2002), Snyman (2007), Cloete *et al.* (2007) and Matebesi-Ranthimo *et al.* (2014). The issue of genetic and environmental factors affecting FWEC still needs to be investigated using a larger dataset to increase the level of accuracy in the results.

33

The objective of this study was thus to determine environmental and genetic sources of variation in the FWEC data of the Elsenburg Merino flock that was divergently selected for the ability of ewes to rear multiple offspring. Phenotypic and genetic trends in FWEC of the divergently selected lines were also inspected for possible divergence indicative of correlated responses to the divergent selection regime. Simultaneously, the reciprocal cross between the two lines was assessed for possible heterotic effects in FWEC.

3.3 Materials and Methods

Data were obtained from the Elsenburg Merino flock that was divergently selected for their ability to rear multiple offspring. Details on the selection procedure for the resource flock and experimental site have been documented in literature (Cloete & Scholtz, 1998; Cloete *et al.*, 2004; 2009; Scholtz *et al.*, 2010). Briefly, two lines of sheep that differ in reproductive performance were developed from 1986. One line was selected for increased reproductive performance (H-line) based on their ability to rear more than one lamb per lambing opportunity. The other line (L-line) was selected based on zero lamb output at one or more lambing opportunities i.e. ewes were barren or lost all lambs born at least once. Initial selection of rams and ewes were based on maternal ranking values for number of lambs weaned (see Cloete *et al.*, 2004). Selection was thus based on performance in the previous generation. From 2002, following on from results reported by Cloete *et al.* (2004), predicted breeding values from single-trait repeatability models were used for aiding selection decisions. During the early stages of the selection experiment, ewes that reared a single lamb per lambing opportunity were occasionally accepted in both lines depending on reproduction rates and replacement needs. As expected, very few offspring were available in the L-line in recent years due to downward selection; so, the progeny from ewes that rear at least a single lamb per mating often had to be selected to maintain the line. Selection decisions were preferably based on three or more maternal joinings, especially for rams.

Divergent selection for reproductive traits resulted in lines that differ in the reproduction traits selected for (Cloete *et al.*, 2004) lamb survival (Cloete *et al.*, 2009), susceptibility to breech strike (Scholtz *et al.*, 2010), behaviour (Cloete *et al.*, 2005; Cloete *et al.*, 2010), and adrenal function (Van der Walt *et al.,* 2009; Hough *et al.*, 2015). In all the mentioned studies, the H-line showed a superior ability to survive, resist breech strike and adapt to stressful situations compared to the L-line. Both lines were maintained at the Elsenburg Research Farm as a single flock, except during joining in single sire groups to 2-7 rams. The experimental farm is

34

situated ~10km north of Stellenbosch at 33° 51'S and 18° 50'E. The climatic conditions at the site are Mediterranean, with 77% total rainfall of 606mm recorded between April and September.

There was no direct selection for low FWEC in any of the lines. The description of management of experimental animals and the pastures they utilized was documented by Cloete *et al.* (2004; 2009), while the faecal grab sampling procedures were detailed by Cloete *et al.* (2007). Rectal faecal grab samples were collected from individual animals born in 1995-1996; 1999 and 2001-2013, aged between nine and 11 months. Two data sets were considered: 1869 FWEC records of animals born in the divergently selected lambs during the birth years provided above, and 851 records of the divergently selected lines and the reciprocal cross between them born from 2003-2008. Sampling was conducted after drenching had been withheld for at least 6 - 10 weeks, generally in April except for in 2013, when the individual sample grabs were collected in February. At that time, the animals were likely to be infected with a mixture of helminthic nematodes with the genera *Teladorsargia* (*Ostertagia*) and *Trychostrongylus spp* present as major species and *Haemonchus contortus* as a minor species (Reinecke *et al.*, 1987). Individual faecal samples were analysed at Stellenbosch Provincial Veterinary Laboratory, using the McMaster technique, with a sensitivity of 100 eggs per gram (epg) of wet faeces (Van Schalkwyk *et al.*, 1994; Matebesi-Ranthimo *et al.*, 2014).

FWEC is known to be exceedingly variable and skewed, needing transformation prior to analysis (Greeff *et al.*, 1995; Khusro *et al.*, 2004; Morris *et al.*, 2005; Cloete *et al.*, 2007). Commonly used transformations applied to FWEC data is the cube root transformation and the log-transformation. Both these transformations were previously used to normalise FWEC data (Morris *et al.*, 2005; Cloete *et al.*, 2007; Matebesi-Ranthimo *et al.*, 2014). The log transformation involved the calculation of the natural logarithm of FWEC, after 100 were added to FWEC to account for zero counts. ASREML software (Gilmour *et al.*, 2009) was used to analyse the fixed effects and to estimate variance components in single-trait analyses. The first analysis involved fitting various combinations of fixed effects to obtain an operational model, including the effects of selection line (H or L), birth year (as specified previously), sex (ram and ewe), age of dam (2-7+ years) and birth type (singles and pooled multiples). All two-factor interactions were considered initially, but only the birth year x sex interaction was significant and retained in the operational model along with the selection line x birth year

interaction. The latter interaction would be indicative of phenotypic divergence possibly associated with correlated responses to the selection regime implemented. Random terms were sequentially added to the operational model, yielding the following models for analyses (in matrix notation):

$$y = Xb + e \qquad\qquad [1]$$

$$y = Xb + Z_1a + e \qquad\qquad [2]$$

$$y = Xb + Z_1a + Z_2c + e \qquad\qquad [3]$$

$$y = Xb + Z_1a + Z_2m + e \qquad\qquad [4]$$
$$[Co \,var\,iance\,(a, m) = 0]$$

$$y = Xb + Z_1a + Z_2m + e \qquad\qquad [5]$$

$$[Co \,var\,iance\,(a, m) = A\sigma_{am}]$$

$$y = Xb + Z_1a + Z_3m + Z_2c + e \qquad\qquad [6]$$

$$[Co \,var\,iance\,(a, m) = 0]$$

$$y = Xb + Z_1a + Z_3m + Z_2c + e \qquad\qquad [7]$$

$$[Co \,var\,iance\,(a, m) = A\sigma_{am}]$$

In these analyses, y was a vector of observations for either untransformed FWEC, cube root transformed FWEC and log transformed FWEC, and b, a, m and c were vectors of fixed effects, direct genetic variances, maternal genetic variances and maternal permanent environmental variances respectively. X, Z_1, Z_2 and Z_3 represented the corresponding incidence matrices relating the respective effects to y and e was the randomly distributed vector of residuals. A was the numerator relationship matrix, and σ_{am} the covariance between direct and maternal additive genetic effects. It was assumed that:

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

With I representing identity matrices; σ_a^2, σ_m^2, σ_c^2, and σ_e^2 being the direct genetic, maternal genetic, maternal permanent environmental (PE) and residual variances respectively. Ratios corresponding to additive genetic and permanent environmental variances were computed from these estimates. These variances were expressed relative to the total phenotypic variance. Likelihood Ratio tests (LRT) were used to test the contribution of each random term

to improvements in the operational model for significance. The LRT is based on testing twice the increase in the Log-likelihood resulting from adding an additional random term to the model as a Chi^2 statistic. For two models with the same number of random terms the model with the higher value for the LRT fits the data better, provided that identical fixed effects were modelled.

Animal solutions, reflecting additive estimated breeding values (EBV's) for log-transformed FWEC were obtained for individuals. These breeding values were added to the overall log-transformed mean and transformed back to the observed scale. The overall geometric mean was again subtracted from the individual values obtained and averaged for the respective selection lines within birth years. Genetic trends derived in this way were inspected for differences between lines, using standard errors of the means to inspect line differences within birth years for significance. EBV's were obtained from an analysis where selection line and its interactions with other fixed effects were excluded from the operational model.

Additionally, data of 851 progeny were extracted from the raw data file to represent the purebred H and L lines, as well as the reciprocal cross between them for the 2003-2008 birth years. The same fixed effects were fitted to this data but the two crossbred genotypes were added to the two purebred lines considered initially. A linear contrast was defined in ASREML to compare the reciprocal crossbred progeny with the midparent value of the two purebred lines. All the genetic analyses included the full pedigree file for the data set, consisting of 5596 individuals, the progeny of 242 sires and 1552 dams.

3.4. Results

The standard deviation of raw FWEC records across lines exceeded the mean value, recorded values ranging from 0 to 27600 epg of wet faeces (Table 3.1). The distribution of FWEC data was improved appreciably by the appropriate transformation thereof, resulting in a coefficient of variation (CV) of 21% for log-transformed FWEC.

Least squares means of fixed effects for log-transformed FWEC are presented in Table 3.2. Conclusions derived from analyses on untransformed FWEC and cube root transformed FWEC were in close correspondence with the results presented and are therefore omitted. Log-transformed faecal worm egg counts (LFWEC) was markedly affected by birth year (P <0.001), means ranging from 111 epg of wet faeces in 2013 to 3646 epg of wet faeces in

2011. The overall LFWEC of ram lambs almost doubled that of ewe lambs (P <0.001). In contrast, LFWEC was not affected by dam age, selection line and sex (P >0.20).

LFWEC was also affected by the interaction between birth year and sex (Figure 3.1). Generally, the least squares means for rams were mostly above those of ewes, in many cases significantly so. However, this pattern was interrupted during 2010, when ewes had markedly higher LFWEC means than rams. No significant sex differences could be discerned in other years, contributing to the observed sex x birth year interaction. In contrast with the sex x birth year interaction, there was no evidence of an interaction between selection line and birth year in phenotypic means (Figure 3.2). The lines for the H and L lines followed each other closely and, even though absolute differences could occasionally be discerned between lines, none of these were significant (P >0.05).

Log-likelihood values for the analyses on FWEC suggest a significant improvement from the model with fixed effects only to the model also including direct additive genetic variation for untransformed FWEC as well as for cube root-transformed and log-transformed FWEC (P <0.05; Table 3.3). However, the addition of further random effects failed to result in an additional improvement to the goodness of fit of the model employed. As a result, the heritabilities in this chapter were estimated using model 2.

All heritability estimates for LFWEC reached a level of at least double the corresponding standard error and therefore differed from zero (P <0.05; Table 3.4). Although transformation resulted in higher heritability estimates in absolute terms, even transformed FWEC remained lowly heritable at 0.09 – 0.10.

There was no compelling evidence of genetic change in back-transformed FWEC in either line during the course of the experiment, as most annual means oscillated between -45 and 54 epg wet faeces during the course of the experiment (Figure 3.3). According to the standard errors provided, there were only a few years during which significant (P <0.05) differences occurred between the averaged estimated breeding values derived for the respective purebred lines. It thus seems as if the resistance of the experimental animals to gastro-intestinal nematodes, as reflected by LFWEC, was largely independent of the divergent selection practices for the ability of ewes to rear multiples applied in the resource population. Overall mean breeding values (± s.e.) across years amounted to -9.2 ± 1.7 epg wet faeces in the H line and -11.2 ± 3.6 epg wet faeces in the L line.

Log-transformed FWEC was independent of genotype in the reciprocal crossbreeding study conducted from 2003-2008 (Table 3.5). Means for the purebred lines were similar (P >0.05), as in Table 3.2. The reciprocal crossbred progeny also did differ from either purebred line or the midparent value (P >0.05).

3.5. Discussion

In this paper, the environmental and genetic factors affecting FWEC, an indirect measure of parasite resistance in Merino lines divergently selected for reproductive performance, was explored. A dataset of 2720 records enabled some unique statistical analyses to be run. There was relatively a high individual variation of FWEC across the lines ranging from 0-27600. Extreme individual variation of FWEC is commonly reported in literature. Studies by Cloete *et al*. (2007), Snyman (2007) and Matebesi-Ranthimo *et al*. (2014) reported an individual variation for FWEC ranging from 0-13700, 0-87800 and 0-32700 epg wet faeces respectively. In a study by Khusro *et al*. (2004) means for FWEC was 736 for hoggets and 779 for yearling Merino sheep, while the individual variation for FWEC ranged from 0-50000 epg in both age groups. The transformations used in this study are commonly applied to improve the extreme variation in data of this nature. Safari & Fogarty (2003) documented genetic parameters of sheep among others for FWEC. In their review, 26 heritability estimates for FWEC were reported, 12 of which a cube transformation was applied and the other 14 a log-transformation was applied. Means in these studies ranged from 2.75 to 22.6 for cube transformed data and 6.88 to 7.49 for log transformed data. In a study by Cloete *et al*. (2007) and Matebesi-Ranthimo *et al*. (2014) the coefficient of variation in FWEC records exceeded 100% before transformation and reduced to below 20% after log transformation. Similar results were found in this study but, the magnitude of CV was slightly higher i.e. up to 21% after transformation. Higher CV values are indicative of appreciable phenotypic variation, which could enable genetic gains even at modest levels of heritability. The results provided in this study are consistent with those reported in the literature.

 Pertaining to the results for the interaction between birth year and sex, the results obtained in this study are in accordance with the results obtained by Khusro *et al*. (2004), Cloete *et al*. (2007) and Matebesi-Ranthimo *et al*. (2014). In all three studies, the effects of birth year and sex were involved in a significant interaction. In a study by Khusro *et al*. (2004) the direction of the magnitude of difference in FWEC varied between yearling animals and hoggets. In yearling animals, ewes excreted more eggs than rams, while, the opposite was true for

hoggets. Cloete *et al.* (2007) and Matebesi-Ranthimo *et al.* (2014) on the other hand, observed fewer eggs in ewes than in rams but the magnitude was different between years resulting in a significant interaction. A significant interaction effect of birth year by sex observed in this study could potentially be attributed to the following causes: i) It could be random, or ii) it could be a sign that there is no uniform environment. Males and females were kept on different paddocks and therefore, they are grazed separately. So, it is possible that males were generally grazed on paddocks with a higher parasite load compared to females. One of the challenges of doing an experiment based on natural challenge is that, the researcher does not have much control of the magnitude of challenge that the experimental units receive, while some environments do not support an adequate helminth challenge. Therefore some studies resort to the use of artificial challenge to ensure an adequate challenge throughout. However, artificially challenging animals with nematodes is labour intensive and costly, it could be debated on ethical grounds and it could be problematic to source infective FWEC larvae on a sustainable basis. Gauly *et al.* (2006) evaluated the effect of sex on resistance to sheep lambs to an experimental *Haemonchus contortus* infection. In their study, male lambs accordingly excreted more FWEC compared to females, suggesting that females were more resistant than males. This sex difference was confirmed by worm counts following slaughter. While the sex x year interaction is clearly related to the grazing of separate pastures, there also seems to be some support for a contention that ewes are generally better able to resist nematode infestation than rams.

The heritability estimates reported in this study were fairly low at 0.10 ± 0.04 after transformation, suggesting a fairly small genetic component for LFWEC and that genetic progress is likely to be slow. The present heritability estimates are on the lower end of the range of literature values. Published heritability estimates for FWEC in Merino flocks under natural challenge in South African conditions were moderate, ranging from 0.14 ± 0.02 to 0.24 ± 0.02 (Niewoudt *et al.*, 2002; Cloete *et al.*, 2007; Matebesi-Ranthimo *et al.*, 2014). In a study by Niewoudt *et al.* (2002), the log-transformed FWEC data yielded the heritability estimate of 0.24 ± 0.02. Cloete *et al.* (2007) reported heritability estimates of 0.14 ± 0.02 to 0.18 ± 0.03 (depending on transformation of the data) in 13 to 16-months old Merino sheep sampled in the spring. Similar results were found by Matebesi-Ranthimo *et al.* (2014) on the same flock and utilizing a larger data set. The heritability estimates reported in South African literature are however; lower than the mean value of 0.27 derived from a mixture of artificial and natural challenge (reviewed by Safari *et al.*, 2005). Previous reports on heritability estimates for

FWEC in Merino sheep have been reported in Australia. The results showed a range of 0.18 to 0.40 for weaners, 0.17 to 0.34 after weaning and 0.15 to 0.40 in one-year-old sheep, with standard errors ranging from 0.04 to 0.12 (Clarke, 2002). Moreover, in New-Zealand, the heritability estimates for FWEC was 0.37 in naturally challenged Romney sheep in a temperate environment (Baker *et al.*, 1991). Studies by Woolaston & Piper (1996) and Karlsson & Greeff (2006) reported that selection for parasite resistance resulted in realized gains.

Scientific literature reports that FWEC can be influenced by seasonal variation, management practices and different geographical areas (Greeff *et al.*, 1995). Gregory *et al.* (1940), also found seasonal variation as one of the factors affecting parasite resistance. Greeff *et al.* (1995) estimated the genetic constitution of FWEC at different times of the year in Merino lambs born in a Mediterranean environment. In their study, the heritability estimates for FWEC under natural challenge was high during the period of June to October (i.e. 0.21 to 0.25), and low from February to April (0.00 to 0.03), while a peak of 0.51 was reached in July. In the same study, Greeff *et al.* (1995) found a larger variation of FWEC between months within years, and also across different years suggesting that the effect of season should not be neglected when planning genetic evaluation studies of parasite resistance. The environment to which the animals are subjected is often characterized by seasonal rainfall events and temperature fluctuations at different times of the year. As a result, the quality and quantity of pasture and the development of infective larvae varies from season to season. Studies by Niewoudt *et al.* (2002), Cloete *et al.* (2007) and Matebesi-Ranthimo *et al.* (2014) collected faecal sample between July and September when the environment was condusive for the development, growth and migration of infective larvae.Their results reported moderate heritability estimates for FWEC. However, in the present study, the faecal samples were collected in late summer and autumn from irrigated pastures. It is unclear why the present study yielded low heritability estimates for FWEC despite adequate challenge (as evidenced by the range of individual faecal worm egg counts and the poportion of zero counts). It is possible that some parasite eggs were probably in the hypobiosis, the arrested state of larvae development. Apart from that, the lower heritability estimates for FWEC in our study could result from using a relatively low accuracy of 100 epg of wet faeces compared to some other studies (Notter, 2003). In a study by Notter (2003) the heritability estimates for FWEC were 0.42, 0.22 and 0.25 at 3, 4 and 5 weeks post infection with *H. contortus* in sheep. In their study, the faecal worm egg counts were calculated at a sensitivity of 50 epg.

Realised genetic responses in relation to the respective phenotypic means in the H line amounted to 1.3% for number of lambs born and 1.5% for number of lambs weaned (Cloete *et al.*, 2004). Corresponding downward trends in the L line amounted to 0.6 and 1.0% respectively. It is clear that responses in reproduction were clearly divergent in the selection lines in contrast with those for FWEC in Figure 3.3, suggesting no statistical evidence of genetic change in both divergently selected lines. Based on these results, a negligible genetic relationship between reproduction and FWEC can be assumed. Studies by Pickering *et al.* (2012) and Morris *et al.* (2010) agree with these findings in the sense that they also reported no evidence of sizable genetic correlations between FWEC and reproduction. Pickering *et al.* (2012) reported that both FWEC1 (faecal worm egg count in summer) and FWEC2 (faecal worm egg count in autumn) were not highly correlated with number of lambs born per ewe (respectively 0.03 ± 0.03 and 0.04 ± 0.03). Morris *et al.* (2010) accordingly reported a non-significant genetic correlation between FWEC and litter size. However, a small correlated genetic response to FWEC selection was observed in another study by Morris *et al.* (2000) with litter size being greater (i.e. 0.11 more lambs weaned/ewe) in the parasite-resistant line compared to the control line. In contrast, the present study failed to provide any evidence of a correlated response in FWEC to selection for reproduction, and seem to be consistent with the reported genetic correlations.

3.6 Conclusion and future direction

The present study indicated that, while FWEC was lowly heritable in the resource population studied, that selection would be aided by adequate levels of phenotypic variation. The lack of phenotypic or genetic change in the divergently selected lines suggests that the genetic correlation of number of lambs weaned per ewe mated with FWEC was likely to be negligible. This finding was supported by genetic correlations cited from the literature, albeit on a different reproduction trait namely number of lambs born. Since the experimental animals in this study were only challenged in autumn, the results thereof may not be applicable to a situation where the challenge was applied in a different season. Future work to determine the effect of season on the genetic components of internal parasite resistance in South African conditions is needed.

3.7. Literature Cited

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3.8 Annexes of Figures and Tables
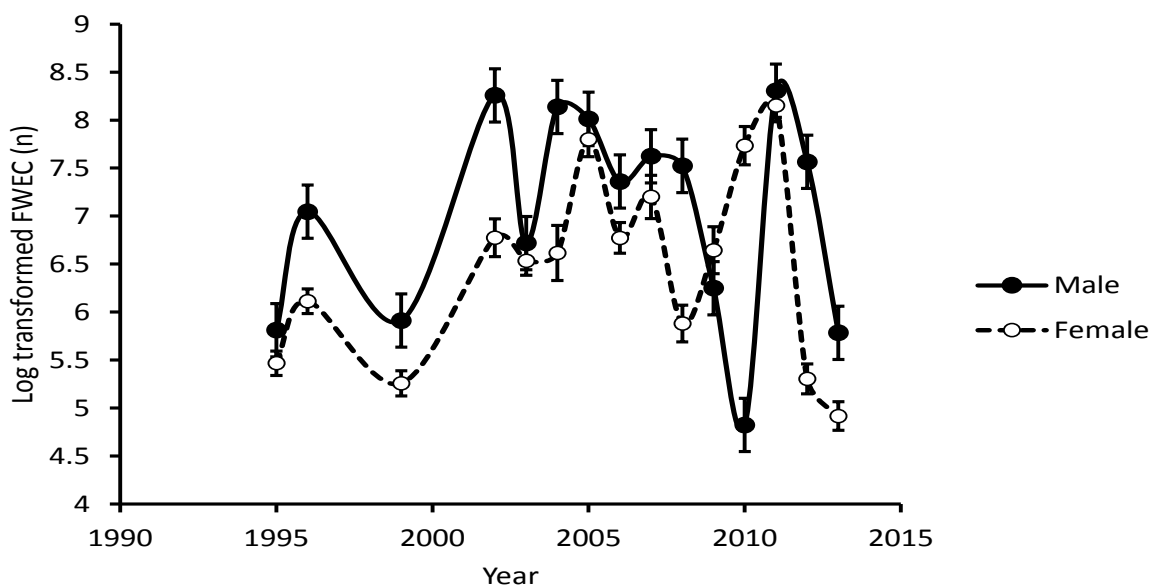
Figure 3.1 Least squate means (s.e as vetical bars about the mean) depicting the birth year *sex interaction for log-transformed FWEC
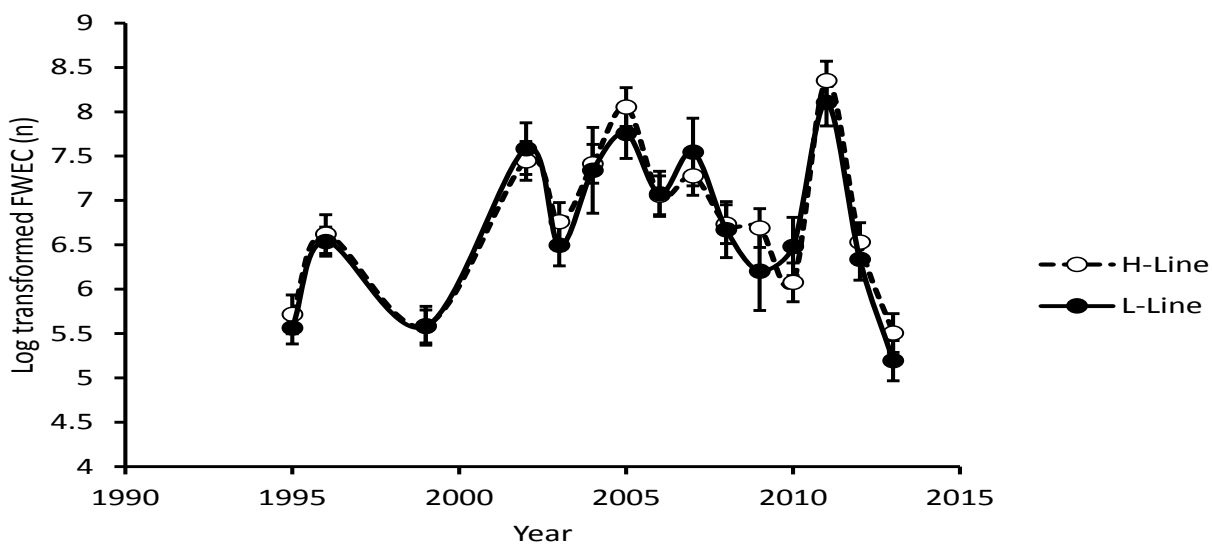
Figure 3.2 Least square means (s.e. as vertical bars about the mean) depicting the selection line x birth year interaction for log-transformed FWEC

47
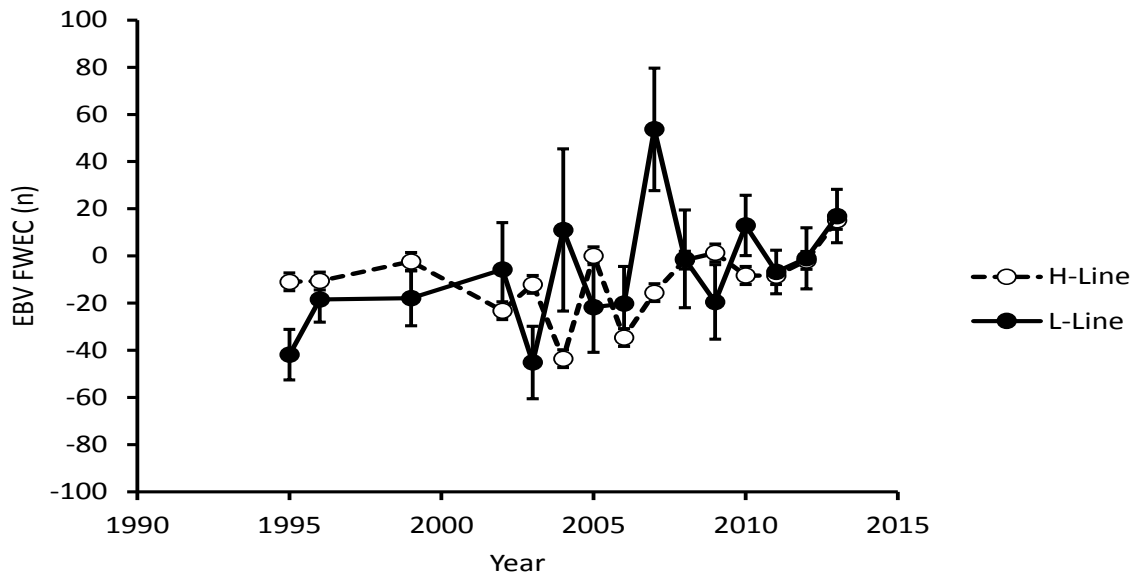
Figure 3.3 Annual means (s.e. as vertical bars about the mean) of back-transformed estimated breeding values (EBV) for faecal worm egg counts to indicate genetic change that took place during the duration of the experiment

Table 3.1 Descriptive statistics for faecal worm egg counts (FWEC) of 1869 Merino progeny before and after transformation

Trait analysed	Mean	SD	CV (%)	Range
Raw FWEC	1774	2767	148	0–27600
Cube root of FWEC	9.02	6.07	67	0–30.2
Log of FWEC	6.65	1.41	21	4.61–10.2
	Total records		Zero Counts	Percentage (%)
FWEC	1869		353	18.9

SD: Standard deviation, CV: Coefficient of Variation

Table 3.2 Least square means (±s.e.), as well as estimated back transformed values (± approximate s.e. derived from ASREML) for log transformed faecal worm egg counts (FWEC) as affected by birth year, sex, selection line, age of dam and birth type

Fixed effect and level	Number of observations	Log transformed FWEC	Geometric mean
Birth year		***	
1995	148	5.64 ± 0.11	181 ± 32
1996	169	6.58 ± 0.11	620 ± 76
1999	121	5.58 ± 0.12	166 ± 31
2002	94	7.52 ± 0.16	1737 ± 297
2003	115	6.63 ± 0.13	655 ± 101
2004	77	7.38 ± 0.25	1498 ± 409
2005	105	7.91 ± 0.16	2612 ± 428
2006	147	7.07 ± 0.14	1072 ± 168
2007	125	7.41 ± 0.20	1555 ± 336
2008	127	6.70 ± 0.17	714 ± 140
2009	100	6.45 ± 0.23	530 ± 147
2010	114	6.28 ± 0.18	433 ± 94
2011	140	8.23 ± 0.15	3646 ± 553
2012	145	6.43 ± 0.14	522 ± 84
2013	142	5.35 ± 0.13	111 ± 28
Sex		***	
Ram	888	7.01 ± 0.08	1006 ± 88
Ewe	981	6.48 ± 0.08	550 ± 52
Selection line		NS	
H Line	1569	6.79 ± 0.08	787 ± 74
L Line	300	6.70 ± 0.13	711 ± 102
Age of dam (year)		NS	
2	399	6.79 ± 0.09	785 ± 80
3	627	6.69 ± 0.08	705 ±68
4	311	6.78 ± 0.08	777 ± 80
5	248	6.78 ± 0.09	780 ± 83
6	162	6.73 ± 0.10	738 ± 87
7+	122	6.69 ± 0.11	708 ± 89
Birth type		NS	
Single	871	6.76 ± 0.08	766 ± 68
Multiple	998	6.72 ± 0.08	731 ± 67

*** $P < 0.001$, actual significant levels for $P > 0.05$, NS: Not significant

Table 3.3 Log-likelihood (LogL) values for modelsa fitting different random effects for FWEC in single-trait animal model analysis. The best model is denoted in bold

Model[a]	Raw FWEC	Cube root transformed FWEC	Log transformed FWEC
FE	-4975.18	-3566.26	-884.434
FE + σ_a^2	**-4972.00**	**-3563.26**	**-881.284**
FE + σ_a^2 + σ_c^2	-4971.34	-3561.80	-879.981
FE + σ_a^2 + σ_m^2	-4971.40	-3562.33	-880.085
FE + σ_a^2 + σ_c^2 + σ_m^2	-4971.22	-3561.72	-879.733
FE + σ_a^2 + σ_m^2 + r_{AM}	-4971.24	-3562.23	-880.084
FE + σ_a^2 + σ_c^2 + σ_m^2 + r_{AM}	-4971.09	-3561.65	-879.753

[a] FE: fixed effects only; σ_a^2: direct genetic effect; σ_m^2: dam genetic effect; σ_c^2: dam PE effect

Table 3.4 Variance components and ratios (±SE) for raw and transformed FWEC estimated from single-trait analyses

Trait analysed	σ_a^2	σ_e^2	h^2
Raw FWEC	280669	4475170	0.06 ± 0.03
Cube root of FWEC	1.462	15.489	0.09 ± 0.04
Log of FWEC	0.084	0.804	0.10 ± 0.04

σ^2_a: direct additive variance; σ^2_e: residual variance; h^2: direct, additive heritability

Table 3.5 Least squares means (±s.e.) for log-transformed FWEC of the divergently selected H and L lines and the reciprocal cross among them for the period 2003-200

Sire line	Dam line	Number of observations	Log transformed FWEC	Geometric mean
H line	H Line	622	7.13 ± 0.04	1152 ± 52
	L Line	55	7.22 ± 0.19	1262 ± 264
L line	H Line	100	7.24 ± 0.10	1301 ± 140
	L Line	74	7.21 ± 0.12	1284 ± 68

CHAPTER 4: GENETIC VARIATION IN AND RELATIONSHIP BETWEEN FAECAL WORM EGGS RECORDED IN DIFFERENT SEASONS OF THE YEAR AT THE TYGERHOEK FARM IN SOUTH AFRICA

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4.1 Abstract

Gastrointestinal nematodes result in severe economic and production losses to the sheep industry. An increase in resistance of the nematodes to chemicals used for control, as well as a demand of consumers for meat products free from chemicals, has fostered research on alternative control strategies. Breeding for resistance to gastrointestinal nematodes offers a sustainable alternative to control parasitism but its effectiveness depends on genetic variation in faecal worm egg count (**FWEC**), an indirect measure of parasite resistance. A historic dataset of FWEC from four Merino lines subjected to natural parasite challenge was used to estimate genetic parameters for FWEC in three seasons (autumn, winter and spring) using a repeated records animal model analysis, followed by a three-trait animal model analysis treating FWEC in different seasons as separate traits. The effects of selection line, birth year, sex, the sex x birth year interaction, season and the season x year interaction were significant when using 4994 records recorded from 1997-2000 respectively (P < 0.001). The heritability of log transformed FWEC amounted to 0.09 ± 0.02, with no contribution from the animal permanent environmental variance to the between animal variation across seasons. Three-trait heritability estimates for log transformed FWEC amounted to 0.07 ± 0.05 in autumn, 0.13 ± 0.05 in winter and 0.19 ± 0.05 in spring. These results suggest sufficient genetic variation in FWEC to support selection for lower log transformed FWEC. However, the best time to record data for selection is after the break of the season in winter and in spring, when sheep are stimulated by a greater intake of infective larvae from the pasture after the first rains. Genetic correlations among FWEC in the respective seasons were moderate to high, ranging from 0.55 to 0.89. Phenotypic correlations, on the other hand, were significant but lower in

magnitude, ranging from 0.09 to 0.16. These results provide useful information for developing strategies for the genetic improvement of ovine resistance to gastrointestinal nematodes under Mediterranean conditions in South Africa by using FWEC as an indicator trait.

Keywords: Gastrointestinal nematodes, heritability estimates, genetic and phenotypic correlations

4.2 Introduction

The profitability of meat and its products in sheep production relies, in part, on the efficient application of proper strategies to reduce nematode infestations under challenge conditions. At present, the major control strategy for nematodes is the use of chemical drenches to treat and prevent production and economic losses associated with infestation. However, development of parasite resistance to chemicals is common (Waller 1994; Swarnkar & Singh 2011; Rialch *et al.* 2013). In addition, consumer perception is in favour of the usage of minimum chemicals during the meat production process. These developments force sheep producers and researchers to consider alternative strategies relying less on chemicals, like an integrated pest management programme, including selection for parasite resistance to control parasitism over the long term (Karlsson & Greeff, 2006).

Genetic variation for ovine resistance to nematode infestation is well documented in the literature. Genetic variation exists among different breeds (Baker *et al.* 1999, 2002; Gruner *et al.* 2003; Nimbkar *et al.* 2003) and within breeds (Morris *et al.* 2000; Woolaston & Windon 2001) when considering different nematode species. The most commonly used criterion to indirectly measure parasite resistance is faecal worm egg count or FWEC (Karlsson & Greeff, 2006; Kemper *et al.*, 2010). Alternative approaches like applying the FAMACHA$^{©}$ set of measurements (Bath & Van Wyk 2009) may also play a role in helminth control in the summer rain areas of South Africa. However, it may not be as directly applicable to dryland conditions in the Mediterranean part of South Africa (Cloete *et al.* 2016), leaving FWEC as the main criterion available for selection against gastrointestinal helminths. Heritability estimates of FWEC reported in literature range from 0 to 0.52 (Greeff *et al.* 1995; Lôbo *et al.* 2009; Mpetile *et al.* 2015). Breeding for a reduced FWEC has been successful in Australia (Karlsson & Greeff 2006; Greeff *et al.* 1999; 2006) and New-Zealand (Morris *et al.* 2005). So far, no comparable results on response to selection for a lower FWEC have been published in South African conditions.

Environmental conditions during natural challenge are characterized by large seasonal and across-year variation in temperature and rainfall. These factors markedly affect the prevalence of parasite populations on pastures between months within years and across years (Greeff *et al.* 1995; O'Connor *et al.* 2006), thus affecting the genetic variation observed in FWEC.

Against this background, a historic dataset of FWEC from four Merino lines maintained at the Tygerhoek Research farm was utilized to identify the most appropriate time to test sheep for parasite resistance under natural challenge conditions. The objectives of this study was to determine the heritabilities and genetic and phenotypic correlations among FWEC records obtained in the different seasons.

4.3 Materials and Methods

The data used in this study came from four lines of Merino sheep that were selected for an increased clean fleece weight with a limit on fibre diameter (Cloete *et al.* 1998, 2007; Matebesi-Ranthimo *et al.* 2014), for a reduction in fibre diameter (Cloete *et al.* 2013; Matebesi-Ranthimo *et al.* 2014), for an increased reproductive efficiency using the "wet and dry" method (Cloete *et al.* 2007; Matebesi-Ranthimo *et al.* 2014), as well as an unselected control line (Cloete *et al.* 1998; 2007; 2013; Matebesi-Ranthimo *et al.* 2014). The experimental animals were maintained at the Tygerhoek research farm in the Southern Cape of South Africa. Details on these lines and selection of the experimental animals, husbandry practices, climate at the experimental site, sampling procedures and experimental design have been adequately reported in the literature cited. The animals were maintained, managed and recorded under clearance from the Departmental Ethical Committee for Research on Animals (DECRA reference number R12/76) at the Western Cape Department of Agriculture. Briefly, the progeny of all lines was maintained as a single flock within birth year cohorts, but separated by gender of each year group throughout the entire trial. The climate at the experimental site is Mediterranean, with an average annual rainfall of 425 mm, 60% of which falls during winter. The long-term mean daily temperature at the site ranges from 10.2^0C to 22.4 respectively. Animals in the study relied on dry pastures precisely the dryland Lucerne (Medicago sativa), and medic (M. truncatula). Animals were also supplemented with oat (Avena sativa) fodder crops during winter and spring as well as wheaten stubblelands in summer.

In this study there was no direct selection for parasite resistance in either line (Cloete *et al.* 2016). Faecal grab samples were obtained from individual animals after drenching was withheld for a period of at least 10 weeks in autumn, winter and spring, respectively. Faecal

grab samples were sent to Western Cape Provincial Veterinary Laboratory for analysis, using the McMaster technique with a sensitivity of 100 eggs/gram of wet faeces (Van Schalkwyk *et al.* 1994). The pathogen species commonly present under dryland conditions in the region were a mixture of Teladorsagia, Trichostronglyus and Nematodirus spp (Reinecke 1994), although traces of Haemonchus contortus might have been observed (Cloete *et al.* 2007). To reduce the variation of FWEC, the data was transformed to natural logarithms after 100 was added to account for zero counts.

The data were initially analysed for fixed effects and variance components across seasons using a single-trait repeatability model analyses in ASREML (Gilmour *et al.* 2009). To obtain the best operational model the fixed effects of selection line (as reported previously), birth year (1997-2000), birth type (multiple or single), sex (ram or ewe), age of dam (2-7+ years) and season (autumn, winter or spring) were fitted. In addition, all two-factor interactions were initially included in the model but only the birth year x sex interaction and the birth year x season interaction was statistically significant and retained in the operational model along with the other significant fixed effects for subsequent analysis. Random effects were then added to the model, giving the following models for analyses (matrix notation):

$$y = Xb + e \qquad [1]$$

$$y = Xb + Z_1 a + e \qquad [2]$$

$$y = Xb + Z_1 a + Z_2 c + e \qquad [3]$$

In these analyses, y was a vector of observations for log transformed FWEC across seasons, and b, a and c were vectors of fixed effects, direct genetic variances and animal permanent environmental (PE) variances respectively. X, Z_1 and Z_2 represented the corresponding incidence matrices relating the respective effects to y and e was the randomly distributed vector of residuals. It was assumed that:

$$V(a) = A\sigma_a^2; \; V(c) = I\sigma_c^2; \; V(e) = I\sigma_e^2$$

With A representing the numerator relationship matrix, I representing identity matrices; σ_a^2, σ_c^2, and σ_e^2 being the direct genetic, animal PE and residual variances respectively. Ratios corresponding to additive genetic and PE variances were computed from these estimates and were expressed relative to the total phenotypic variance.

The later analysis assumed equal genetic variances for log transformed FWEC across seasons, as well as unity genetic correlations among expressions of log transformed FWEC in each season. To test these assumptions, the analyses were followed by within season single-trait analyses for records obtained during autumn, winter and spring respectively. To obtain the best operational model for these analyses, the fixed effects selection line (as reported previously), birth year (1997-2000), birth type (multiple or single), sex (ram or ewe) and age of dam (2-7+ years) were fitted within seasons. In addition, all two-factor interactions were initially included in the model but only the birth year x sex interaction was retained in the operational model along with the other significant fixed effects for subsequent analyses. Random effects were then added to the operational model, resulting in the following models for analyses in matrix notation:

$$y = Xb + e \qquad [1]$$

$$y = Xb + Z_1 a + e \qquad [2]$$

$$y = Xb + Z_1 a + Z_2 c + e \qquad [3]$$

$$y = Xb + Z_1 a + Z_3 m + e \qquad [4]$$

$$[Co\,var\,iance\,(a, m) = 0]$$

$$y = Xb + Z_1 a + Z_3 m + Z_2 c + e \qquad [5]$$

$$[Co\,var\,iance\,(a, m) = A\sigma_{am}]$$

In these analyses, y was a vector of observations for log transformed FWEC within seasons, and b, a, m and c were vectors of fixed effects, direct genetic variances, maternal genetic variances and maternal PE variances respectively. X, Z_1, Z_2 and Z_3 represented the corresponding incidence matrices relating the respective effects to y and e was the randomly distributed vector of residuals. A was the numerator relationship matrix, and σ_{am} the covariance between direct and maternal additive genetic effects. It was assumed that:

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

With I representing identity matrices; σ_a^2, σ_m^2, σ_c^2, and σ_e^2 being the direct genetic, maternal genetic, maternal PE and residual variances respectively.

Ratios corresponding to additive genetic and permanent environmental variances were computed from these repeatability and single-trait within-season analyses. These variances were expressed relative to the total phenotypic variance. Likelihood Ratio tests (LRT) were used to test the contribution of each random term to improvements in the operational model for significance. The single-trait within-season analyses were followed by a three-trait analysis treating FWEC in different seasons as separate traits. This analysis also allowed the calculation of season-specific heritability estimates, as well as genetic and phenotypic correlations among FWEC expressions in different seasons. The full pedigree file, including 4650 animals born from 1989-2000 as the progeny of 357 sires and 1447 dams, were used in all analyses.

4.4 Results

The descriptive statistics of FWEC showed an extreme variation and a non-normal distribution before transformation, as shown in Table 4.1. The distribution of the data was improved by transformation to natural logs resulting in coefficients of variation (CV) that were below 20%. Only results obtained from the log transformed analysis on the repeatability model analysis will be presented. The fixed effects of selection line, birth year, sex, season, the sex x birth year interaction and the season x year interaction influenced the data significantly ($P < 0.001$). Seasonal effects of FWEC differed quite markedly across years (Figure 4.1). Log transformed FWEC means recorded in autumn declined quite markedly from 1997 to 2000; those recorded in winter were higher in 1997 and 2000 and lower in 1998 and 1999, while those recorded in spring declined from 1997 to 1998 to stabilise at the lower levels.

Log-likelihood values for the repeatability model analysis on log transformed FWEC amounted to -1932.02 for the fixed-effect operational model prior to the addition of the additive genetic effect of animal. When animal genetic effects were added to the analysis, the Log-likelihood value improved to -1904.87 ($P < 0.05$ tested as a Chi-square statistic at 1 degree of freedom). The addition of animal permanent environment as another random effect did not result in a further improvement of the Log-likelihood value, which stayed at -1904.87. Log-likelihood values for the subsequent analyses on within-season FWEC accordingly suggested a significant improvement from the model with fixed effects only to the model also including direct additive genetic variation for log-transformed FWEC ($P <0.05$; Table 4.2). However, the adding of additional random effects failed to result in further improvements to the goodness of fit of the models fitted.

Log transformed FWEC was lowly heritable in the across-season repeatability model analysis at 0.09 ± 0.02. The derived season-specific heritability estimates of log transformed FWEC were 0.07 ± 0.05 in autumn, 0.13 ± 0.04 in winter and 0.19 ± 0.05 in spring (Table 4.3). Relative to the standard errors associated with these heritability estimates, the estimate derived in spring were higher than the one derived in autumn. These results therefore suggested significant genetic variation for FWEC in winter and spring, but not in autumn. Selection for a lower FWEC can be feasible when data recorded during winter and spring are used.

Table 4.3 also presents genetic and phenotypic correlations among FWEC in different seasons of the year. The genetic correlations among FWEC records from different seasons ranged from 0.55 to 0.89, suggesting that selection for a reduced FWEC in one season would also improve FWEC in other seasons. Phenotypic correlations, on the other hand, were significant but low and ranged from 0.09 to 0.16.

4.5 Discussion

Extreme individual variation of FWEC data is commonly reported in literature, ranging from 0-50000 epg (Khusro *et al.* 2004; Snyman 2007; Cloete *et al.* 2007; Matebesi-Ranthimo *et al.* 2014; Mpetile at al. 2015). Log transformation is traditionally applied to reduce the individual variation of FWEC and to improve the properties of the data (Safari & Fogarty 2003; Cloete *et al.* 2007; Matebesi-Ranthimo *et al.* 2014; Mpetile *et al.* 2015). In a study by Safari & Fogarty (2003) about 14 of the 26 heritability estimates for FWEC were log transformed, resulting in mean values that range from 6.88–7.49 after transformation. Cloete *et al.* (2007) and Matebesi-Ranthimo *et al.* (2014) reported a highly variable, skewed and leptokurtic data for FWEC before transformation. Log transformation improved the properties of their data, resulting in coefficients of variation that were below 20%. Similar results were reported in this study. The high CV value obtained in this study indicates sufficient phenotypic variation which in turn has a potential to improve genetic gains should selection for low FWEC be desired.

The results pertaining to the birth year x sex interaction were consistent with those reported by Cloete *et al* (2007). Previous research attributed this interaction to a lack of control of the challenge on the pastures utilised by the ram and ewe hoggets which are grazing in single-sex flocks at that stage (Cloete *et al.* 2007; Matebesi-Ranthimo *et al.* 2014). A significant interaction of season x year was also observed in this study, suggesting that there is no uniform environment. It is conceivable that short-term climatic conditions hugely impacts on log transformed FWEC, resulting in these trends (Pandey *et al.* 1993; Greeff *et al.* 1995;

Pfukenyi *et al.* 2007; Kumba *et al.* 2003). Animals are routinely exposed to different climatic conditions as a result; the parasite population also fluctuates with season between years and also across years (Greeff *et al.* 1995; Cloete *et al.* 2007; Matebesi-Ranthimo *et al.* 2014). The general trend for FWEC in relation to year and season is reported in literature (Rahman 1992; Greeff *et al.* 1995; Kumba *et al.* 2003). In a study by Kumba *et al.* (2003) the least square means for FWEC were 2140 during the warm, wet season, 430 during cold, dry months and 653 during hot, dry months in goats on communal farms of Namibia. Another study by Rahman (1992) also in goats has reported a higher FWEC in the wet season, a moderate FWEC in the hot season and lowest values of FWEC in the cold, dry season. Therefore, when planning a breeding program for parasite resistance, seasonal variation of FWEC should be considered.

The across-season heritability derived for this study from the repeatability model was low at 0.09. However, the three-trait analysis suggested that the magnitude of the genetic variance component for log transformed FWEC was increased by 87% from 0.046 in autumn to 0.086 in winter. The genetic variance component of log transformed FWEC in spring was increased by an order of magnitude exceeding 3.5 in comparison to FWEC in autumn. Phenotypic variance components were not affected to the same extent, ranging from 0.64 to 0.88 (Table 4.3). These results seem to suggest that the expression of genes associated with log transformed FWEC in different seasons differed quite appreciably. The heritability of the natural logarithm of FWEC accordingly amounted 0.07 in autumn, but it improved appreciably to 0.13 in winter and further to 0.19 in spring. The increase in heritability estimates for FWEC in winter and spring coincided with the growth of pastures after the first rains in the Mediterranean environment and the hatching of parasite eggs during the wet season. The better nutritional conditions during this time of the year seem to have improved the ability of resistant hosts to mount an immune response at the genetic level which in turn affected the expression of parasite resistance, leading to improved heritability estimates. Studies by Nieuwoudt *et al.* (2002), Cloete *et al.* (2007) and Matebesi-Ranthimo *et al.* (2014) conducted in South Africa from the data that was collected in spring reported moderate to high heritability estimates (0.14 to 0.24) for FWEC of Merino sheep under natural challenge. These results suggest genetic variation in FWEC and that selection for low FWEC would result in future generation gains. In chapter 3, using data that was collected in autumn from the Elsenburg Merino flock under natural challenge in South African conditions, reported lower but still significant heritability estimates of 0.10 for FWEC, suggesting that genes for parasite resistance are not well expressed in autumn. Therefore, should selection for low FWEC be

58

desired, the animals must be assessed sometime after the break of season in winter and in spring under Mediterranean conditions, when temperature and rainfall are favourable for the development, survival and migration of infective larvae onto pastures (O'Connor *et al.* 2006). Our results accord with those obtained by Greeff *et al.* (1995) when estimating the genetic variation of FWEC in Merino lambs in different seasons under Mediterranean conditions in Western Australia. Relative to standard errors associated with heritability estimates, the estimates derived in their study were low in autumn (h^2 = 0.00 to 0.03), moderate during winter to late spring (h^2 = 0.21 to 0.25), and reached a high of 0.51 during mid-winter. However, the current study, along with studies by Greeff *et al.* (1995) on Merino lambs; Rahman (1992), Rinaldi *et al.* (2009) and Kumba *et al.* (2003) on goats reported a significant effect of season on FWEC, suggesting that seasonal variation of FWEC should also be considered when planning breeding programs for an improved parasite resistance.

Overall, the heritability estimates of FWEC in our study under South African conditions, although moderate, were somewhat lower than the mean value of 0.27 that was derived from 16 literature sources documented in a major review article by Safari *et al.* (2005). In a study by Greeff & Karlsson (1997), heritability estimates for FWEC were 0.40 for Merino weaners and 0.22 for hoggets under natural challenge. Similar results were conveyed by Yadav *et al.* (2006) and Morris *et al.* (2005) with h^2 estimates for FWEC of 0.24 in Muzaffarnagari sheep and 0.22 in 22-week-old Perendale sheep, respectively. Comparable results were produced by Clarke (2002), in Merino sheep with heritability estimates ranging from 0.18-0.40 for weaners, 0.17-0.34 during the post weaning period and 0.15-0.40 in yearlings. Another study by Brown *et al.* (2010) on Merino sheep yielded heritability estimates for FWEC ranging from 0.29-0.38 for yearlings and from 0.29-0.41 for hoggets depending on the model used. A different study in New-Zealand reported the heritability of FWEC as 0.37 in naturally challenged Romney sheep (Baker *et al.* 1991). Hence, it is not surprising that selection for low FWEC has resulted in marked genetic gains in New Zealand and Australia (Woolaston & Piper 1996; Greeff *et al.* 1999; Morris *et al.* 2005; Karlsson & Greeff 2006). Similar results can also be expected in South Africa if proper data collection measures, as well as the best sampling period for FWEC are duly noted and effectively applied.

The lower magnitude of heritability estimates for FWEC obtained in our study could be attributed to a greater variation of FWEC between months within seasons, between seasons within years and also across countries (Greeff *et al.* 1995). Moreover, the lower magnitude of

our heritability estimates for FWEC could be due to the fact that our study used an accuracy of 100 epg wet faeces compared to more accurate counts in other studies (Notter 2003). The latter author reported heritability estimates of 0.42, 0.22 and 0.25 at 3, 4 and 5 weeks after artificial challenge with Haemonchus contortus larvae in sheep. FWEC were counted with a sensitivity of 50 epg wet faeces in their study.

Genetic correlations among log transformed FWEC in different seasons were moderate to high and positive. Log transformed FWEC thus seems to be governed by mostly the same genes, irrespective of the season. Although genetic correlations among log transformed were not significantly different from each other as indicated by standard errors, it is notable that the genetic correlation between FWEC in autumn and in spring was only slightly above 0.50. The large standard error accompanying this correlation is possibly due to a smaller additive variance component derived in autumn. High positive correlations of FWEC in autumn and winter and winter and spring observed in this study seem to suggest that individual free-ranging animals susceptible to nematode infestation in one season will also be at risk in other seasons. Animals that consume higher volumes of the infected pastures are likely to host greater parasite loads (Zajac 2006). A study by Rinaldi *et al.* (2009) in goats reported a positive relationship between worm burden and parasite load, suggesting that an increase in worm burden would also increase FWEC. Similar results were obtained for goats by Cringoli *et al.* (2008) where FWEC and worm burdens were positively correlated with each other. Although the latter studies were conducted in goats, their results could be extended to sheep since small ruminants share many of the same parasite genera and species. Moreover, a strong relationship between FWEC and parasite load supports the use of FWEC to indirectly measure parasite prevalence as well as the level of infestation (Eysker & Ploeger 2000).

Finally, it is relevant to consider whether FWEC and other traits involving host resistance should form part of formal sheep recording in South Africa. Cloete *et al.* (2014) suggested that disease resistance traits should be considered for inclusion in this recording scheme, as is the case in Australia (Khusro *et al.* 2004; Brown *et al.* 2010; 2015) and New Zealand (Pickering *et al.* 2012). Cloete *et al.* (2014) argued that hard-to-measure traits like disease resistance should be targeted for genomic selection procedures in the national sheep flock. Clues as to how to achieve this could be taken from Australia and New Zealand where such initiatives are already in place (Swan *et al.* 2014; Pickering *et al.* 2015).

4.6 Conclusion

Genetic variation for FWEC exists. Selection for low parasite load is likely to pay dividends in South Africa, as in overseas countries. However, this study suggested that the best time to challenge sheep for deriving breeding values to assist with selection for parasite resistance is some time after the break of season in winter and/or spring, when greater numbers of infective larvae after the first rains provide an adequate natural challenge under Mediterranean conditions. This study has an implication for the timing of data collection to allow breeding for parasite resistance under South African Mediterranean conditions.

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61

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*4.8 Annexes of Figures and Tables
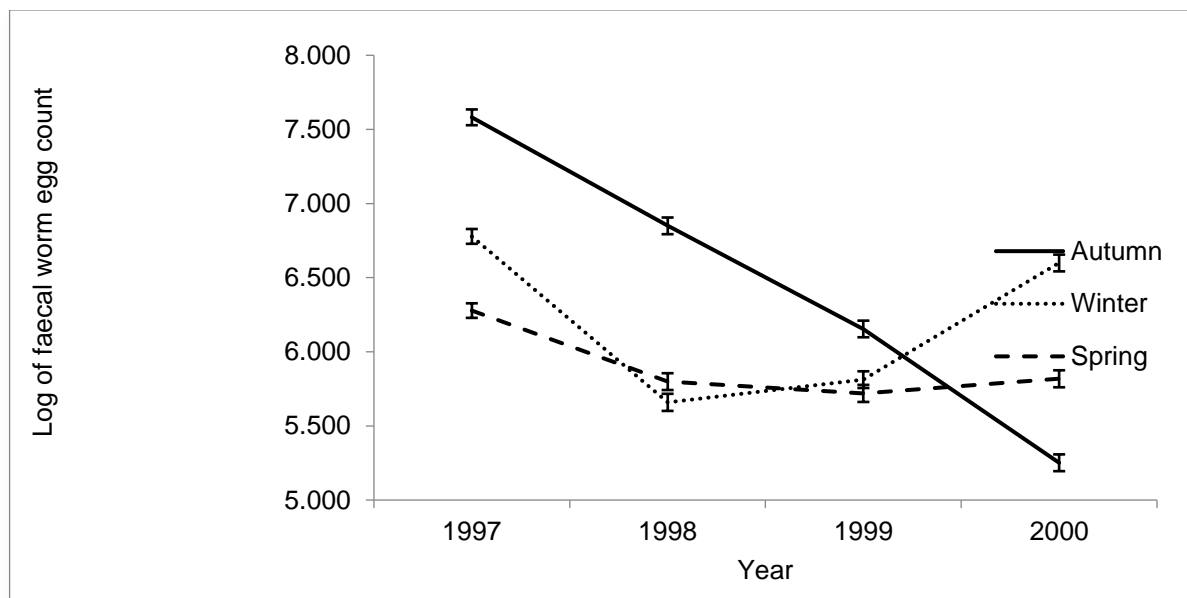
Figure 4.1 Least-squares means depicting the interaction of year by season for the natural log of FWEC in the study population

Table 4.1 Descriptive statistics for faecal worm egg counts (FWEC) of Merino sheep before and after transformation

Trait	Mean ± SD	Range	CV %	Skewness	Kutorsis
FWEC 1	891 ± 1570	0 – 37200	177.3	8.81	165.37
FWEC 2	524 ± 1001	0 – 14900	191. 10	5. 17	46. 44
FWEC 3	665 ± 920	0 – 14300	138. 40	3. 77	33. 32
LFWEC1	6.17 ± 1.12	4.55 -10.53	19.78	0.18	-1.00
LFWEC2	5.72 ± 1.12	4.61 – 9.62	19.6	0.61	-0.62
LFWEC3	6.04 ± 1.12	4.61-9.57	18. 62	0. 14	-1. 17
	Total records	Zero Counts		Percentage (%)	
FWEC 1	1658	309		18.6	
FWEC 2	1678	337		20.1	
FWEC 3	1659	540		32.5	

FWEC1 – untransformed faecal worm egg count in autumn, FWEC2 – untransformed faecal worm egg count in winter, FWEC3 – untransformed faecal worm egg count in spring; LFWEC1 - log transformed faecal worm egg count in autumn, LFWEC2 – log transformed faecal worm egg count in winter, LFWEC3 – log transformed faecal worm egg count in spring

Table 4.2 Log likelihood ratios for random effects model fitted to FWEC data of Tygerhoek Merino resource flock with "best" model in bold

Model	FWEC1	FWEC2	FWEC3
Fixed	**-500.908**	-556.152	-757.517
Fixed +h2	-500. 908	**-547.427**	**-750.294**
Fixed +h2 + m2	-499.296	-547.427	-750.294
Fixed +h2 + c2	-499.876	-547.07	-750.294
Fixed +h2 + m2 + c2	-499.296	-547.07	-750.294

FWEC1- faecal worm egg count in autumn, FWEC2- faecal worm egg count in winter,

FWEC3- faecal worm egg count in spring

Table 4.3 Variance components and ratios (±SE) for log transformed faecal worm egg counts (FWEC) estimated from the three-trait analysis with genetic (below diagonal) and phenotypic correlations (above diagonal) between expressions of FWEC in different seasons

Trait Analysed	LFWEC1	LFWEC 2	LFWEC 3
Variance components*			
σ^2a	0.046	0.086	0.166
σp^2	0.639	0.674	0.88
(Co)variance ratios (h^2 on the diagonal in bold italics)			
LFWEC1	**0.07 ± 0.05**	0.12 ± 0.02	0.09 ± 0.03
LFWEC2	0.89 ± 0.34	**0.13 ± 0.04**	0.16 ± 0.03
LFWEC3	0.55 ± 0.30	0.78 ± 0.18	**0.19 ± 0.05**

*σ^2_a: direct additive variance; σ_p^2: phenotypic variance, h^2: direct, additive heritability; LFWEC1: log transformed faecal worm egg count in autumn; LFWEC2: log transformed faecal worm egg count in winter; LFWEC3: log transformed faecal worm egg count in spring.

CHAPTER 5: GENETIC PARAMETERS FOR FAECAL WORM EGG COUNT AND SUBJECTIVE AND OBJECTIVE WOOL AND BODY TRAITS IN ELSENBURG MERINO SHEEP

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5.1 Abstract

Gastrointestinal nematodes adversely affect the welfare and health of domestic ruminants world-wide. Faecal worm egg count (**FWEC**) is traditionally used as indicator to measure parasite resistance. The objective of this study was to estimate genetic and phenotypic parameters for FWEC and 17 traits recorded in Elsenburg Merino flock, covering live-weights, wool traits, subjective traits and testis dimensions. The heritability estimates for log transformed FWEC were low but significant at 0.09 ± 0.04, suggesting that genetic progress is likely to be slow. Direct heritability estimates for production traits were moderate to high, ranging from 0.17 ± 0.03 for birth weight (**BW**) to 0.60 ± 0.03 for clean yield. Maternal additive effects ranged from 0.03 ± 0.01 for total fold score to 0.21 ± 0.04 for BW and dam permanent environmental effects ranged from 0.03 ± 0.01 for standard deviation of fibre diameter to 0.11 ± 0.03 for BW. Genetic correlations of FWEC with the other traits were not significant, ranging from -0.24 ± 0.18 with crimps per 25 mm to 0.30 ± 0.23 for weaning weight. These results suggested that selection for parasite resistance is unlikely to compromise genetic progress in these production and conformation traits.

Keywords: Gastrointestinal nematodes, faecal worm egg counts, genetic evaluation, live weight testis dimensions

5.2 Introduction

Anthelmintic resistance by nematodes and a growing concern of consumers to the chemicals used in meat production calls for a more sustainable solution to control parasitism in small ruminants (Waller, 2006; Besier, 2007). As a result, genetic improvement of the host resistance to nematodes has been seen as an alternative measure to control parasitism (Karlsson & Greeff, 2006; Greeff *et al.*, 2006) as part of an integrated programme.

Faecal worm egg count (**FWEC**) measurements are widely used to estimate parasite resistance (Karlsson & Greeff, 2006; Kemper *et al.*, 2010). It is genetically variable trait, derived heritability estimates ranging from 0 - 0.52% (Greeff *et al.*, 1995; Clarke, 2002). Breeding for reduced FWEC has been successful in Australia (Woolaston & Piper, 1996; Karlsson & Greeff, 2006; Greeff *et al.*, 1999, 2006) and New-Zealand (Morris *et al.*, 2005). So far, no comparable results on responses to selection for a low FWEC have been published in South African conditions. Although that is the case, South African scientists have advocated the inclusion of health traits in breeding program to promote the economic gains in livestock production (Cloete *et al.*, 2007; Matebesi-Ranthimo *et al.*, 2014a; Cloete *et al.*, 2016). This suggestion was based on low to moderate levels of genetic variation in local flocks linked to adequate levels of phenotypic variiation.

The role of sheep breeders is to make profit from wool and meat production. Several live weight and wool traits have thus been identified as economically important. It is important to ascertain how the inclusion of a health trait like FWEC would impact on these traits by studying genetic correlations of FWEC by these traits. Genetic correlations of FWEC with wool and live weight traits in South Africa is limited to the studies of Matebesi-Ranthimo *et al.* (2014 a, 2014 b) on the Tygerhoek Merino flock.

The objectives of this paper were therefore to estimate the heritabilities, as well as genetic and phenotypic correlations of FWEC with live-weight traits, wool traits, subjective traits and testis dimensions in South African Merinos of the Elsenburg flock.

5.3 Materials and methods

Since 1986, a population of Merino sheep was divergently selected for reproductive performance (the high (**H**) and low (**L**) line). Details on the establishment of lines can be found in papers by Cloete *et al.* (2004, 2009) as well as in preceding chapters. The flock is at present housed at Elsenburg Research Farm, which is located in the Boland region, about 10 km north of Stellenbosch in Western Cape Province of South Africa, at an elevation of about 177 m above the sea level with coordinates of 33° 51' S, 18° 3D' E. The climate in this region is Mediterranean with an average rainfall of 605 mm which mostly falls from April to September. The animals belonging to both lines were maintained in the same flock from birth but progeny were grazed in separate flocks based on sex from approximately 2 months post weaning. Both groups were subjected to similar management practices and were kept on dryland

pastures consisting of lucerne (*Medicago sativa*) and oat (*Avena sativa*) fodder crops. Irrigated lucerne and kikuyu (*Pennisetum clandestinum*) paddocks were also strategically available.

A dataset ranging from 1766 records for staple strength to 4311 records for birth weight (BW) was available to correlate FWEC with 17 traits of economic importance recorded between 1986 and 2014 in the flock described above. Animals were not directly selected for low FWEC in either line as confirmed by estimated breeding values for FWEC reported by Mpetile *et al.* (2015). All animals were naturally challenged with nematodes for a period of 6-10 weeks in autumn as described by the latter authors. At this stage sheep were likely to be infected with a mixture of *Trychostronglyus spp*, *Osterstagia* spp and *Haemonchus contortus*. After the challenge, faecal sample grabs were collected directly from the rectum of individual sheep and were sent to Stellenbosch Provincial Veterinary Laboratory for analysis. The faecal samples were calculated using the McMaster technique, with a sensitivity of 100 eggs per gram of wet faeces (Van Schalkwyk *et al.*, 1994).

The traits included in the analyses were faecal worm egg count (**FWEC**), birth weight (**BW**), weaning weight (**WW**), post weaning weight (**PWW**), Greasy fleece weight (**GFW**), clean yield (**CY**), clean fleece weight (**CFW**), staple length (**SL**), staple strength (**SS**), fibre diameter (**FD**), Standard deviation of fibre diameter (**SDFD**), Coefficient of variation of fibre diameter (**CVFD**), Crimps per 25 mm (**CPI**), Comfort factor (**CF**), birth coat score (**BCS**), total fold score (**TFS**), scrotal circumference (**SC**) and testis diameter (**TD**). In order to normalize and improve the distribution of the data, FWEC was transformed to natural logarithms (after a base number of 100 was added to each value to account for zero counts). Covariance components were derived from single- and two-trait analyses using ASREML software (Gilmour *et al.*, 2015). However, before the analysis, a thorough observation of the data structure was done in order to identify and eliminate any abnormalities that may be present. All animals with a missing record for a particular trait of interest were not included in the analysis for that particular trait. Initially, the analysis involved fitting various combinations of fixed effects to obtain an operational model. Fixed effects fitted in these analyses included the selection line (H or L), birth year (1986 - 2014, depending on trait), sex (ram or ewe), age of dam (2-7+ years) and birth type (singles or pooled multiples). All two-factor interactions were considered, but only those attaining significance (P < 0.05) were retained in the final model. The birth year x sex and selection line x birth year interaction were significant on occasion and retained in the

operational model. Random effects were successively added to the model, resulting in the following models for analyses (in matrix notation):

$$y = Xb + e \qquad [1]$$

$$y = Xb + Z_1a + e \qquad [2]$$

$$y = Xb + Z_1a + Z_2c + e \qquad [3]$$

$$y = Xb + Z_1a + Z_3m + e \qquad [4]$$

$$[Co\,var\,iance\,(a,m) = 0]$$

$$y = Xb + Z_1a + Z_2m + e \qquad [5]$$

$$[Co\,var\,iance\,(a,m) = A\sigma_{am}]$$

$$y = Xb + Z_1a + Z_3m + Z_2c + e \qquad [6]$$

$$[Co\,var\,iance\,(a,m) = 0]$$

$$y = Xb + Z_1a + Z_3m + Z_2c + e \qquad [7]$$

$$[Co\,var\,iance\,(a,m) = A\sigma_{am}]$$

Where y was a vector of observations for FWEC; and b, a, m and c were vectors for fixed effects, direct additive variances, maternal/dam additive variances and dam permanent environmental variances; and e denoted the randomly distributed residual error. X, Z_1, Z_2 and Z_3 are denoted as the corresponding incidence matrices relating the fixed and random effects. A denoted the numerator relationship matrix and σ_{am} the covariance between direct and maternal additive genetic effects.

It was assumed that:

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

Where I represented an identity matrix; σ_a^2, σ_m^2, σ_c^2, and σ_e^2 were the variance components that indicating the direct genetic, maternal genetic, maternal permanent environmental (PE) and residual (error) variances, respectively. The phenotypic variance was derived as the total of all the estimated variance components. The heritability estimates were calculated by dividing the additive genetic variance by the phenotypic variance, the maternal heritability as the maternal additive variance divided by the phenotypic variance and the maternal PE effect was derived as a ratio of the phenotypic variance.

Likelihood Ratio tests (LRT) were used to test the significance of random effects. A random effect was considered significant when its inclusion in the model improved the log likelihood ratio, and the Chi^2 distribution was used as a test statistic. The best model (with higher value for LRT) was then used in the subsequent analysis. Genetic, environmental and phenotypic correlations of FWEC with wool, live weight, subjective and testis dimension traits were estimated by fitting a two-trait model incorporating FWEC and the other trait. The initial values for co-variance components of in two-trait models were obtained from the single-trait analyses that were fitted initially.

5.4 Results

Table 5.1 shows the descriptive statistics for live weights, wool traits, subjectively assessed traits, testis dimensions and FWEC. Means and standard deviations for the traits reported ranged from 2.89 ± 1.69 for clean fleece weight to 98.9 ± 18.0 for comfort factor.Transforming faecal worm egg count data normalised the data, rendering it suitable for statistical analyses; only the results from the log transformed data will thus be presented. The fixed effects of sex, birth year and the sex x birth year interaction were significant for FWEC (P < 0.01), Table 5.2. In addition to the aforementioned fixed effects for FWEC, the effects of selection line, the selection line x birth year interaction, dam age and the selection line x dam age were significant (P < 0.05) for some wool and live weight traits and were therefore retained in the model for subsequent analyses.

The log likelihood ratio test has shown the model with direct additive genetic variation for log transformed FWEC to fit the data best in the present study (Table 5.3). However, different random effects models were best for some wool and live weight traits. The direct additive genetic variation as a single random effect fitted the data best for CY, SL, SS, CVFD, CPI, BCS, SC and TD. Random direct additive and maternal genetic effects fitted the data best for CFW, CFW and TFS. The analysis on PWW additionally included the direct-maternal covariance. Direct genetic and maternal PE effects were chosen for the analyses on FD, SDFD and CF. Analyses on BW and WW included direct additive, maternal genetic and maternal PE effects.

The direct single-trait heritability for log transformed FWEC were low but significant at 0.09 ± 0.04 (Table 5.4). Other traits of economic importance showed moderate to high heritability estimates (from h^2 = 0.17 ± 0.03 for BW to 0.60 ± 0.03 for CY) suggesting that genetic improvement can be achieved. Maternal additive effects ranged from 0.03 ± 0.01 for TFS to

0.21 ± 0.04 for BW and dam PE effects from 0.03 ± 0.01 for SDFD to 0.11 ± 0.03 for BW. Table 5.5 shows genetic and phenotypic correlations of FWEC with traits of economic importance. Genetic correlations of FWEC with the other traits were not significant, ranging from -0.24 ± 0.18 with CPI to 0.30 ± 0.23 for WW. Genetic correlations with FWEC equal to or exceeding an absolute value of 0.10 were observed for CY (0.10), SL (27), SS (-19), CPI (-0.24), BCS (0.14) and TD (-0.18). However, most genetic correlations did not reach significance, as evidenced by standard errors larger than half the corresponding estimate.

5.5 Discussion

5.5.1 Descriptive statistics

Individual FWEC records were highly variable, ranging from 0 - 31500 and not normally distributed. Data could be normalised by transforming data points to natural logarithms after 100 was added. This transformation is commonly applied to normalise data in studies of this nature (Cloete *et al.*, 2016; Snyman, 2007). Previous chapters (3 and 4) and studies by Cloete *et al.* (2016) and Snyman (2007) reported ranges for FWEC from 0 – 27600, 0 – 37200, 0 - 34100 and 0 - 87800, respectively. However, after transformation the reported means (±SD) were respectively 6.15 ± 1.15, 6.17 ± 1.17, 6.87 ± 1.24 and 6.65 ± 1.47. The means reported in this study were similar to those reported by Matebesi-Ranthimo *et al.* (2014 a) for the Tygerhoek Merino flock. The mean estimates reported for live weight traits, wool traits, subjective traits and testicular dimensions traits were within the reported literature values (Groenewald *et al.*, 1999; Duguma *et al.*, 2002; Cloete *et al.*, 2003 a, b; 2004; Olivier, 2014; Matebesi-Ranthimo *et al.*, 2014a).

5.5.2 Fixed effects

Selection line (H and L) affected live weight traits, some wool traits, subjective traits as well as testis dimensions. These results are consistent with those reported in the literature (Cloete *et al.*, 2004; Matebesi-Ranthimo *et al.*, 2017). The effect of birth year was significant for all the traits recorded in this study. The significant effect of birth year on traits of economic importance may be related to differences in feed quality and availability caused by different climatic conditions experienced throughout the years in some cases augmented by management decisions. Significant effects of year has previously been reported by several authors on live weight traits (Duguma *et al.*, 2002), on wool traits (Matebesi-Ranthimo *et al.*, 2014a), on subjective traits (Matebesi-Ranthimo *et al.*, 2014a) on testis dimensions (Duguma *et al.*, 2002) and on FWEC (Mpetile *et al.*, 2015, 2017).

The fixed effect of sex in the present study was significant for live weight, wool and subjectively assessed traits. Similar results were reported in various literature studies (Cloete *et al.*, 2007, 2009; Safari *et al.*, 2007 a, b; Zishiri *et al.*, 2014). In the latter study, the mean birth weights of male lambs were higher than those of females in all three breeds of sheep studied. Moreover, single born lambs were heavier than multiples (Zishiri *et al.*, 2014). In chapter 3 and 4, there was a generally higher parasite load in males compared to females overall. This could be due to different feeding behaviour as well as an indication that the sexes were not exposed to a uniform environment (males grazed in different paddocks and may have been subjected to a different parasite challenge).

The present study showed a significant influence of dam age on live weight traits, subjective scores; testis dimensions traits and some wool traits. The significant effect of dam age on birth weight were commonly reported in literature (Cloete *et al.*, 2002 a; Notter *et al.*, 2005); with mature ewes giving birth to heavier lambs compared to the younger ewes (Zishiri *et al.*, 2014). Such differences between ewes of different age groups may result from differences in uterine environment. Moreover, younger ewes may still be growing themselves and there may thus be competition for nutrients between the need for dam growth and the need for the development of the foetus. Older ewes on the other hand are well developed. There is no competition for nutrients needed for their own growth and the development of the foetus. With this said, this could explain the variation in BW of newborn lambs between younger and mature ewes. Zishiri *et al.* (2014) also observed differences in weaning weight and post weaning weight between lambs from younger ewes and older ewes. In their study, the 2- and 3-year-old ewes had lambs which were lighter than the lambs from 5-year-old ewes. This difference could be explained by differences in maternal experience between young and older ewes. Younger ewes are likely to have little experience in taking care of the lambs i.e. nursing/feeding the lambs which may ultimately affect the weaning weight of lambs. These weight differences are likely to be carried over to post-weaning weights.

Sex by year interactions commonly impacted on a range of live weight and wool traits as well as FWEC (Cloete *et al.*, 2007; Mpetile *et al.*, 2015, 2017; Matebesi-Ranthimo *et al.*, 2014 a, 2017). Selection line by year interactions were significantly different for all the traits measured in this study except for SDFD, CVFD and FWEC. These interactions were likely to have been caused by genetic change associated with the selection regime practiced (Cloete *et al.*, 2003, 2005, 2013).

75

5.5.3 Random effects

Genetic parameters are of vital importance in the application of breeding programs and evaluation of genetic progress so the accuracy of their prediction should be taken into consideration. According to Van Wyk *et al.* (2003) and Satoh *et al.* (2002) the inclusion of appropriate random effects in the model eliminates bias and increases the accuracy of prediction of breeding values. LRT tests for FWEC indicated that a model only fitting direct, additive effects provided the best fit, as was reported by Matebesi-Ranthimo *et al.* (2014 a) and in chapter 3 and 4. Direct and maternal genetic effects are commonly reported for CFW, while direct genetic effects are generally more important for other wool traits (Olivier *et al.*, 1994; Cloete *et al.*, 1998; Cloete et al., 2002b). In a study by Zishiri *et al.* (2014) the most appropriate model for fitting all live weight traits included direct additive, maternal additive, maternal PE and the direct-maternal genetic correlation for Dormer and Ile de France sheep. However, in Merino Landsheep, the best model was direct additive effects for BW, maternal additive, maternal PE and the direct-maternal genetic correlation for WW. It is important to note that in the latter breed (Merino Landsheep) Zishiri *et al.* (2014) found it difficult to partition the additive maternal and dam permanent environmental effects possibly due to inadequate genetic ties because of the structure of data across years (Zishiri, 2009; Zishiri *et al.*, 2014).

The best model for most wool traits (CY, SL, SS, CVFD and CPI) in the present study was for only direct additive genetic effects. Similar results for CY, SL, SS, and CVFD were obtained by Matebesi-Ranthimo *et al.* (2014 a) and Khusro *et al.* (2004). Therefore, to eliminate bias and improve the accuracy of the estimates, all the random effects must be included in the analysis and retained in the model if they are significant. Failure to do so could overestimate the breeding values.

5.5.4 Heritability estimates

Weight traits. It is important to note that genetic parameters may differ according to breed and statistical modelling across studies. Therefore, breed differences and models used should be considered when comparing studies of this nature. The direct heritability for BW (0.17 ± 0.03) in the present study were consistent with the results obtained by Cloete *et al.* (2001) in Merinos (0.18) and Borg *et al.* (2009) in Targhee sheep (0.19). Lower direct heritability estimates were obtained in the weighted mean of 0.13 from four estimates in wool breeds reviewed by Fogarty (1995) (0.13), 0.12 in a study by Cloete *et al.* (2003 a) on Merinos and 0.11 in a study on Dorpers (Neser *et al.*, 2001). Safari *et al.* (2005) and Zishiri *et al.* (2014) on

the other hand reported higher direct heritability estimates (0.21 and 0.23) for BW in wool breeds. However, all studies indicated that BW could be changed by genetic selection.

The results pertaining to direct heritability for WW in the present study (0.19 ± 0.04) were moderate and in agreement with a value of 0.19 obtained by Assan *et al.* (2002) in Dorpers but higher than the value of 0.13 reported for Merinos (Cloete *et al.*, 2003 a). Other studies by Fogarty (1995), Cloete *et al.* (2001), Safari *et al.* (2005) and Zishiri *et al.* (2014) reported higher heritability estimates for WW in wool breeds, ranging from 0.23 to 0.33. These results clearly indicated that WW can be improved through selection.

PWW was highly heritable at 0.31 ± 0.05, a value which is consistent with the weighted mean of 0.33 derived from 18 estimates in wool breeds (Safari *et al.*, 2005). The present heritability estimate, on the other hand, was higher than the range of 0.21 to 0.28 reported for PWW in meat and dual-purpose breeds (Fogarty, 1995; Safari *et al.*, 2005). Genetic factors like mothering ability and non-genetic factors like the availability of quality and quantity of feed, ambient climate, changes in husbandry and management could all have an influence on PWW. Differences in heritability estimates for this trait could be attributed to effects such as these.

Maternal genetic effects obtained in this study were high for BW at 0.21 ± 0.04, followed by a reduction to 0.09 ± 0.03 at weaning and a further reduction to 0.06 ± 0.02 at the post weaning stage. The importance of maternal effects at birth emphasises the important role of maternal traits like the uterine environment provided by the dam for the development of lamb. However, the direct genetic effect of the dam is reduced at the weaning and post weaning stages. In a study by Snyman *et al.* (1995) in Afrinos the maternal genetic effects were high for BW at 0.17; they decreased to 0.09 at weaning and reduced to 0.06 at 18 months. Literature shows evidence of diminishing maternal genetic effects on live weight over time as the animal ages. Assan *et al.* (2002) accordingly reported a direct heritability of 0.24 for BW which was reduced to 0.09 at weaning. Similarly, Hanford *et al.* (2003) reported maternal heritability estimates for BW to be twice as large as that of WW, i.e. 0.20 vs 0.11. In a study by Brown *et al.* (2016) the maternal effects for WW and PWW were low at respectively 0.06 and 0.05. The diminishing maternal effects in wool breeds amounted to 0.21 for BW, 0.16 for WW and 0.10 for PWW (Safari *et al.*, 2005). Corresponding maternal heritability estimates were 0.18, 0.10 and 0.04 in dual-purpose breeds and 0.24, 0.10 and 0.08 in meat breed (Safari *et al.*, 2005). Estimates from studies by Neser *et al.* (2000) in the Dorper and Zishiri *et al.* (2014) in three terminal

sheep breeds did not follow the usual trend that is often reported in literature for maternal heritability estimates of live weight traits. Neser *et al*. (2000), reported maternal heritability estimates of 0.09 for BW, 0.10 for 42-day weight and 0.095 for 100-day weight, respectively. Zishiri *et al*. (2014), on the other hand, reported estimates of 0.05 for BW, 0.07 for WW and 0.17 post weaning weight (PWW) in Dormer sheep. Corresponding results were respectively 0.10, 0.25 and 0.02 for the lle de France breed. For the Merino Landsheep breed, maternal effects could not be estimated for BW and WW. However, PWW had a maternal estimate of 0.07 (Zishiri *et al*., 2014). Other literature estimates for maternal heritability of PWW were slightly higher than the values presented here (0.07 to 0.12 vs 0.06) (Swan & Hickson, 1994; Wuliji *et al*., 2001; Safari *et al*., 2007a, 2007b). Lower estimates for maternal effects as the animal ages suggest that maternal effects diminished as the lambs grew older.

The results pertaining to the dam permanent environmental effects obtained in this study were moderate for both BW (0.11± 0.03) and weaning weight (0.10 ± 0.02). These results were consistent with a value of 0.10 reported by Safari *et al*. (2005) for BW based on the weighted means of six estimates from wool breeds. Similar results were reported by Neser *et al*. (2000) in Dorper sheep with maternal PE amounting to 0.12 for BW, 0.11 for 42-day weight and 0.08 for 100-day weight. The results obtained in this study are in line with those reported by Snyman *et al*. (1995) for BW (0.12) and slightly higher than those reported by Safari *et al*. (2005) and Mousa *et al*. (1999) (0.09). Variance ratios for dam PE effects were low for WW (0.06 and 0.07) both in wool and dual-purpose breeds (Safari *et al*., 2005).

The literature is undecided with reference to the genetic correlation between direct and maternal additive effects (Neser *et al*., 2001; Safari *et al*., 2005). In the review by Safari *et al*. (2005), the reported r_{AM} estimates for live weight traits in wool breeds were mostly negative with the exception of PWW (0.18). A higher estimate of the direct-maternal correlation was found for PWW in the present study (0.46 ± 0.21). A positive genetic correlation between direct and maternal effects could pose the opportunity to simultaneously improve both direct and maternal breeding values for the trait under consideration.

Wool traits. All the wool traits considered in this study were moderately to highly heritable, estimates ranging from 0.18 ± 0.03 for CPI to 0.60 ± 0.03 for CY, suggesting that all the wool traits would potentially benefit from selection. The direct heritability estimates were high at 0.39 ± 0.04 for GFW and 0.35 ± 0.04 for CFW and were within the literature values. The present results accord well with those reported by Asadi Fozi *et al*. (2005) in fine wool Merinos,

as well as with values of 0.40 for GFW and 0.36 for CFW reported by Safari *et al.* (2005) in wool breeds. Cloete *et al.* (2002 b), Babar (1994) and Hanford *et al.* (2002, 2003, 2006) on the other hand reported higher (0.41 to 0.68) direct heritability estimates for GFW on various sheep breeds. Similarly, higher estimates for CFW, ranging from 0.40 to 0.51 were reported in other studies conducted on Merino and dual-purpose breeds (Safari *et al.*, 2005; Naidoo & Cloete, 2006; Olivier *et al.*, 2006; Matebesi *et al.*, 2009). Therefore, both traits can respond to purposeful selection.

The maternal genetic effects for GFW and CFW in the present study were low at 0.06 ± 0.02 and 0.07 ± 0.02, respectively. These estimates are consistent with the figure of 0.08 reported in wool breeds for GFW by Safari *et al.* (2005) and 0.08 for CFW in Merinos (Cloete *et al.*, 2005). The maternal heritability estimates should be included in the analysis in order to ensure that selection for direct breeding values is optimized.

The direct heritability of CY in the present study was high at 0.60 ± 0.03. These results accorded with a mean value of 0.58 reported by Safari *et al.* (2005) from the weighted means of 15 estimates derived from wool breeds. The present estimate was higher than the value of 0.46 obtained in Australian Merinos by Lewer *et al.* (1994). Higher estimates were also reported in Merinos from various literature studies ranging from 0.63 to 0.68 (Cloete *et al.*, 1998; 2002 b; Matebesi *et al.*, 2009). These estimates of genetic variation suggested that this trait can be improved by well-directed selection, should it be desired.

Direct heritability estimates for FD, SDFD and CVFD obtained in this study were all high at 0.54 ± 0.03, 0.55 ± 0.04 and 0.58 ± 0.04, respectively – suggesting that all traits would respond to purposeful selection. The heritability estimates obtained in this study for FD (0.54) were consistent with the value of 0.53 obtained by Cloete *et al.* (2005) also in Merino sheep. However, other studies reported higher heritability estimates for FD, ranging from 0.57 to 0.75 in various sheep breeds (Fogarty, 1995; Safari *et al.*, 2005; Olivier *et al.*, 2006; Brown *et al.*, 2010). Lower (but, but still highly heritable) estimates for FD were also reported by Safari *et al.* (2005) (0.51) in wool breeds. The dam PE effect derived in this study was very low at 0.03, indicating a limited contribution to the observed phenotypic variation.

Direct heritability estimates pertaining to SDFD in the present study (0.55 ± 0.04) were slightly higher than the value of 0.50 reported by Li *et al.* (1999). Higher heritability estimates for SDFD were reported in various studies conducted on Merino sheep, with a range from 0.57 to 0.61

79

(Ponzoni *et al.*, 1995; Hill, 2001; Matebesi *et al.*, 2009), indicating that direct selection for this trait would be successful. Dam PE effects were low at 0.03.

CVFD in the present study was highly heritable at 0.58 ± 0.04, an estimate slightly higher in magnitude than the value of 0.52 reported by Safari *et al.* (2005) in wool breeds and 0.50 reported by Naidoo *et al.* (2004) in Merinos. Studies by Hill (2001), Naidoo & Cloete (2006), Cloete *et al.* (2003 b) and Matebesi *et al.* (2009) also reported higher heritability estimates for CVFD in Merino sheep ranging from 0.60 to 0.74.

The direct heritability estimate of 0.35 ± 0.06 for SS in the present study was similar to the value of 0.34 derived from 11 estimates in wool breeds (Safari *et al.*, 2005). Cloete *et al.* (2005) and Herselman *et al.* (2006) on the other hand reported lower but, still moderate heritability estimates for SS in Merino's (h^2 = 0.13 and 0.23 respectively). A higher estimate of 0.39 was reported by Greeff *et al.* (2006) in Merinos. With this in mind, it can be concluded that SS would respond to genetic selection.

The direct heritability estimate for SL obtained in the present study was high at 0.36 ± 0.04, a value according with an estimate of 0.34 in Menz sheep (Gizaw *et al.*, 2006). Studies by Naidoo *et al.* (2004) and Naidoo & Cloete (2006) reported lower, but still moderate, heritability estimates for SL in Merinos (h^2 = 0.25 and 0.28, respectively). The estimate in the latter study was derived from a repeatability model and possibly not directly comparable to the present results. Higher heritability estimates than the value reported in this study were reported for SL, h^2 ranging from 0.43 to 0.48 in various sheep breeds (Olivier *et al.*, 2006; Safari *et al.*, 2005; Notter *et al.*, 2007).

CPI was moderately heritable at 0.18 ± 0.03. Direct heritability estimates for CPI in Australian Merino's were respectively 0.40 and 0.29 in 10 and 16 months old sheep (Ponzoni *et al.*, 1995). Similarly, Fogarty (1995) reported an estimate of 0.41 from six literature sources studying wool breeds.

The direct heritability estimates for CF were high at 0.44 ± 0.05 and in accordance with a value of 0.49 obtained by Ciappesoni *et al.* (2013) also in Merinos. These values were higher than the estimates of 0.26 and 0.38 obtained in Merinos and Targhee sheep, respectively (Pollot & Greeff, 2004; Notter *et al.*, 2007). The highest direct heritability estimate of 0.91 for this trait was also reported in Merinos by Olivier & Greyling (2008).

Subjective traits. Heritability estimates in the present study were 0.52 ± 0.04 for total fold score and 0.59 ± 0.04 for birth coat score, indicating that selection for both traits would lead to genetic change, should it be desired. Direct heritability estimates for TFS in South African Merinos were moderate to high, ranging from 0.15 to 0.54 respectively (Lewer *et al.*, 1995; Cloete *et al.*, 1998; Groenewald *et al.*, 1999; Cloete *et al.*, 2005). Literature values for BCS on the other hand were slightly higher in Merinos, ranging from 0.66 to 0.70 (Ponzoni *et al.*, 1996; Cloete *et al.*, 2003 a; Kemper *et al.*, 2003).

Testis dimensions. Direct heritability estimates for testicular dimensions amounted to 0.31 ± 0.06 for SC and 0.26 ± 0.06 for TD, suggesting that both these traits would respond to selection. These derived heritability estimates fell within the range of literature values (Fogarty, 1995; Duguma *et al.*, 2002; Safari *et al.*, 2005). Fogarty (1995) summarised the heritability estimates for SC as ranging from 0.08 to 0.50 with a corresponding range of 0.10 to 0.69 for TD.

FWEC. The heritability estimate of 0.09 ± 0.04 for FWEC has been extensively discussed in a previous study on the same resource population (in Chapter 3) as well as in the literature. This discussion will not be repeated here.

Correlations. In Table 5.5, the genetic correlations between FWEC and live weight traits were all positive in sign but did not differ from zero (according to the corresponding standard errors). It is considered logical to suggest that selection for low FWEC would improve growth potential of lambs (Vanimisetti *et al.*, 2004). Various literature studies have reported low but, negative genetic correlations between FWEC and live weight traits in various sheep breeds. In a study by Yadav *et al.* (2006) the genetic correlation between FWEC and BW in Muzaffarnagari Sheep were -0.26. Khusro *et al.* (2004) also reported low but negative genetic correlations between FWEC and yearling (-0.14) and hogget weights (-0.10) in Australian Merinos. Similarly, Bisset *et al.* (1992) reported low but, negative genetic correlations (-0.05) between FWEC and WW in Romney sheep and it increased to -0.29 post weaning. Pollot *et al.* (2004) on the other hand reported varying correlations between body weight and FWEC in Merinos, ranging from 0 at weaning to -0.63 at hogget age. Furthermore, the genetic relationships between FWEC and 5-month-old weight of Scottish Blackface sheep were high at -0.63 (Bishop *et al.*, 1996). These literature results suggest that selection for low FWEC would improve live weight traits in sheep so, selection for low FWEC should be emphasised in breeding objectives as the robust method in lowering the parasite load and improving live

weight traits (Bishop *et al.*, 2004). Despite that, genetic correlations between FWEC and live weight traits are not always favourable. In a study by McEwan *et al.* (1992) genetic correlations between FWEC and PWW were moderate and positive at 0.37. In addition, Greeff & Karlsson (1998) also reported low positive correlations (0.11 to 0.14) between FWEC and live weight traits at various ages. The latter results are consistent with the results reported in the present study. The unfavourable correlations between FWEC and live weight traits in some studies suggested that the traits should be combined in a selection index to ensure progress in all traits of economic importance.

The phenotypic correlations between FWEC and BW and WW were positive at 0.05 ± 0.02 and 0.03 ± 0.02, correspondingly. A study by Pollot & Greeff (2004) also reported a positive phenotypic correlation between FWEC and BW (0.04).

The genetic correlations between FWEC and all the wool traits obtained in the present study were below double the corresponding standards errors and thus not significant. The relationship between FWEC and GFW; and FWEC and CFW obtained in the present study were unfavourable (i.e. positive) and lower than the standard error at 0.07 ± 0.20 and 0.09 ± 0.21, respectively. Ciappesoni *et al.* (2010), Pollot & Greeff, (2004) and Matebesi-Ranthimo *et al.* (2014a) also reported low and positive relationships between FWEC and GFW with the value of 0.027 (with no reported standard error), 0.04 ± 0.05 and 0.17 ± 0.095, respectively. Similarly, Cloete *et al.* (2007) and Matebesi-Ranthimo *et al.* (2014a) also reported low estimates of 0.19 ± 0.09 and 0.16 ± 0.10 between FWEC and CFW in the Tygerhoek Merino flock. A positive direction of the correlation between FWEC and wool weight traits, although not significant indicates that an increase in wool weights would also increase FWEC. This direction of the expected genetic response is unfavorable as far as the parasite load is concerned because high parasite loads are not desirable.

FWEC and SL were lowly moderately correlated at 0.27 ± 0.20 but the correlation was not significant. Genetic correlations of FWEC with SL varied from -0.08 to 0.21 in Merino sheep studied by Greeff & Karlsson (1998). In another study by Ciappesoni *et al.* (2013), also on Merinos, the genetic relationship of FWEC with SL amounted to -0.14 ± 0.04. Similar results were reported by Ciappesoni et.al. (2010), Pollot & Greeff (2004) and Matebesi-Ranthimo *et al.* (2014a) with correlations of FWEC with SL ranging from -0.006 to -0.101. Combining the results obtained in this study and those found in literature, it can be concluded that selection for low FWEC would have very little to no effect on SL.

82

FWEC and SS were negatively correlated but the correlation was low and not significant at -0.19 ± 0.27. The direction of this correlation indicates that selection for low FWEC could improve SS. Genetic correlations between these two traits were negative but low at -0.17 ± 0.096 (Pollot & Greeff, 2004). Cloete *et al.* (2007) and Matebesi-Ranthimo *et al.* (2014 a), on the other hand, reported the higher favourable genetic correlations between FWEC and SS i.e. -0.49 and -0.54, respectively. With this in mind, it can be deduced that selection for low FWEC is likely to improve SS.

Genetic correlations between FD and FWEC were low in magnitude but, positive in direction with a very high standard error. A similar correlation was reported by Khusro *et al.* (2004) amounted to 0.01. Conversely, other literature values for the genetic correlation between FWEC and FD were low and negative in direction, ranging from -0.18 to -0.03 (Pollot & Greeff, 2004; Cloete *et al.*, 2007; Ciappesoni *et al.*, 2013; Matebesi-Ranthimo *et al.*, 2014a). However, all of these independent correlations were small and mostly not significantly different from zero. It thus seems as if the genetic correlation of FWEC with FD is likely to be negligible.

The two measures of variation in FD, namely SDFD (0.03 ± 0.17) and CVFD (0.01 ± 0.17) were marginally genetically correlated with FWEC. A small dataset used in this study could have been the cause of the very large standard errors obtained. Matebesi-Ranthimo *et al.* (2014a) reported a positive genetic correlation between FWEC and SDFD amounting to 0.25 ± 0.073. This correlation was higher than values of 0.09 and 0.10 reported by Greeff and Karlsson (1998).

Various literature sources reported positive genetic correlations between FWEC and CVFD, namely values of 0.09 ± 0.045 (Pollot *et al.*, 2004), 0.298 ± 0.089 (Cloete *et al.*, 2007), 0.037 (with no reported standard error) (Ciappesoni *et al.*, 2010) and 0.33 ± 0.072 (Matebesi-Ranthimo *et al.*, 2014a). Ciappesoni *et al.* (2013) also reported a positive genetic correlation of 0.18 ± 0.04 between FWEC and CVSD. It can be concluded from these literature values that selection for low FWEC could be favourable both for SDFD and CVFD.

The genetic correlation of FWEC with CPI was negative but not significant (-0.24 ± 0.18). There were no other reports on correlations between FWEC and CPI in the literature.

The genetic relationship of FWEC with CF was marginal at 0.03 ± 0.20. Comparable results were reported by Ciappesoni *et al.* (2013) with an estimate amounting to 0.01 ± 0.03. Pollot & Greeff (2004) on the other hand reported a low but negative genetic correlation between

83

FWEC and CF (-0.04 ±0.072) using results derived from a sire model. A similar genetic correlation of -0.01± 0.086 was derived when using an animal model.

The phenotypic correlations obtained in this study between FWEC and the wool traits were very low, ranging from -0.03 to 0.03. An increase or decrease in FWEC would thus have little or no effect on wool traits. In a study by Khusro *et al.* (2004) the phenotypic correlations between FWEC and various wool traits were correspondingly low at 0.04 with GFW, 0.02 with CFW and 0.01 with FD in yearling animals. Corresponding correlations in hoggets were respectively 0.03, 0.02 and 0.02. In a study by Matebesi-Ranthimo *et al.* (2014 a) on the other hand, the phenotypic correlations of FWEC with GFW, CFW, CY, CVFD and CVFD were positive at respectively 0.040 ± 0.014, 0.051 ± 0.014, 0.007 ± 0.015, 0.060 ± 0.015 and 0.060 ± 0.015 but negative with FD (−0.029 ± 0.016), SS (−0.036 ± 0.014), SL (−0.009 ± 0.016).

BCS and FWEC were positively but, not significantly correlated at the genetic level at 0.14 ± 0.15. No comparable results were found in literature in the relationship between FWEC and BCS.

The genetic correlation between TFS and FWEC was also positive and not significant at 0.07 ± 0.16, implying that selection for low FWEC would have no effect on TFS. Matebesi-Ranthimo *et al.* (2014a) on the other hand, reported the correlations between FWEC and TFS to be 0.15 ± 0.08.

Genetic correlations of FWEC with testis dimensions were low and negative in direction for both SC (-0.08 ± 0.23) and TD (-0.18 ± 0.24). The direction of these correlations was favourable. However, it was not significant implying that selection for low FWEC would not affect testis dimensions. In a study by Matebesi-Ranthimo *et al.* (2014b) the genetic correlations of FWEC with SC and SD amounted to -0.38 ± 0.15 and -0.64 ± 0.37, respectively, suggesting that selection for low FWEC would likely result in an increased TD and SC which is expected to benefit overall flock fertility.

Phenotypic correlations between FWEC and testis dimensions were negative and low for both SC (-0.06 ± 0.03) and TD (-0.04 ± 0.03). Comparable results were reported by Matebesi-Ranthimo *et al.* (2014b) with the estimates of -0.10 between FWEC and SC and -0.04 between FWEC and TD.

5.6 **Conclusions and recommendations:**

Most production traits reported in this study were moderate to highly heritable; suggesting that selection for most traits would result in responses in the desired direction. A low but significant heritability estimate for FWEC suggests additive genetic variation for this trait, but also that selection gains are likely to accrue slowly. The genetic correlations of FWEC with the other traits of economic importance were variable in sign and low to moderate in magnitude and not significant. Genetic gains in an overall breeding objective using economic weights and a balanced selection index thus seem to be feasible. Further work on the relationships among FWEC and the other production traits of economic importance across flocks is recommended.

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91

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5.8 Annexes of Tables

Table 5.1 Descriptive statistics for the traits considered in the analyses

Traits	Abbre-viation	Number of observations	Mean ± SD	Skewness	Kurtosis	Range
Live weight (kg)						
Birth	BW	4311	3.91 ± 0.81	-1.09	1.39	1-7
Weaning	WW	4255	21.6 ± 4.7	-1.08	0.51	6-38
Post-weaning	PWW	4223	38.1 ± 7.3	1.3	1.09	14-74
Wool traits						
Greasy fleece weight (kg)	GFW	4076	3.31 ± 1.53	0.79	0.57	0.7-9.1
Clean yield (%)	CY	4231	74.5 ± 4.9	-0.42	0.79	60-87
Clean fleece weight (kg)	CFW	4066	2.43 ± 1.01	0.57	0.32	0.5-6.4
Staple length (mm)	SL	3403	77.2 ± 19.1	-0.1	-0.83	31-139
Staple strength (N/ktex)	SS	1766	47.0 ± 11.3	-0.28	-1.48	5-83
Fibre diameter (µm)	FD	4232	19.3 ± 1.6	-0.18	0.48	14-29
SD of fibre diameter (µm)	SDFD	2671	3.97 ± 0.71	-0.55	0.67	2.3-7.0
CV of Fibre diameter (%)	CVFD	2671	21.0 ± 3.3	-0.01	0.44	13-37
Crimps per 25mm (n)	CPI	3212	10.4 ± 2.0	1.41	0.28	6-25
Comfort factor (% < 30µm)	CF	2670	98.2 ± 2.2	0.02	0.52	79-100
Subjective traits						
Birth coat score	BCS	3097	3.19 ± 0.88	-0.39	-1.32	1-5
Total fold score	TFS	4224	7.96 ± 2.73	-0.17	0.2	3-17
Testicular dimensions						
Scrotal circumference (cm)	SC	1964	28.7 ± 3.8	0.36	-1.72	14-40
Testis diameter (mm)	TD	1964	92.4 ± 19.1	0.47	-1.56	36-138
Faecal worm egg count	FWEC	2087	1641 ± 2657	4.29	27.58	0-26800
	Log-FWEC	2087	6.19 ± 1.12	0.63	1.44	4.6-10.2

		Total records	Zero Counts		Percentage (%)	
FWEC		2087	428		20.5	

Table 5.2 Significance of fixed effects fitted to the respective traits

Trait	Selection line (Gr)	Birth year (BY)	Sex	Dam age	Birth type	Gr x BY	Sex x BY
Live weights							
BW	**	**	**	**	**	**	0.51
WW	**	**	**	**	**	**	**
PWW	**	**	**	**	**	**	**
Wool traits							
GFW	*	**	*	**	**	**	**
CY	*	**	**	0.45	0.79	**	**
CFW	*	**	**	**	**	**	**
SL	**	**	**	0.49	0.23	**	**
SS	**	**	0.16	0.28	0.35	**	**
FD	**	**	**	**	*	**	**
SDFD	0.08	**	**	0.07	0.12	0.7	**
CVFD	0.66	**	**	0.19	0.13	0.17	0.11
CPI	**	**	**	*	*	**	**
CF	0.7	**	**	0.29	0.64	**	**
Subjective traits							
BCS	**	**	**	**	0.64	*	0.32
TFS	**	**	0.73	**	**	**	**
Testis dimensions							
SC	**	**	N.A.	*	**	**	N.A.
TD	**	**	N.A.	*	**	**	N.A.
FWEC	0.53	**	**	0.44	0.18	0.89	**

* - P < 0.05; ** - P < 0.01; Actual significance level for P > 0.05; N.A. - Not applicable

Table 5.3 Log likelihood values for all traits for 7 fixed- and random-effects models

Trait	Fixed effects	$+ \sigma^2_A$	$+ \sigma^2_A + \sigma^2_C$	$+ \sigma^2_A + \sigma^2_M$	$+ \sigma^2_A + \sigma^2_M + \sigma_{AM}$	$+ \sigma^2_A + \sigma^2_M + \sigma^2_C$	$+ \sigma^2_A + \sigma^2_M + \sigma^2_C + \sigma_{AM}$
Weights							
BW	-406.857	-200.648	-46.6046	-21.9055	-18.8048	**-13.9707**	-12.4761
WW	-7674.43	-7583.82	-7826.96	-7528.16	-7527.36	**-7519.39**	-2718.64
PWW	-8634.5	-8486.08	-8474.92	-8469.52	**-8466.8**	-8468.75	-8466.51
Wool traits							
GFW	164.568	323.894	328.175	**330.148**	331.298	330.414	331.577
CY	-7865.76	-7572.64	-7572.64	-7572.64	N.C.	-7572.64	N.C.
CFW	1365.97	1487.36	1490.82	**1496.16**	1496.32	1496.16	1496.32
SL	-9032.22	-8938.63	-8938.63	-8938.45	-8936.5	-8938.45	-8936.5
SS	-4960.23	-4923.77	-4923.62	-4923.72	-4923.63	-4923.62	-4923.5
FD	-3147.54	-2885.79	**-2880.09**	-2880.29	-2878.79	-2878.8	-2877.89
SDFD	-164.89	82.1006	**84.2721**	82.3837	83.8746	84.2721	86.3237
CVFD	-4226.67	-3976.3	-3975.58	-3976.3	-3975.75	-3975.98	N.C.
CPI	-3706.68	-3665.8	-3665.47	-3665.8	N.C.	-3665.47	N.C.
CF	-3175.53	-3039.29	**-3031.43**	-3038.48	-3037.37	-3031.43	N.C.
Subjective traits							
BCS	-1056.94	-800.43	-799.044	-799.773	-799.522	-799.03	-798.677
TFS	-5393.71	-5129.14	-5127.76	**-5127.05**	-5125.54	-5126.89	-5125.13
Testis traits							
SC	-2905.39	-2883.33	-2883.1	-2882.74	-2881.54	-2882.72	-2881.43
TD	-5434.64	-5413.38	-5412.24	-5412.67	-5411.39	-5412.15	-5410.78
FWEC	-999.67	-996.394	-995.158	-995.853	-995.601	-995.15	-995.13

σ^2_A: Direct, additive genetic effects; σ^2_M: Maternal genetic effects; σ^2_C: Dam permanent environmental effects; σ_{AM}: The covariation between direct and maternal effects; N.C.: Analysis failed to converge

Table 5.4 The total phenotypic variance components of all traits, as well as the applicable variance ratios for the direct additive, maternal genetic and maternal permanent environmental effects, as well as the correlation between direct and maternal effects

Trait	σ^2_P	h^2	m^2	c^2	r_{AM}
Weights					
BW	0.421	0.17 ± 0.03	0.21 ± 0.04	0.11 ± 0.03	-
WW	14.082	0.19 ± 0.04	0.09 ± 0.03	0.10 ± 0.02	-
PWW	24.157	0.31 ± 0.05	0.06 ± 0.02	-	0.46 ± 0.21
Wool traits					
GFW	0.3329	0.39 ± 0.04	0.06 ± 0.02	-	-
CY	16.65	0.60 ± 0.03	-	-	-
CFW	0.1824	0.35± 0.04	0.07 ± 0.02	-	-
SL	80.385	0.36 ± 0.04	-	-	-
SS	112.13	0.35 ± 0.06	-	-	-
FD	1.6775	0.54 ± 0.03	-	0.04 ± 0.01	-
SDFD	0.3914	0.55 ± 0.04	-	0.03 ± 0.01	-
CVFD	8.884	0.58 ± 0.04	-	-	-
CPI	3.623	0.18 ± 0.03	-	-	-
CF	4.07	0.44 ± 0.05	-	0.06 ± 0.02	-
Subjective traits					
BCS	0.7478	0.59 ± 0.04	-	-	-
TFS	4.9526	0.52 ± 0.04	0.03 ± 0.01	-	-
Testis dimensions					
SC	7.325	0.31 ± 0.06	-	-	-
TD	103.44	0.26 ± 0.06	-	-	-
FWEC	0.9017	0.09 ± 0.04	-	-	-

σ^2_P: Total phenotypic variance; h^2: Direct heritability; m^2: Maternal heritability; c^2: Common maternal permanent environment; r_{AM}: The correlation between direct and maternal genetic effects

Table 5.5 Genetic, phenotypic and environmental correlations of FWEC with the other traits considered

Trait	Genetic correlation	Phenotypic correlation	Environmental correlation
Live weights			
BW	0.09 ± 0.21	0.05 ± 0.02	0.04 ± 0.04
WW	0.30 ± 0.23	0.03 ± 0.02	-0.01 ± 0.03
PWW	0.01 ± 0.20	-0.06 ± 0.03	-0.09 ± 0.04
Wool traits			
GFW	0.07 ± 0.20	0.01 ± 0.03	-0.00 ± 0.04
CY	0.10 ± 0.16	0.03 ± 0.02	0.01 ± 0.05
CFW	0.09 ± 0.21	0.02 ± 0.03	0.00 ± 0.04
SL	0.27 ± 0.20	-0.01 ± 0.04	-0.07 ± 0.05
SS	-0.19 ± 0.27	0.00 ± 0.03	-0.04 ± 0.05
FD	0.05 ± 0.16	0.01 ± 0.03	-0.01 ± 0.04
SDFD	0.03 ± 0.17	0.01 ± 0.03	0.01 ± 0.05
CVFD	0.01 ± 0.17	0.00 ± 0.03	0.00 ± 0.05
CPI	-0.24 ± 0.18	-0.03 ± 0.02	0.01 ± 0.03
CF	0.03 ± 0.20	0.02 ± 0.03	0.02 ± 0.04
Subjective traits			
BCS	0.14 ± 0.15	0.01 ± 0.03	-0.05 ± 0.04
TFS	0.07 ± 0.16	0.06 ± 0.02	0.06 ± 0.04
Testis dimensions			
SC	-0.08 ± 0.23	-0.06 ± 0.03	-0.05 ± 0.04
TD	-0.18 ± 0.24	-0.04 ± 0.03	-0.02 ± 0.05

98

CHAPTER 6: ESTIMATION OF GENETIC PARAMENETS FOR FAECAL WORM EGG COUNT AND REPRODUCTIVE TRAITS IN MATURE EWES OF THE ELSENBURG MERINO FLOCK

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6.1 Abstract

Gastrointestinal nematodes are a common problem world-wide. Traditional control of gastrointestinal nematodes with chemical drenches has led to the worldwide development of resistance by the nematodes. As a result, selection for parasite resistance has been suggested as part of an integrated approach to control parasitism in the long term. Faecal worm egg counts (**FWEC**) are traditionally used to measure parasite load. Records from the divergently selected Elsenburg Merino ewe breeding flock, from ages of 2 to 7+ years were used to estimate the genetic parameters of FWEC measured in autumn, and its relationship with reproductive traits, namely number of lambs born (NLB) and number of lambs weaned (NLW) per ewe mated. Heritability estimates for FWEC after log and cube root transformation were low and not significant at 0.03 ± 0.03. However, ewe permanent environmental effects also contributed 0.06 ± 0.03 to the phenotypic variance, resulting in a repeatability estimate of 0.09 ± 0.03. These results suggested that current flock selection for parasite resistance is likely to lead to slow gains, but that genetic change in mature ewes would be difficult to achieve. Reproductive traits on the other hand were moderately heritable at 0.19 ± 0.03 for NLB and 0.11 ± 0.03 for NLW, suggesting a greater likelihood for genetic selection to be successful. Genetic correlations of FWEC with reproductive traits were high and negative at -0.71 ± 0.32 for NBL and -0.78 ± 0.34 for NLW. These correlations suggested that higher reproducing ewes would also have a lower FWEC. This study provides important information pertaining to the relationship between FWEC and reproduction in adult Merino ewes.

Key words: nematode resistance, genetic improvement, reproduction

6.2 Introduction

Infestation with gastrointestinal nematodes is a global problem because it affects the health and welfare of ruminants. Scientists, farmers and government institutions (Perry & Randolph,

1999; Kelly *et al.*, 2010; Van Houtert & Sykes, 2010; Roeber *et al.*, 2013) have long recognized economic and production losses resulting from nematode infestations. The economic impact of the nematodes in ruminants stems from the direct cost of anthelmintic treatment and labour to drench the animals. In addition, an indirect cost stemming from production losses in meat, milk, fibre production, reproductive efficiency and death of infected animals (in severe cases) also contribute to economic losses. In South Africa alone, the estimated cost for treating *Haemonchus contortu*s is 50 million U.S. dollars/yr (Waller & Chandrawathani, 2005). This cost is even larger on a worldwide scale (McLeod, 1995; Sackett & Holmes, 2006). In addition to the costs, the use of chemical drenches in livestock production is not without problems. Misuse and overuse of such drenches resulted in resistance to the chemicals by the nematodes (Waller *et al.*, 1995; van Wyk, 2001; Bessier & Love, 2003). In extreme instances, resistance by the nematodes made it impossible for South African sheep farmers to continue farming (van Wyk *et al.*, 1989). Alternative measures to control parasitism, such as breeding ruminants for resistance to parasites, have been advocated as part of an integrated strategy to alleviate the impact of parasitism in livestock (Karlsson & Greeff, 2006; Kemper *et al.*, 2010).

Traditional breeding strategies for genetic improvement, using phenotypes and pedigree information to estimate breeding values for individual animals, allowed sustained, cumulative genetic gains in economically important traits in South Africa (Schoeman *et al.*, 2010). In Australia and New Zealand, selection for resistance to parasites has accordingly resulted in substantial realized genetic gains (Woolaston & Piper, 1996; Greeff *et al.*, 1999; Morris *et al.*, 2005; Karlsson & Greeff, 2006). Faecal worm egg count (FWEC) is a tool to measure parasite burden. It requires animals to be infected with nematodes either naturally or artificially. FWEC is widely variable, with coefficients of variation often exceeding the mean in untransformed data (Cloete *et al.*, 2007). Part of the observed variation is genetic in origin, heritability estimates ranging from 0 to 0.52 (Greeff *et al.*, 1995; Safari *et al.*, 2005; Lôbo *et al.*, 2009).

Infestation with gastrointestinal nematodes in sheep production is influenced by age related immunity (Barger, 1988), a peri-parturient rise in ewes (O'Sullivan & Donald, 1970), season of collection (Greeff *et al.*, 1995), sex (Greeff *et al.*, 1995; Cloete *et al.*, 2016), the type of nematode infecting the host (Beraldi *et al.,* 2007) and the host breed (Baker *et al.*, 1999, 2002; Gruner *et al.*, 2003; Nimbkar *et al.*, 2003). Most South African studies estimated genetic variation of FWEC in lambs, hoggets or yearlings. Such animals are more prone to mortality and morbidity after challenge than mature animals. Mature ewes are generally more resilient

to parasitism than lambs (Burke & Miller, 2002; Vanimisetti *et al.*, 2004). Therefore, they could be challenged by helminths at a reduced risk.

The sheep industry would prefer breeding animals expressing favourable production and reproduction traits, while also having an increased resistance to internal parasites. However, breeding for animals for a selection objective combining these traits could prove to be challenging. Against this background, it was surprising to find a dearth of genetic correlation estimates between FWEC and ovine reproduction in Chapter 3.

No information on the genetic relationship between FWEC and reproduction of mature ewes could be sourced from the South African literature. The objectives of this study were to derive genetic parameters for FWEC and reproduction in mature Merino ewes, while also estimating genetic and phenotypic correlations between FWEC and the reproductive traits.

6.3 Material and Methods

Starting in 1986, two lines of Merino sheep were divergently selected for reproductive efficiency from the same base population using maternal ranking values for number of lambs weaned per mating (Cloete & Scholtz, 1998; Cloete *et al.*, 2004; 2009). In short, two lines of sheep that differ markedly in reproductive efficiency were developed. The high line (H Line) was selected upwards based on the ability of their dams to rear one or preferably more lambs per joining. The low line (L Line), on the other hand, were descended from ewes that reared less than one lamb per joining (i.e. were either barren or lost all lambs prior to weaning on at least one occasion). Both lines were maintained as a single flock at the Elsenburg research farm. In January-February the ewes were separated according to selection line and joined to individual rams for mating. They lambed in June-July in randomly divided groups of 20-30 in 0.3 - 0.4 ha Kikuyu paddocks. During lambing, these groups were inspected twice daily. At the morning inspection, lambs were identified with their dams and birth type, sex and birth weight were recorded within 24hrs of birth. At 3 days after lambing, ewes with lambs were moved from the kikuyu pastures to lucerne pastures, where they were maintained in groups of 30-40 until their tails were docked at the second palpable joint at about three weeks. A more detailed description of the environment, climate, husbandry methods and management of the resource flock can be found in literature (Cloete *et al.*, 2004, 2009).

In this study, no animals were intentionally selected for parasite resistance (low FWEC) in either line. Ewes were naturally challenged with parasites over a period of 6 – 10 weeks in autumn. During this period, the animals were likely to be infested with a mixture of *Trycostronglyus spp*, *Teladorsagia spp* and *haemonchus contortus* (Reinecke, 1987). Following the challenge, faeces samples were collected from the rectum of individual ewes 6-8 weeks prior to the commencement of lambing in early June. These samples were sent to the Stellenbosch Provincial Veterinary Laboratory for determining FWEC by using the McMaster technique, at a sensitivity of 100 eggs per gram of wet faeces (Van Schalkwyk *et al.*, 1994).

Between 1581 (FWEC) and 1633 (NLB and NLW) repeated records of 609 ewes were available for analysis (Table 6.1). The distribution of the categorical reproduction traits approached normality, as reflected by the frequency distribution in Figure 6.1 as well as the descriptive statistics in Table 6.1. FWEC was extremely variable and was transformed either to natural logarithms after 100 were added (FWEC) or to cube roots (CRFWEC). Conclusions

102

were similar between the sets of analyses, and only results from log transformed FWEC data were used to estimate genetic correlations with reproduction traits. The estimation of the fixed effects and the subsequent derivation of variance components and ratios for FWEC, NLB and NLW in single-trait repeated-records animal models were conducted in ASREML (Gilmour *et al.*, 2015). Fixed effects were lambing year (2007-2015), selection line (H or L line) and ewe age (2-7+ years). Initial analyses involved fitting various combinations of fixed effects and interactions between them to obtain an operational model, including regressions of FWEC on the reproduction traits. Random terms to reflect between-animal variance components were then added, resulting in the following repeated-records animal models for analyses (in matrix notation):

$$y = Xb + Z_1 a + e \tag{1}$$

$$y = Xb + Z_1 a + Z_2 c_{ewe} + e \tag{2}$$

In these models, y was a vector of observations consisting of repeated FWEC, NLB or NLW records; b, a, and c_{ewe} were, respectively, vectors of fixed effects, direct, additive genetic effects and ewe permanent environmental (PE) effects; X, Z_1, and Z_2 were the corresponding incidence matrices relating the respective effects to y, and e the vector of residuals.

It was assumed that:

$$V(a) = A\sigma^2_a; \ V(c_{PE}) = I\sigma^2_{ewe}; \ V(e) = I\sigma^2_e,$$

In these assumptions, A was the numerator relationship matrix, I an identity matrix; σ^2_a the direct, additive genetic variance, σ^2_{ewe} the ewe PE variance, and σ^2_e the environmental (residual) variance. All analyses included the full pedigree file, consisting of 8233 individuals, the progeny of 231 sires and 1750 dams.

Three-factor interactions between lambing year, selection line and ewe age were not significant (P>0.05) for any of the traits considered. The two-factor interactions between lambing year and selection line as well as between selection line and ewe age were sometimes significant and were presented where applicable.

Log likelihood tests were conducted to identify the random effects that should be modeled for each trait in single-trait analyses (Snyman *et al.*, 1996). Subsequent analyses involved a 3-trait repeated-records animal model fitted to all traits. These analyses allowed the calculation

of all relevant genetic and phenotypic correlations among traits, together with their appropriate standard errors.

6.4 Results

6.4.1 Descriptive statistics

Raw FWEC was extremely variable and not normally distributed (Table 6.1). Transformation to either logarithms or cube roots, however, reduced the variation markedly and rendered the data suitable for statistical analysis in terms of normality. Coefficients of variation (CVs) were reduced to 23% for FWEC and 86% for CRFWEC. The reproduction traits were also variable, with CVs of 59% for NLB and 72% for NLW.

6.4.2 Fixed effects

Transformed FWEC was largely independent of the fixed effects modeled, with the exception of lambing year (Table 6.2 and 6.3). The reproduction traits were, in contrast, affected by selection line, ewe age and lambing year, as well as some interactions among these traits. No selection line differences were observed for transformed FWEC, but H line ewes outperformed their L line contemporaries by 26% for NLB and by 53% for NLW. Transformed FWECs were independent of ewe age, but older ewes generally had an improved reproductive performance compared to 2- and 3-year-old ewes.

Selection line interacted with ewe age for NLB (Figure 6.2). This interaction arose from a large line difference of 92% in 2-year-old ewes, becoming smaller at 40% in 3-year-old ewes before no significant line differences were found for 4- and 6-year-old ewes. H line ewes outperformed L line contemporaries by 28-29% at 5- and 7+-years of age.

Selection line and lambing year was also involved in an interaction for both NLB and NLW. This interaction was presented for NLW in Figure 6.3. H line ewes generally outperformed their L line contemporaries by between 49 and 104% for the periods from 2007-2010 and again for 2014-2015. Line differences were substantially smaller in the 2011-2013 period, and not statistically different.

6.4.3 Random effects and genetic (co)variances

The addition of additive genetic and animal PE effects to the operational model improved the log likelihood for all traits (Table 6.4). However, in the case of transformed FWEC the "best" model only included ewe PE effects as a random factor. The "best" model for NLB included

104

both ewe additive genetic and ewe PE effects, while the "best" model for NLW only included ewe additive genetic effects. However, additive genetic effects for ewes were modeled throughout in downstream analyses, as parts of the objectives of the study were to estimate genetic correlations of transformed FWEC with the reproduction traits.

Both LFWEC and CRFWEC were lowly heritable at 0.03 (Table 6.5). Heritability estimates for the reproduction traits were higher, at 0.12 for NLB and 0.10 for NLW. Ewe PE affected transformed FWEC (0.06) and NLB (0.09). The repeatability estimates for the traits analysed were 0.09 for FWEC, 0.20 for NLB and 0.10 for NLW.

The variance associated with ewe PE in NLB in the single-trait model partitioned to the ewe additive genetic variance ratio in the three-trait analysis and ewe PE could be dropped from the model without a change to the observed log likelihood. Heritability estimates for FWEC remained stable at 0.03, increased to 0.19 for NLB and increased marginally to 0.11 for NLW. Genetic correlations among traits indicated that ewes with a better reproduction rate would also have lower values for LFWEC. NLB and NLW were genetically very similar traits, as suggested by a genetic correlation not different from unity between them. Ewe PE of FWEC remained stable at 0.06 in the three-trait analysis. Phenotypic correlations were in the same direction but smaller in magnitude than the corresponding genetic correlations (not significant for the correlations of the reproduction traits with FWEC).

Lastly, not modelling ewe PE for FWEC in the three-trait analysis had the following outcomes: The heritability of FWEC changed to 0.07±0.03, while the heritability of the reproduction traits remained similar at 0.19 for NLB and 0.11 for NLW. The genetic correlations of FWEC with the reproduction traits became somewhat smaller, at -0.52±0.20 for NLB and -0.60 ± 0.22 for NLW. The genetic correlation between the latter traits remained stable at 0.96±0.05. The phenotypic correlations among traits remained similar.

6.5 Discussion

6.5.1 Descriptive statistics

Raw FWEC was extremely variable, skewed and not normally distributed as was commonly reported in the literature (Safari & Fogarty, 2003; Morris *et al.*, 2005; Cloete *et al.*, 2007, 2016). Data were thus transformed to logarithms and cube roots to reduce the variation and normalize the distribution. Both transformations used in this study were commonly reported in the literature (Safari & Fogarty, 2003; Matebesi-Ranthimo *et al.*, 2014). Safari & Fogarty

(2003) listed 26 heritability estimates of FWEC in sheep from various sources, 14 of which were estimated from log transformed data while the other 12 were derived from cube root transformed data. The reported means in these studies ranged from 6.88 to 7.49 where log transformations were applied and 2.75 to 22.6 for cube transformed data. Cloete *et al.* (2007) reported the mean estimates of 6.15 ± 1.15 for log transformed FWEC and 6.93 ± 4.67 for cube root transformed data in Merino sheep. Similar results were reported by Mpetile *et al.* (2015) and Matebesi-Ranthimo *et al.* (2014) also in Merino sheep, with respective means of 6.65 ±1.41 and 2.57 ± 0.51 for log transformed data and 9.02 ± 6.07 and 5.88 ± 4.88 for cube root transformed data. The results from the present study are consistent with these reports.

6.5.2 Fixed effects

Transformed FWEC was independent of the fixed effects fitted, with the exception of lambing year. The effects of lambing year are often transient and unpredictable, depending on a combination of climatic and managerial effects not repeated in other years. Cloete *et al.* (2007), Matebesi-Ranthimo *et al.* (2014) and Mpetile *et al.* (2015) also reported significant birth year effects on transformed FWEC. The regression of FWEC on both reproduction traits also did not reach significance. In contrast, the fixed effects of selection line, ewe age and lambing year as well as some interactions among these effects influenced reproductive traits (P < 0.05). Although no statistically significant differences were observed between the high and low line for transformed FWEC, the high line had slightly lower least squares means for FWEC in absolute terms. The higher reproductive efficiency in the H Line compared to the L Line, clearly indicated a marked phenotypic divergence following selection. Notable differences between the divergent lines in NLB and NLW were also reported by Cloete & Scholtz (1998), Cloete *et al.* (2004) and Naidoo *et al.* (2005), with the H Line clearly outperforming their L Line contemporaries.

The selection line x lambing year interaction seemed to reflect three distinct periods, namely 2007-2010 during which the H Line soundly outperformed the L Line, 2011-2013 when the line difference diminished and 2014-2015 when the H Line superiority was restored. No evident reason for this result exists, except possibly for the introduction of rams from outside the flock since 2008 in the H Line to link the genetic resource flock with industry flocks. The progeny of the single introduced ram would have commenced reproduction in 2010. So, more progeny of outside rams would have been introduced as years progressed from 2010. However, this does not explain the larger line differences in favour of the H Line the most

recent years. The physiological state of the animals as indirectly measured by body condition score had an effect on fertility and fecundity traits in Afshari sheep (Aliyari *et al.*, 2012). These authors reported that ewes with a body condition score of 3.0 had a higher fertility rate and thus a greater number of lambs born per ewe joined at 1.40. While ewes with scores of 3.5 (or more) and less than 3.0 body condition score had the lowest fertility rate with mean estimates for number of lambs born per ewe joined of respectively 1.05 and 1.30. With that in mind, it can be deduced that inconsistencies in feed abundance could translate to variation in reproductive performance of sheep in different years. Several authors have also reported the effects of lambing year on reproductive traits in sheep production (Vatankhah *et al.* 2008; Ceyhan *et al.*, 2009, Mohammadi *et al.*, 2012; Mohammadabadi & Sattayimokhtari, 2013).

Our study showed an effect of age on reproductive traits with ewes showing highest, higher and lowest reproductive performance on 7 +, 4 – 6 and 2 - 3 years old, respectively. The suggestion of an improved reproductive efficiency in ewes of 7+ years was quite unexpected and not in accordance with a contemporary study by Cloete *at al.* (2003), in the same population from the period of 1997 – 2002. In their study, Cloete *et al.* (2003), reported general trends for reproductive traits in 4 – 7+ years old ewes, ranging from 1.23 ± 0.05 to 1.29 ± 0.05, with the highest mean in 5 years old ewes. In the present study, the H Line ewes in the 7+-years-old category were retained in the flock on the basis that they could become sire mothers, whereas most other ewes were cast-for-age at 6 years. This management intervention could have contributed to the better than expected 7+-year-old reproduction. A significant effect of ewe age on reproductive traits is commonly reported in literature, with the lowest reproductive performance reported in 2- and 3-year-old dams (Rosati *et al.,* 2002; Cloete *et al.*, 2003; Mokhtari *et al.,* 2010; Roshanfekr *et al.*, 2015). The significant effect of age on reproductive traits could be attributed to maternal effects, nursing, behavior and experience in mothering ability of dams at different ages. It is an undeniable fact that older dams have more experience in nurturing the young ones compared to the younger dams. As a result, it is not surprising that the older ewes in this study (4 – 6 yrs old) had a greater number of lambs weaned compared to the younger dams (2 – 3 yrs old).

Marked differences in selection line by age interaction was also observed in number of lambs born per ewe mated. The interaction stemmed from a greater line difference in 2-year-old ewes, which later reduced in 3-year-olds and regained momentum in 5- and 7+-year-olds. In the aforementioned ewe ages, the H line outperformed the L line significantly. Cloete &

Scholtz (1998) also reported a significant line by age interaction on divergently selected lines for reproductive efficiency in NLB and NLW. The significant difference in reproductive traits was due to benefits of selecting for higher reproductive efficiency. Contrary to other years, the line difference for NLB at 4 and 6 years of age was not statistically significant. This lack of significance is not well understood at present.

6.5.3 Random effects and genetic (co)variances

The single-trait heritability estimates for LFWEC and CRFWEC were low at 0.03 ± 0.03 with ewe PE effects of 0.06 ± 0.03 and repeatability estimates of 0.09 ± 0.03. These estimates suggest that mature ewe reproduction may be difficult to change by genetic selection. It is not clear why the heritability estimate for LFWEC was zero in the present study. However, it is assumed that sufficient pedigree depth would have been present in the analysis to accurately partition direct genetic and animal permanent environmental effects. It is notable, though, that the repeatability as an indication of the total between-animal variance component was very similar to the heritability estimate for yearlings in the same flock (see Chapters 3 and 5). In the present study FWEC records were collected in autumn, at a time where literature shows a trend for low heritability estimates for FWEC, as previously reported in Chapter 3 and 5 and in a study by Greeff *et al.* (1995). However, the experimental animals used in this study were exposed to irrigated pastures, so the variation of the growth of pastures due to rains was minimized. Although that is the case, the survival of parasites depends on climatic factors such as temperatures, humidity and rainfall. So, in autumn, there is a chance that a lot of parasites were in hypobiosis – an arrested state of parasite development. Although that could have been the case, it is important to note that only 29% of zero counts were obtained in the present study with individual counts ranging from 0 to 25600. Therefore, there seems to have been sufficient challenge for the animals to trigger an immune response. Studies by Watson *et al.* (1995), Morris *et al.* (1998), and Bishop & Stear (2001) reported moderate heritability estimates (h^2 ranging from 0.23 ± 0.05 to 0.37 ± 0.06) for FWEC under natural challenge during the peri-paturient period in Romney, Perendale and Scottist Blackface ewes. Unlike the present study, where FWEC was independent of reproduction, Watson *et al.* (1995) did not fit pregnancy in the model, despite measuring FWEC records in pregnant animals. Morris *et al.* (1998) as well as Bishop & Stear (2001), on the other hand only recorded the FWEC records 1 to 2 months post lambing. With that said, it is not clear why the results by Watson *et al.* (1995) Morris *et al.* (1998), and Bishop & Stear (2001) were not duplicated in the present

108

study. One of the limitations of natural challenge of hosts with GIN is that there may be a lack of control over the actual challenge that were achieved. So, there might have been differences in the parasite challenge between the present study and the literature cited. The timing of sampling (autumn) could have had an effect but it is impossible to be sure of this with our present knowledge. Breed differences, the period in which the faecal sample grabs were collected, physiological status of ewes, age of ewes, ewe birth type, the exclusive use of ewes, as well as the accuracy of counting FWEC may all have had an impact on parasite load and thus, the heritability estimates of FWEC.

Scientific literature reports an existing genetic variation of FWEC in different seasons, with most and least genetic variation from a data that was collected in spring and autumn, respectively as reported by Greeff *et al.* (1995) and in Chapters 3 and 4. In a study by Greeff *et al.* (1995) the heritability estimates of FWEC in Merino lambs under natural challenge were high from winter to spring (i.e. 0.21 to 0.25), and low in autumn (0.00 – 0.03), while the peak was reached in mid-winter (0.52). In Chapter 4, a similar trend was reported with heritability estimates of 0.07, 0.13 and 0.19 in autumn, winter and spring, respectively. An increase in heritability estimates in both studies colluded with the growth of pasture and hatching of nematode eggs during winter and spring. Differences in temperature and rainfall in different seasons affects the prevalence of parasite load on pasture and the genetic variation of FWEC. So, it is possible that autumn might not be the best season to challenge the animals. However, based on the percentage of zero counts, the range of individual counts for FWEC and the mean FWEC the challenge appears to have been adequate. The low heritability estimates of FWEC observed in this study where data collected at Elsenburg were concerned, could be due seasonal variation and sampling period, which occurred at a time where there is a trend of low heritability estimates for FWEC (Greeff *et al.*, 1995).

Ewes are generally known to have lower FWEC compared to rams (Cloete *et al.* 2007; Matebesi-Ranthimo *et al.* 2014). However, during the peri-paturient period, the acquired immunity gets compromised resulting in an increase in parasite load, which pose a major threat to the growth and development of newborn lambs. A study by Woolaston (1992) has shown that sheep that were selected for parasite resistance experienced a peri-paturient rise of FWEC suggesting an existing mechanism in controlling parasite resistance in different classes of animals. Gutierrez-Gil *et al.* (2010) reported low to moderate heritability estimates for FWEC in peri-parturient ewes and pregnant ewes (0.09 ± 0.03 and 0.12 ± 0.04

respectively) suggesting a temporal loss of immunity during the period around lambing. These results may suggest that nutrients may be prioritized to reproductive functions and partitioned away from immune functions (Houdijk *et al.*, 2003). Ewes in our study were also pregnant, having been assessed 6-8 weeks before lambing. Therefore, this could also have been part of the reason for the observed low genetic variation for FWEC.

Williams *et al.* (2006) reported a pattern of FWEC and pasture contamination in resistant and unselected control Merino ewes in a Mediterranean environment. In their study, pasture larvae were high in both lines in the post lambing period compared to pre-lambing period. However, the resistant ewes had less larvae compared to the control line in both periods. Studies conducted in South Africa reported moderate heritability estimates for FWEC when the data was collected in spring (h^2 ranged from 0.14 – 0.24) (Niewoudt *et al.*, 2002; Cloete *et al.*, 2007; Matebesi-Ranthimo *et al.*, 2014). Although the reported heritability estimates were inclusive of rams, it suggested that selection for FWEC can be feasible. With that in mind, the low repeatability estimate obtained in this study suggests that selection for parasite resistance in the current flock is likely to be slow in South Africa.

Ewe age also affected parasite load and ultimately the genetic variation of FWEC. Watson *et al.* (1995) found a reduction in FWEC in ewes during the peri-parturient phase with an increasing ewe age. Hayward *et al.* (2010) reported similar results, with the middle-aged ewes having the lowest FWEC compared to younger and older ewes. Similar to our results, Beraldi *et al.* (2007) also reported a limited genetic variation of FWEC in adult, free-ranging sheep infected with helminths belonging to *Strongyle spp*. In contrast, the same authors found a moderate heritability estimate of 0.26 ± 0.12 for the same trait in lambs, suggesting that selection for a reduced FWEC is likely to be successful in younger animals. Reduced heritability estimates in adult ewes compared to lambs are common in the literature. Goldberg *et al.* (2012) derived heritability estimates of 0.25 ± 0.03 in lambs as compared to 0.08 ± 0.03 in adult ewes. The low heritability estimates in adults compared to young animals may result from different mechanisms controlling the immune system of the respective age groups. It is possible that the worm control mechanisms of adult ewes encompassed genetic factors not properly represented by FWEC as the indicator trait. With this in mind, heritability estimates derived by Davies *et al.* (2006) declined from 0.30 to 0.21 and 0.19 in lambs of respectively four, five and six months of age. In contrast to the results obtained in the present study, direct heritability estimates for FWEC across 3 breeds amounted to 0.10 in lambs compared to 0.31

in adult ewes (Vanimisetti *et al.,* 2004). The latter study did not model breed as a fixed effect, though, and the authors contemplated that the higher heritability estimates in ewes could be attributed to the breed effect not being properly accounted for.

Ewe birth type also influenced the heritability for FWEC. In a study by Hayward *et al.* (2010), lambs born as twins had higher parasite burdens compared to singles. This could be caused by the fact that the twin-bearing dams had to eat more than the single-bearing dams for maintenance and production. This arguably increased the chances of consuming a greater amount of infecting larvae.

Literature reports a general trend of lower parasite load in ewes compared to rams (Mpetile *et al.,* 2015; Hayward *et al.*, 2010**,** Mathebesi-Ranthimo *et al.*, 2014). This could be due to factors such as the behavior of animals while grazing, differences in feed intake between rams and ewes, and different environments to which the animals are routinely exposed to. Rams are generally known to consume more feed than ewes. Therefore, they have more chance to consume greater amounts of the infected pastures. The greater the parasite load, the more chance the animal would have to use its immune system to fight off the nematodes. Therefore, the sex which has a higher parasite load is expected to have higher heritability estimates for FWEC. There is no record of the comparison of FWEC heritabilities between rams and ewes in literature. However, a contemporary study by Mpetile *et al.* (2015), within the same population, estimated the heritability estimates of FWEC in both genders. In their study, FWEC was lowly but significantly heritable at 0.10, suggesting that genetic progress in FWEC is likely to be slow. Although the heritability estimate of 0.10 is low, it is higher than the estimate of 0.03 ± 0.03 in the present study, when rams were excluded. Similar to our study, Mandonnet *et al.* (2006), Beraldi *et al.* (2007) and Goldberg *et al.* (2012) found limited genetic variation of FWEC in small-stock production with heritability and repeatability estimates of 0.10 ± 0.02 and 0.17 ± 0.02 in Creole goats; 0.00 in adult Soay sheep and 0.08 ± 0.03 and 0.18 ± 0.03 in Merino ewes respectively.

The accuracy of calculating FWEC also has an influence on heritability estimates. In this study, FWEC was calculated at a sensitivity of 100 epg wet feaces, which may be a bit low. A sensitivity of 50 epg wet feaces would have been preferred but the service providers routinely counted FWEC at an accuracy of 100 epg and were not willing to do the counts at a greater accuracy. Notter (2003) reported moderate heritability estimates (h^2 ranging from 0.22 to 0.42)

of FWEC in sheep infected with *Haemonchus contortus.* In their study, FWEC was derived at an accuracy of 50 epg of wet faeces.

The reproductive traits, analysed by single-trait analyses, yielded moderate heritability estimates of 0.12 ± 0.04 for NLB and 0.10 ± 0.03 for NLW, with a ewe PE effect of 0.08 ± 0.04 for NLB. The three-trait-analysis yielded estimates of 0.19 ± 0.03 for NLB and 0.11 ± 0.03 for NLW. Linked to appreciable levels of phenotypic variation, as reflected by high CVs, these estimates suggested that reproduction traits should react positively to purposeful selection. Compared to our study, the heritability estimates reported in literature for NLB and NLW stemming from a repeated-records model were inconclusive. The heritability estimates for NLB range from 0.00 ± 0.01 to 0.19 ± 0.06 with ewe permanent environmental effects ranging from 0.00 ± 0.05 to 0.07 ± 0.03, suggesting an existing genetic variation in NLB and that selection for NLB may be possible (Brash *et al.*, 1994, Fogarty *et al.*, 1994; Cloete *et al.*, 2004). Similar to our results, the heritability estimates reported by Duguma *et al.* (2002), Snyman *et al.*, (1998) and Olivier *et al.* (2001) were to 0.23, 0.19 and 0.26 respectively for NLB, suggesting that genetic variation for this trait do exist. However, in the aforementioned studies, the heritability estimates for NLB were not derived from repeated records as the estimates were stemming from overall or lifetime reproduction.

The heritability estimates reported in this study for NLW was higher than the values reported in literature. In literature, the heritability estimates reported ranges from 0.04 ± 0.01 to 0.06 ± 0.01 with permanent environmental effects ranging from 0.03 ± 0.01 to 0.11 ± 0.03, suggesting that given the same environmental conditions, selection for NLW may be difficult to achieve (Brash *et al.*, 1994; Swan *et al.*, 2001; Hanford *et al.*, 2002).

The genetic correlations of FWEC with the reproductive traits were favourable (i.e. negative) and high at -0.71 ± 0.32 for NLB and -0.78 ± 0.34 for NLW. These correlations suggested that selection for low FWEC would increase reproductive efficiency i.e. NLB and NLW. These correlations suggested that ewes with a better reproduction rate would also have lower means for FWEC. A study by Morris *et al.* (2000) also reported a favourable realised correlated response to selection for parasite resistance in Romney sheep, with the line selected for a reduced FWEC having 0.11 more lambs weaned per ewe mated compared to the high line. In contrast to these results, Pickering *et al.* (2012) found no evidence of a genetic association of FWEC with NLB in New-Zealand dual-purpose ewes. In their study, FWEC in summer and autumn was not correlated with NLB (0.03 ± 0.03 and 0.04 ± 0.03, respectively). Based on

these results and the very low genetic variance component for FWEC in the present study, the genetic correlations of FWEC with reproduction traits should be interpreted with caution. It is also not sure how these results would fit in with the resource allocation model proposed by Van der Waaij (2004). Further research is therefore indicated.

6.6 Conclusions and Recommendations

Heritability estimates for FWEC was low and not different from zero in mature ewes at Elsenburg. Since this study reported data that was collected during autumn, the results obtained may be different in other seasons. Marked variation in the heritability of reproductive traits in mature ewes was evident, indicating that other considerations may affect genetic variation in FWEC in older ewes. Further research on the heritability of FWEC in mature animals and its correlations with reproduction is needed.

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6.8 Annexes of Figures and Tables
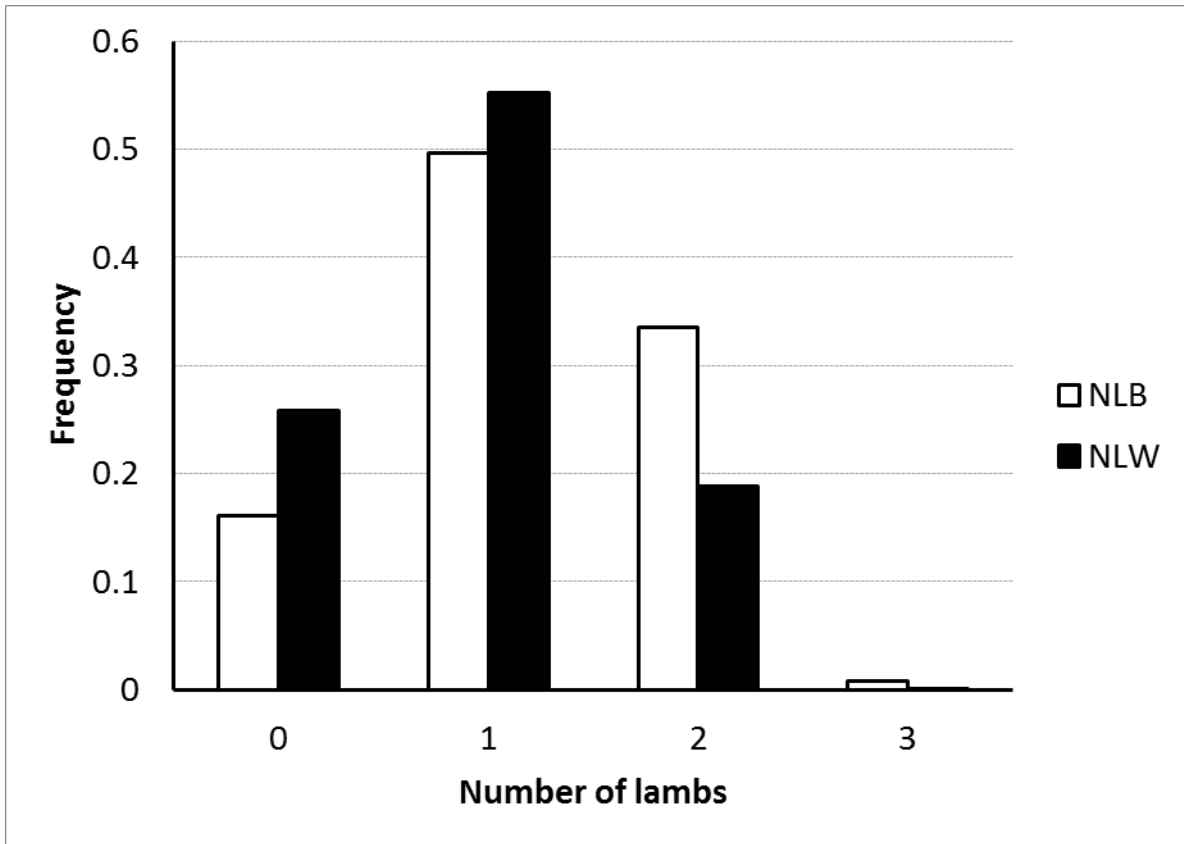
Figure 6.1 Frequency distribution of record for number of lambs born (NLB) and number of lambs weaned (NLW)
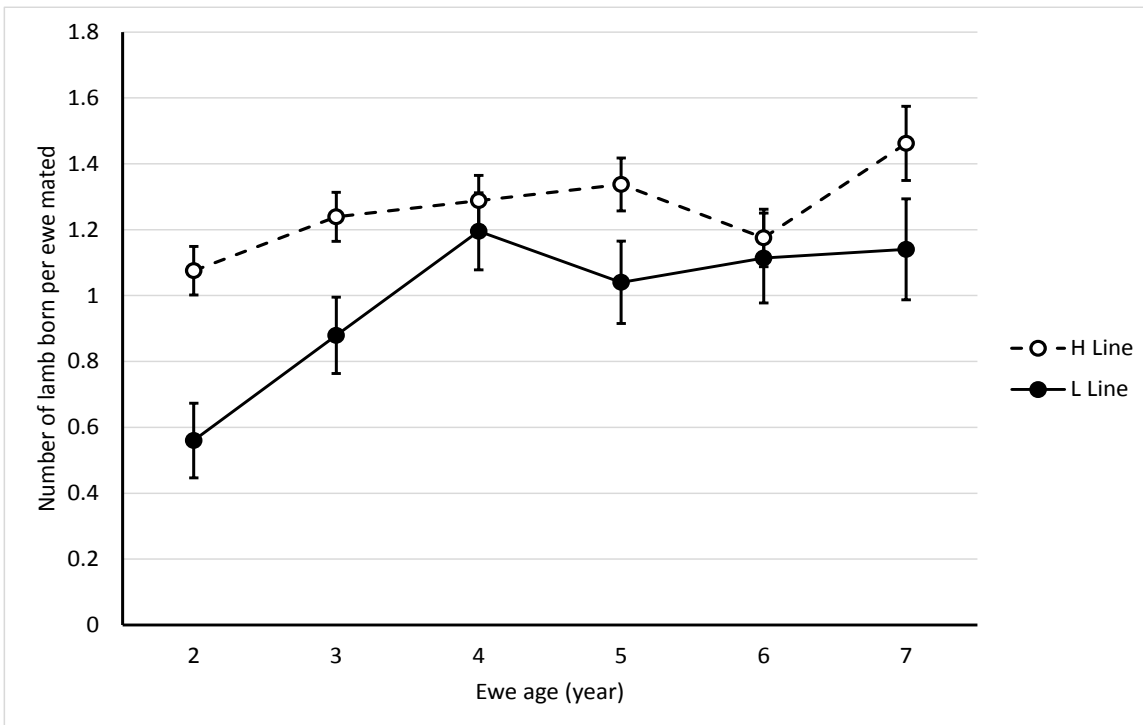
Figure 6.2 Least squares means (±SE) depicting the interaction of selection line x ewe age for NLB
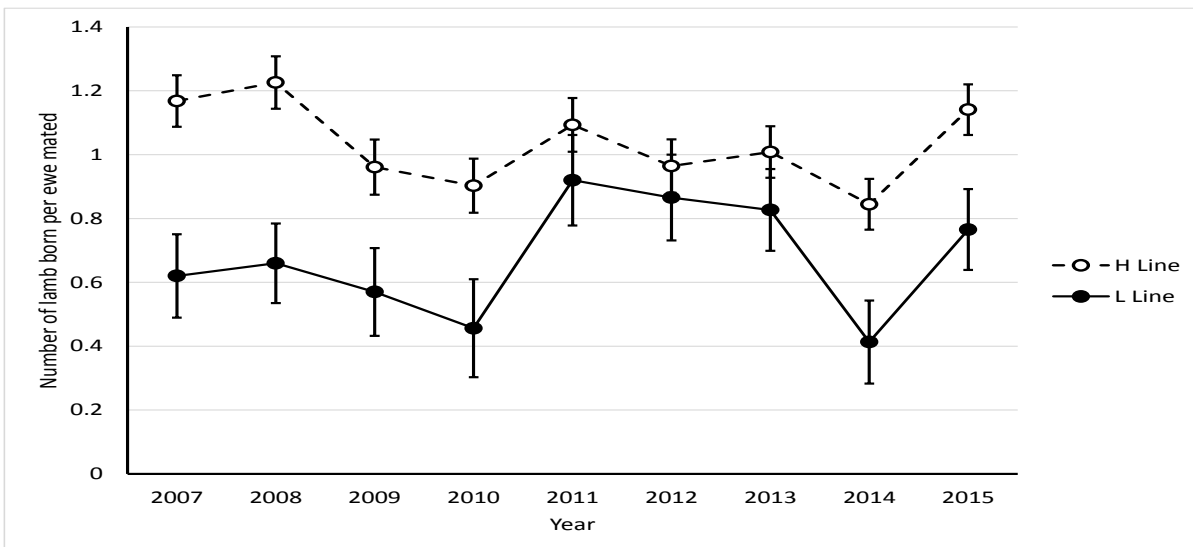
Figure 6.3 Least squares means (±SE) depicting the interaction of selection line x lambing year for NLW

122

Table 6.1 Descriptive statistics for raw and transformed FWEC and reproduction traits used in the study

Trait	Observations	Mean±SD	Range	Skewness	Kurtosis
FWEC	1581	1344±2610	0-25600	3.51	15.77
LogFWEC	1581	6.21±1.43	4.61-10.15	0.51	-0.80
Cube root FWEC	1581	7.22±6.18	0-29.5	0.60	-0.16
NLB	1633	1.18±0.69	0-3	-0.12	-0.67
NLW	1633	0.92±0.66	0-3	0.11	-0.63
	Total count	Zero count	Percentage (%)		
FWEC	1581	458	29		

Table 6.2 Significance of fixed effects and interactions included in the models fitted

Trait	NLB	Line (L)	L x NLB	Age (A)	L x A	Year (Y)	L x Y	NLB x Y
LogFWEC	0.72	0.62	0.51	0.15	0.62	**	0.93	0.63
CR FWEC	0.97	0.61	0.55	0.15	0.70	**	0.93	0.62
NLB	N.A.	**	N.A.	**	**	**	*	N.A.
NLW	N.A.	**	N.A.	**	0.12	**	*	N.A.

* - P<0.05; ** - P<0.01; Actual significance for P>0.05; N.A. – Not applicable for the analysis

Table 6.3 Least-squares means (±SE) depicting the fixed effect of line, ewe age, lambing year and NLB (for FWEC only) on FWEC and reproduction traits

Effect	FWEC		Reproduction	
	Log transformed	CR transformed	NLB	NLW
Lambing year	**	**	**	**
Selection line	0.62	0.61	**	**
H line	6.26±0.08 (423)	7.42±0.36 (409)	1.28±0.07	1.04±0.07
L line	6.33±0.12 (461)	7.75±0.52 (465)	1.00±0.10	0.68±0.09
Ewe Age	0.15	0.15	**	**
2-year	6.34±0.10 (466)	7.66±0.43 (450)	0.82±0.07	0.61±0.06
3-year	6.22±0.10 (404)	7.28±0.43 (386)	1.06±0.07	0.85±0.06
4-year	6.20±0.10 (399)	7.24±0.44 (379)	1.25±0.07	0.95±0.06
5-year	6.50±0.12 (503)	8.51±0.50 (617)	1.20±0.08	0.97±0.07
6-year	6.44±0.14 (523)	8.20±0.60 (551)	1.15±0.08	0.83±0.07
7+-year	6.06±0.16 (341)	6.67±0.70 (297)	1.36±0.10	0.95±0.09
NLB (regression)	0.036±0.047	0.095±0.207	N.A.	N.A.

** - $P<0.01$; Actual significance for $P>0.05$; N.A. – Not applicable for the analysis

Table 6.4 Log Likelihood values for all traits for 3 fixed- and random-effects models with the best model in bold text

Trait	Fixed effects	$+ \sigma^2_A$	$+ \sigma^2_{PE}$	$+ \sigma^2_A + \sigma^2_{PE}$
LFWEC	-1086.32	-1080.14	**-1078.95**	-1078.01
CRFWEC	-3391.26	-3384.71	**-3383.70**	-3382.71
NLB	-134.229	-105.829	-107.974	**-103.232**
NLW	-91.6574	**-82.0924**	-82.5469	-80.6772

Table 6.5 Phenotypic variance components (σ^2_P) and ratios (±SE) for body location specific log and cube root transformed faecal worm egg counts, number of lambs born and number of lambs weaned from single-trait analyses

Trait	σ^2_P	h²±SE	PE²±SE	t±SE
LFWEC	1.4017	0.03±0.03	0.06±0.03	0.09±0.03
CRFWEC	26.659	0.03±0.03	0.06±0.03	0.09±0.03
NLB	0.4278	0.12±0.04	0.08±0.04	0.19±0.03
NLW	0.3502	0.10±0.03	-	0.10±0.03

t: repeatability

Table 6.6 Total phenotypic variance (σ^2_P) as well as (co)variance ratios (±SE) for log transformed FWEC and the reproduction traits NLB and NLW analysed in a 3-trait repeatability model

Trait	LogFWEC	NLB	NLW
σ^2_P	1.402	0.4207	0.3923
(Co)variance ratios: h² in bold on diagonal; r_G below diagonal and r_P above diagonal			
LogFWEC	**0.03±0.03**	-0.01±0.03	-0.06±0.03
NLB	-0.71±0.32	**0.19±0.03**	0.67±0.01
NLW	-0.78±0.34	0.96±0.05	**0.11±0.03**

CHAPTER 7: AN ACROSS-FLOCK ANALYSIS ON FAECAL WORM EGG COUNTS IN MERINO SHEEP AT TYGERHOEK AND ELSENBURG

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7.1 Abstract

Previous South African studies on faecal worm egg count (**FWEC**) in South African Merinos have so far been limited to analyses within flocks. This study details an across-flock-season analysis on FWEC at the Tygerhoek and Elsenburg research farms using 9355 records collected between 1995 and 2016. Three discrete environments were identified, namely an autumn lambing season at Tygerhoek and autumn and winter lambing seasons at Elsenburg. The exchange of sires across environments allowed the estimation of sire x site/season as an indication of the genotype x environment interaction for FWEC. At 0.108 ± 0.020 FWEC was lowly heritable across environments. Additionally, variance ratios for the dam permanent environment and sire x site contributed respectively 0.026 ± 0.010 and 0.015 ± 0.006 to the observed phenotypic variation. It thus seemed as if selection for a reduced FWEC across flocks would result in slow genetic gains, while the probability of a major reranking of sires across site/season appears to be unlikely.

Keywords: genotype x environment, flocks, season

7.2 Introduction

So far, this study focused on the comparison of faecal worm egg count (**FWEC**) across breeds (Chapters 3, 4, 5, 6, 8 9) and lines (Chapter 3) as well as to derive genetic parameters for FWEC as such (Chapters 5) or in correlation with other traits of economic importance. However, all these studies have been done within flocks or localities. For FWEC as an indication of resistance to roundworm infestation to be applied to the national flock, as advocated by Cloete *et al.* (2014), it is important to conduct analyses across flocks. Across-flock analyses for FWEC have become commonplace in other sheep producing countries like Australia (Khusro *et al.*, 2004; Brown & Fogarty, 2016) and New Zealand (Pickering *et al.*, 2012). Sheep farmers in these countries are thus able to benefit from advances brought about

by using across-flock genomic breeding values for FWEC for the selection of replacements with resistance to GIN.

So far, South Africa has been lagging behind as far as these important advances are considered. This study therefore conducts the first across-flock/season analysis for FWEC in South African sheep, unlike for liveweight and fleece traits where across-flock analyses are common. Linkage provided by sires across flock/season groups additionally allowed the estimation of the sire x flock/season variance to serve as an indication of the genotype x environment interaction to be expected for a trait like FWEC.

7.3 Materials and methods

The study combined data from the Merino flocks maintained on the Tygerhoek and Elsenburg research farms. The management, breeding, husbandry and recordings of FWEC in the Tygerhoek flock is well described in the literature (Cloete *et al.*, 2007; Matebesi-Ranthimo *et al.*, 2014) and in this study (Chapter 4). Exhaustive information on these aspects in the Elsenburg Merino flock is also readily available (Mpetile *et al.*, 2015, Chapters 3, 5 and 6). Further information on these topics will thus be omitted from this study. Data at Tygerhoek were recorded on the breeding flock from 1995 to 2016, except for 2004 when no data were available (Cloete *et al.*, 2007). The data at Elsenburg was recorded over the same period, with the exception of 1997-1996 and 2000 (Mpetile *et al.*, 2015). Flock data at Tygerhoek and Elsenburg contributed respectively 6527 and 2563 records to the study.

After consideration it was decided to also include a small set of data consisting of 275 FWEC records obtained from a multiple ovulation and embryo transfer (MOET) project in the study. The MOET project sought to enhance predominantly Low (L) line ewe numbers in the Elsenburg flock although a similar number of High (H) line ewes were also flushed for comparison. Papers by Cloete *et al.* (2004; 2009) can be consulted for detailed information on the establishment, selection methods and responses to selection in these lines. The MOET programme was considered necessary when ewe numbers in the L line dropped below 50 (Naidoo, 2012). The surrogate ewes carrying these lambs lambed in autumn, in contrast with the main flock that lambed during winter. According to previous results (Mpetile *et al.*, 2017; Chapter 4) season had profound effects on the genetic variation of FWEC, with the heritability of FWEC using spring samples being substantially higher than for samples collected in autumn. Both the flock at Elsenburg and the MOET progeny were maintained at Elsenburg. However, they were maintained in separate flocks when FWEC samples were collected for

127

analysis. Also, being born in different seasons (winter for breeding flock progeny and autumn for MOET progeny), resulted sampling for FWEC being done in late summer-autumn for flock progeny and spring for MOET progeny. The different seasons were also well-linked through H and L sires used in both flocks. Surrogate dams, however were not linked, as they were surplus Dormer, SA Mutton Merino, Dohne Merino and Merino ewes from the flocks at Elsenburg and another resource flock at Langgewens involving Merino and Dohne Merino ewes subjected to either pure or crossbreeding (see Cloete *et al.*, 2015).

Given the well-established deviations from normality in FWEC data, individual records were transformed to natural logarithms after 100 was added to account for zero counts. The data so derived were analysed by single-trait analyses using ASREML (Gilmour *et al.*, 2015). Fixed effects fitted included contemporary group (90 levels involving year-site-season-sex combinations), age of dam (2-6+ years) and birth type (single vs. multiple). Previous research at both locations indicated that there was a profound interaction of sex with year at both locations (Cloete *et al.*, 2007; Mpetile *et al.*, 2015, Chapters 3, 4 and 5). These interactions stemmed from the maintenance of rams and ewes in single-sex groups when sampled for FWEC, validating the integration of sex with contemporary group. Random effects were sequentially added to the fixed-effects analysis to include the following models (in matrix notation):

$$y = Xb + e \qquad\qquad [1]$$

$$y = Xb + Z_1a + e \qquad\qquad [2]$$

$$y = Xb + Z_1a + Z_2c + e \qquad\qquad [3]$$

$$y = Xb + Z_1a + Z_3m + e \qquad\qquad [4]$$

$$y = Xb + Z_1a + Z_3m + Z_2c + e \qquad\qquad [5]$$

Where y was a vector of observations for FWEC; and b, a, m and c were vectors for fixed effects, direct additive variances, maternal/dam additive variances and dam permanent environmental variances; and e denoted the randomly distributed residual error. X, Z_1, Z_2 and Z_3 were denoted as the corresponding incidence matrices relating the fixed and random

effects. The covariance between direct and maternal additive genetic effects was not considered, since maternal additive effects proved to be miniscule. It was assumed that:

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

Where I represented an identity matrix; σ_a^2, σ_m^2, σ_c^2, and σ_e^2 were the variance components that indicated direct genetic, maternal genetic, maternal permanent environmental (PE) and residual (error) variances, respectively.

Likelihood Ratio tests (LRT) were used to test the significance of random effects. A random effect was considered significant when its inclusion in the model improved the log likelihood ratio using the Chi^2 distribution as a test statistic (Snyman *et al.*, 1996). Additionally, for a model with the same number of random effects, the model with the highest log likelihood fitted the data best. After the random effects model fitting the data best was determined, the random effect of sire x site/season (encompassing 576 levels) was added to the model by fitting an identity matrix linking sire x site/season effects to the data. The LRT test was then conducted additionally to assess this effect for significance.

Phenotypic variance was expressed as the total of all the estimated variance components. The derived heritability estimates were estimated by dividing significant (P < 0.05) variance components by the phenotypic variance.

7.4 Results

FWEC data were leptokurtic and skewed with extreme individual variation of raw FWEC records ranging from 0 to 32700 epg of wet faeces (Table 7. 1). The log transformation improved the distribution of the data appreciably resulting in a coefficient of variation of 17.9% for transformed data.

Environmental effects impacting on FWEC in the flocks under study were comprehensively dealt with in previous publications (Cloete *et al.*, 2007; Mpetile *et al.*, 2015) and chapters (Chapters 3 and 4) and are not discussed here. It is, however, important to note that contemporary group exerted a marked effect on the data (P < 0.001), while FWEC data depended less on age of dam (P = 0.57) and birth type (P = 0.07).

The LRT suggested that the log likelihood improved markedly from a model consisting of only fixed effects to a model including additive genetic effects (Table 7. 2). The addition of maternal

129

additive effects did, however, not result in a further improvement (P > 0.05). Adding maternal PE effects resulted in a further improvement in the log likelihood, as did the inclusion of sire x site/season.

Variance components and ratios for additive genetic, dam PE and sire x site/season effects are presented in Table 7. 3. It was evident that the across flock heritability of FWEC was relatively low at 0.108. Additionally, dam PE and sire x site/season contributed respectively 2.6 and 1.6 % to the observed phenotypic variation for FWEC.

7.5 Discussion

The nature of untransformed FWEC data and the improvement made by a log transformation have been discussed at length in the preceding chapters (Chapters 3, 4, 5, 6) and literature (Cloete *et al.*, 2007; Snyman, 2007; Matebesi-Ranthimo *et al.*, 2014). The observed descriptive statistics will thus not be covered in detail here, as it will overlap with previous discussions. It is important, though, to comment that the observed coefficient of variation is indicative of adequate phenotypic variation in FWEC to yield genetic gains should selection be prioritised.

The observed phenotypic variation was backed up by a relatively low across-flock heritability of 0.108 for FWEC. It should be noted that dam PE did not affects FWEC in previous studies in this thesis. The exclusion of this variation possibly resulted in a slightly lower heritability. However, it will be possible to obtain genetic gains across flocks although these gains may not necessarily be fast. The estimated heritability is within the ranges of 0.00 to 0.52 reported in the literature (Greeff *et al.*, 1995; Cloete *et al.*, 2007; Matebesi-Ranthimo *et al.*, 2014) and a fair reflection of previous heritability estimates in the flocks contributing the bulk of the data to this study (Cloete *et al.*, 2007; Matebesi-Ranthimo *et al.*, 2014; Chapters 3, 4, 5, 6 and 9). It is important though to start to collect more comprehensive data on FWEC in the local small stock genetic resource to allow the incorporation of this important input cost trait in the formal evaluation scheme.

The dam PE estimate of 0.026 is somewhat lower than comparable estimates of 0.048 – 0.051 derived previously for the Tygerhoek flock (Cloete *et al.*, 2007). It may well be that the accrual of additional dam, grand-dam and great grand-dam data assisted in the partitioning of animal variances away from dam PE in the present study. In a study by Safari & Fogarty, (2003) the values for permanent environmental effects were variable from 0.02 to 0.16.

Although the observed variation for sire x site/season was significant, it contributed less than 2% to the overall phenotypic variation. This variance ratio is consistent with previous estimates of between 2.2 and 2.5% variation attributed to sire x contemporary group for production traits in an across-flock analysis on South African Dohne Merinos (van Wyk *et al.*, 2008). No other comparable studies were obtained in literature. However, it is important to note that a marked reranking of sires in different flock/season groups appears to be unlikely.

7.6 Conclusion and future direction

This study confirmed significant across-flock genetic variation in FWEC in local sheep flocks. It therefore paves the way for further exploration of the genetic improvement of FWEC as an input trait in the local ovine genetic resource. It is important to note that the derived heritability was not particularly high, but still backed up by sufficient levels of phenotypic variation to sustain genetic progress. Moreover, it is foreseen that further across-flock studies incorporating more flocks will provide more accurate estimations of other sources of variation, such as maternal effects and sire x flock/season effects. The preliminary results obtained in the present study used the sire x flock/season variance which served as an indication of the genotype x environment interaction.

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7.8 Annexes of Tables

Table 7.1 Descriptive statistics for the faecal worm egg count data (n=9355) recorded in the Tygerhoek and Elsenburg Merino flocks and used in this study

	Trait		
Statistic	Raw FWEC	Log transformed FWEC + 100	
Mean	1960	6.97	
Standard deviation	2599	1.25	
Coefficient of variation (%)	133	17.9	
Skewness	4.029	-0.318	
Kurtosis	29.781	-0.581	
Range	0 – 34000	4.61 – 10.44	
	Total records	Zero counts	Percentage (%)
FWEC	9355	2466	26.4

Table 7.2 Log likelihood ratios for the various models fitted in the across-flock analysis conducted on the Tygerhoek and Elsenburg Merino flocks (deviations from the model including additive animal as a single random variable are given in brackets for those modes containing >1 random effect)

Effect fitted	Log likelihood value
Fixed effects (FE) only	-3853.61
FE + σ^2_a	-3790.71
FE + σ^2_a + σ^2_m	-3789.18 (1.53)
FE + σ^2_a + σ^2_{pe}	-3787.56 (3.15)
FE + σ^2_a + σ^2_m + σ^2_{pe}	-3787.55 (3.16)
FE + σ^2_a + σ^2_m + σ^2_{pe} + $\sigma^2_{sire:site/season}$	-3783.74 (6.97)
FE + σ^2_a + σ^2_{pe} + $\sigma^2_{sire:site/season}$ (model of choice)	-3783.76 (6.95)

σ^2_a = additive genetic variance; σ^2_m = maternal genetic variance; σ^2_{pe} = dam permanent environmental variance and $\sigma^2_{sire:site/season}$ = sire by site/season variance

Table 7.3 Estimated variance components and ratios for FWEC in the across-flock analysis of Merinos from Tygerhoek and Elsenburg

Variances Components	Value
$\sigma^2 a$	0.08827
$\sigma^2 pe$	0.02136
$\sigma^2_{sire:site/season}$	0.01333
$\sigma^2 e$	0.6952
$\sigma^2 p$	0.81815
Ratios (± SE)	
h^2	0.108 ± 0.020
pe^2	0.026 ± 0.010
sire x site/season	0.015 ± 0.006

σ^2_a = additive genetic variance; σ^2_{pe} = dam permanent environmental variance and $\sigma^2_{sire:site/season}$ = sire by site/season variance; σ^2_e = residual (error) variance; σ^2_p = phenotypic variance; h^2 = heritability; pe^2 = dam permanent environmental variance ratio

CHAPTER 8: FAECAL WORM EGG COUNTS IN DORMER AND SA MUTTON MERINO LAMBS AND EWES

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8.1 Abstract

South African studies on faecal worm egg count (**FWEC**) following at least 10 weeks of natural parasite challenge as an indirect measure of parasite resistance have so far been limited to Merinos. This study involves the comparison of Dormer and SA Mutton Merino lambs and ewes for FWEC under Mediterranean conditions. Parasite eggs were counted using the McMaster technique, with a sensitivity of 100 eggs /g wet faeces. The fixed effects of breed, ewe age, sex as well as the interactions of breed x birth year, sex x birth year and breed x lambing year were significant, respectively (P < 0.01). Overall, in the analysis on lambs had higher means for FWEC compared to ewes suggesting that they might be more susceptible to the nematodes compared to the adult animals. SA Mutton Merinos accordingly had higher means for FWEC than Dormer in the analysis on mature ewes. However, the magnitude of the breed differences varied among years. Future work is needed to determine the effect of parasite load on production traits between the two breeds.

Keywords: Gastrointestinal nematodes, faecal worm egg counts, breed differences

8.2 Introduction

Despite many years of availability of anthelmintic drenches to treat and control parasitism; combined in some cases with pasture management, gastrointestinal nematodes remain a major threat in small stock production. Misuse and overuse of anthelmintics has led to continuing development of anthelmintic resistance by the parasites (Kenyon *et al.*, 2009; Molento *et al.*, 2011). In addition, the consumer perception on use of chemicals in meat production is forcing the producers to look for other alternatives in dealing with parasitism (Halbrendt *et al.*, 1991; Tackie *et al.*, 2015). Therefore, alternative strategies to control GIN's like selecting for sheep breeds that are genetically resistant to gastrointestinal nematodes is appropriate for consideration.

Variation in parasitism is influenced by both environmental and genetic factors. Breed differences are commonly regarded as indicative of genetic variation in traits where insufficient data for the estimation of genetic parameters is available. Studies on the genetic variation in faecal worm egg count (**FWEC**) as an indirect measure of parasite resistance have so far been limited to Merinos in South Africa. FWEC has been traditionally used as an indicator trait to identify resistant sheep (Karlsson & Greeff, 2006; Kemper *et al.*, 2010; Morris *et al.*, 2010; 2011). Literature reports overwhelming evidence of an existing genetic variation for FWEC between and within breeds (Baker *et al.*, 1999; 2002; Morris *et al.*, 2000; Woolaston & Windon, 2001; Gruner *et al.*, 2003; Nimbkar *et al.*, 2003). It is contended that the use of genetically resistant sheep breeds in livestock production would improve the overall production and animal well-being. Moreover, such breed differences have a potential to provide the prospect to investigate the unique mechanisms of parasite resistance that may not be available in susceptible breeds (Guo *et al.*, 2016). At present, there are no studies available in the South African literature about differences in parasite loads between Dormer and SA Mutton Merino breeds. As respectively the dominant terminal sire breed and the most important dual-purpose breed in South Africa (Cloete & Olivier, 2010) it is important to study FWEC in these breeds.

Against this background, the objectives of this study were to evaluate the effect of breed and sex on FWEC of yearling Dormer and SA Mutton Merino progeny maintained under Mediterranean conditions within the same flock, as well as differences in faecal load in mature breeding ewes.

8.3 Materials and methods

The data from this study came from the registered Dormer and SA Mutton Merino studs maintained at the Elsenburg Research Institute near Stellenbosch. Details on the description of these flocks, their origin and early breeding are detailed by Van der Merwe (1976) and Vosloo (1967) respectively. More recently Van Wyk *et al.* (2003; 2008) updated information on the Dormer flock, while Cloete *et al.* (2004b) provided updated information on the SA Mutton Merino flock. The location of the experimental site is in Boland region, about 10 km north of Stellenbosch in Western Cape Province of South Africa, at an altitude of about 177 m above the sea level (33° 51' S, 18° 3D' E). The climate is Mediterranean with an average annual precipitation of 605.8 mm which mostly falls in winter. Animals of both breeds in this study were maintained as a single flock throughout the year, except at mating to single sires

in small groups in October-November. Lambs were identified with their dams within 24 hours of birth in an autumn lambing season (March-April), allowing information on the pedigree and breed to be updated. Lambs of both breeds grazed in a single flock until weaning but were separated according to sex shortly after weaning at approximately 4 months. Sex-specific groups were maintained under similar management practices and were primarily kept on dryland pastures consisting of lucerne (*Medicago sativa*) and oat (*Avena sativa*) fodder crops. They also occasionally had access to irrigated kikuyu (*Pennisetum clandestinum)* and lucerne pastures. The study involved lambs that were born from 2007-2014 as well as those born in 2016. FWEC data of the 2-5-year-old dams of these lambs were available for the period from 2006-2017.

None of the animals used in this study were selected for parasite resistance. In October-November, the animals were naturally challenged with parasites for a period of at least 10 weeks at an age of approximately 8 months. During that period, the animals were likely to be infected with a mixture of *Trycostronglyus spp*, *Osterstargia* and *haemonchus contortus*. Following this challenge, faecal samples were collected directly from the rectum of individual lambs and were sent to Stellenbosch Provincial Veterinary Laboratory for analysis. Samples were collected in the ewes using the same methods, but the samples were collected in summer (February) approximately 6 weeks before lambing commenced. The faecal samples collected from both ewes and lambs were counted using the McMaster technique, with a sensitivity of 100 eggs per gram of wet faeces (Van Schalkwyk *et al*., 1994).

The data was analysed using ASREML software (Gilmour *et al*., 2015). The fixed effects fitted were breed (Dormer vs SA Mutton Merino), birth year (2007 – 2014; 2016), sex (male or female), age of dam (2-6 years of age) and birth type (single or multiple), as well as two-factor interactions between these fixed effects. The analysis on ewes included breed, lambing year and ewe age as fixed effects, as well as significant two-factor interactions between these effects. Heritability estimates for FWEC were not derived in this study as it was reported (and published) in Chapter 9 along with the FAMACHA© traits for the lambs studied.

8.4 Results

Descriptive statistics indicated FWEC data for Dormer and SAMM sheep were leptokurtic and skewed with extreme individual variation of raw FWEC records ranging from 0 to 34000 epg of wet faeces in lambs and 0 to 39600 in ewes; with estimated means across breeds

exceeding the standard deviation (Table 8.1 and 8.2). The log transformation improved the distribution of the data appreciably resulting in coefficients of variation of 17.9% in lambs and 22.2% in ewes.

The least squares means portraying the effects of breed, sex and birth type on log transformed FWEC in Dormer and SA Mutton Merino lambs are presented in Table 8.3. The fixed effects of breed and sex significantly affected FWEC (P < 0.01), with the least-squares-means of SA Mutton Merino lambs and rams being higher than those of Dormers ewes, respectively. Means of FWEC for birth type were significantly different. Additionally, the regression of log transformed FWEC on age of the lamb amounted to -0.015 ± 0.003, suggesting that older lambs had lower values for FWEC. Transformed FWEC was also independent of dam age (P = 0.50).

Breed also impacted on the FWEC of mature ewes (P < 0.01), with Dormer maintaining lower FWEC compared to SA Mutton Merinos (Table 8.4). Ewe age was also statistically significant with 2- and 6-year-old ewes showing the highest parasite load compared to 3- to 5-year-old ewes.

Breed interacted with birth year for log-transformed (FWEC + 100) (Figure 8.1). The back transformed FWEC of Dormer lambs exceeded that of SAMM lambs by almost 8-fold during 2007 (P < 0.01; 480 epg wet faeces in SAMM lambs vs. 3807 epg in Dormers). Subsequent years were characterised by generally lower back transformed FWEC values in Dormers. This advantage in favour of Dormers (i.e. lower counts) reached significance in 2008, 2009, 2011, 2012, 2013 and 2014 (P < 0.05). Significant breed differences in favour of Dormers ranged from 36% in 2008 (1850 for SA Mutton Merinos vs. 1364 for Dormers) to almost 3-fold in 2011 (2222 vs. 793 respectively) and 2014 (1385 vs. 482 respectively). Differences were independent of breed (P > 0.05) in 2010 and 2016, although absolute means still favoured Dormers.

Breed was also involved in a significant interaction with lambing year for log-transformed (FWEC + 100) in mature ewes (Figure 8.2). In contrast to the overall means, the back-transformed mean for FWEC in Dormer ewes in 2011 exceeded that of SA Mutton Merino ewes by almost 4-fold (4872 in Dormers vs. 1227 in SA Mutton Merinos; P < 0.05). Interestingly, absolute means for Dormers also exceeded those of SA Mutton Merinos in years surrounding 2011, namely from 2009-2012. In the remaining years, absolute means favoured

mature Dormer ewes throughout. Significant differences in favour of the latter breed ranged from 41% in 2007 (1521 vs. 2138) to more than 2-fold in 2008 (780 vs. 2004), 2013 (129 vs. 259) and 2016 (85 vs. 183; P < 0.05).

Log transformed FWEC was similarly affected by the interaction of sex x birth year in young sheep (P < 0.05; Figure 8.3). Generally, the annual least-squares means for ram lambs were higher than those of their ewe contemporaries in 2007, 2008, 2010, 2011 and 2012, the advantage in favour of ewes ranging from 44% in 2008 (1906 for rams vs. 1323 for ewes) to almost 7-fold in 2010 (1391 vs. 205 respectively; P < 0.01). No conclusive advantages in favour of either rams or ewes were found for 2009, 2013, 2014 and 2016 (P > 0.05).

8.5 Discussion

Historic datasets consisting of records from Dormer and SAMM lambs and ewes was used to investigate the effect of breed, sex and age on log transformed FWEC. Descriptive statistics suggested a marked variation in FWEC, ranging from 0 to 39600 epg of wet faeces. Individual variation for raw FWEC is commonly reported in literature, with standard deviations commonly exceeding the corresponding mean and coefficients of variation exceeding 100% (Khusro *et al.* 2004; Snyman 2007; Matebesi-Ranthimo *et al.* 2014). The log transformation was applied in this study to reduce the variation and improve the statistical properties of the data. Log transformation of the data is commonly reported in literature (Bishop *et al.*, 1996; Baker *et al.*, 2003; Cloete *et al.*, 2007). The log transformation improved the distribution of the data appreciably, yielding a coefficient of variation of 17.9% and 22.2% in lambs and ewes, respectively. These values suggest sufficient phenotypic variation of FWEC to yield genetic gains should selection be required.

The fixed effect of breed on FWEC was significant (P < 0.01), with the overall least-squares-mean of SAMM lambs and ewes being higher than in Dormers. Appreciable variation exists amongst different ovine hosts in their reaction to gastrointestinal nematodes. This variation exists between (Gruner *et al.*, 2003; Good *et al.*, 2006) and within breeds when considering different helminth species (Woolaston *et al.*, 1990; Woolaston & Windon, 2001). FWEC variation between and within breeds is influenced by host differences in the ingestion of infective larvae, harnessing an immune response and by the type of parasite infesting the host (Stear *et al.*, 2007; Valilou *et al.*, 2015). Good *et al.* (2006) similarly reported a significant effect of breed on FWEC. In their study, Texel sheep were more resistant to natural infection than

Suffolk sheep. Other literature sources also reported various sheep breeds being able to resist helminth infestation, i.e. Red Massai (Baker *et al.*, 2003), Dorper (Vannimiseti *et al.* 2004) and Florida sheep (Díaz *et al.* 2000). The identification of breeds being able to tolerate or resist gastrointestinal nematodes may reduce the need for anthelmintic treatments. It is notable that Dormer sheep (both ewes and lambs) in this study seemed to be able to resist infestation by what is likely to be a mixed challenge at the experimental site better than SA Mutton Merino ewes in most years. No previous studies on FWEC in these breeds could be sourced, but it is accepted that breed differences in traits not yet subjected to genetic analyses may reflect underlying genetic variation. Significant genetic variation in FWEC was indeed reported for Dormer and SA Mutton Merino lambs (Chapter 9; Cloete *et al.*, 2016). However, breed differences were not consistent across years for either lambs or ewes. Although Dormers generally outperformed SA Mutton Merinos for FWEC in most years, contrasting results were found in a single year for both ewes and lambs. As this is the first study comparing FWEC means to our knowledge for these breeds we did not find comparable results in the literature. The reason for this lack of stability in breed means is not known at present and should be studied further. It is known that Dormers are generally fatter than SA Mutton Merinos at slaughter (Cloete *et al.*, 2004a). The same trend was seen of subjective fat scores in Chapter 9. Brown & Swan (2016) reported that the genetic correlation of ultrasound fat depth with FWEC was negative in direction, indicating that fatter animals may have lower FWECs. It is not sure at present how these results contribute to the breed difference in this chapter.

The repeatability of a trait is often regarded as the upper limit of heritability. The observed repeatability in the mature-ewe analysis suggested limited genetic variation, as did the results of Chapter 6. Further research on the genetics of FWEC in mature ewes is indicated.

Male lambs seemed to be more susceptible to natural challenge compared to female lambs. Higher means for FWEC in male lambs compared to females is commonly reported in literature (Cloete *et al.*, 2007; Idris *et al.*, 2012; Matebesi-Ranthimo *et al.*, 2014). The significant effect of gender on FWEC could be caused by various reasons, including: i) the lack of a uniform environment as the animals grazed in different flocks, as indicated in chapter 3 ii) Different hormonal profiles between male and female lambs which may affect the immune response of lambs to infection (Gauly *et al.*, 2006) (iii) the morphology or physiological status of each sex (Zuk & McKean, 1996) and iiii) different feeding behaviour between the two sexes, with males having been shown to be more aggressive feeders than females. Abuargob *et al.*

140

(2015) did not report a significant sex effect for FWEC. Khusro *et al.* (2004) on the other hand reported variable results. In their study, yearling rams had a lower faecal load compared to females but the opposite was true in hoggets. With that in mind, it is important for the researchers to always consider sex x birth year effects when interpreting results of this nature. It is important to include this effect in the statistical model for the variation it controls.

The interaction between birth year x sex was statistically significant in the present study, agreeing with other studies by Khusro *et al.* (2004), Cloete *et al.* (2007), Matebesi-Ranthimo *et al.* (2014). This interaction was discussed in Chapters 3 and 4 and will not be repeated here.

Ewe age was statistically significant for log transformed FWEC, with 2- and 6-year-old ewes showing highest faecal worm egg count compared to 3-5-year-old ewes. These results suggest that younger animals are more susceptible to infection compared to older animals but, the ability to resist the worm challenge may decline with age above 5 years. This observation could be attributed to the fact that younger ewes are still growing themselves while having to sustain pregnancy. So, there might be an increase in demand of nutrients for growth which competes with the ability of younger ewes to fight infection. The ability of ewes to resist infection is improved in animals in the prime phase of their lives (i.e. from 3-5 years of age). This ability to withstand parasite challenge may then diminish as the ewes reach 6 years. No comparable results were observed in literature.

8.6 Conclusion and future direction

The Dormer sheep breed was apparently more resistant to natural challenge with gastrointestinal nematodes compared to SA Mutton Merino lambs, although this breed superiority was not uniform across years in either lambs or mature ewes. The reason for the overall breed difference is poorly understood at present as neither of the breeds has been selected for a reduced FWEC. It would also be informative to understand the causes for the variability of the breed effect across birth year groups. Additionally, further research on the genetic and phenotypic correlations of parasite load with production traits is needed in these breeds.

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8.8 Annexes of Figures and Tables
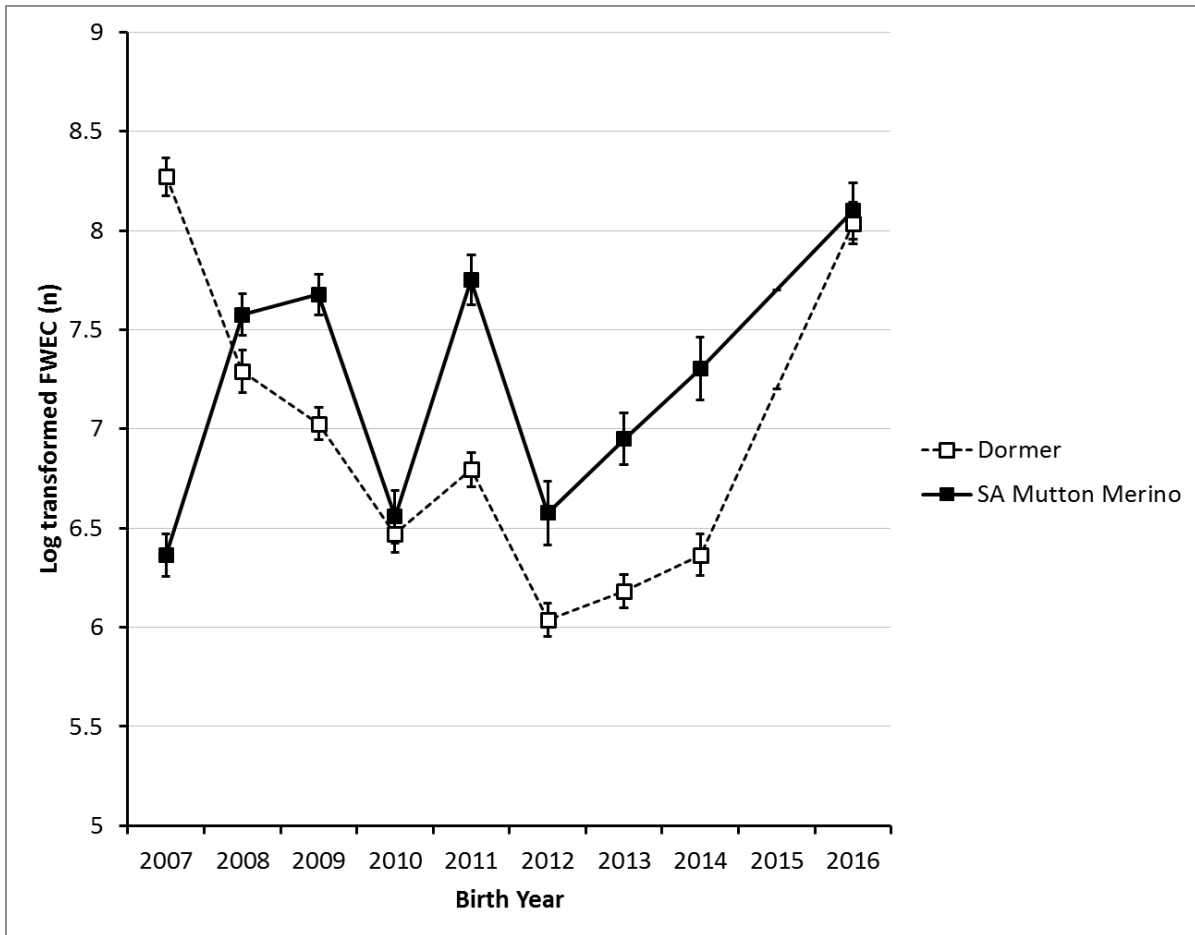
Figure 8.1 Least-squares means depicting the interaction of breed (Dormer and S.A. Mutton Merino) of lambs with birth year for the natural logarithm of faecal worm egg count (FWEC)
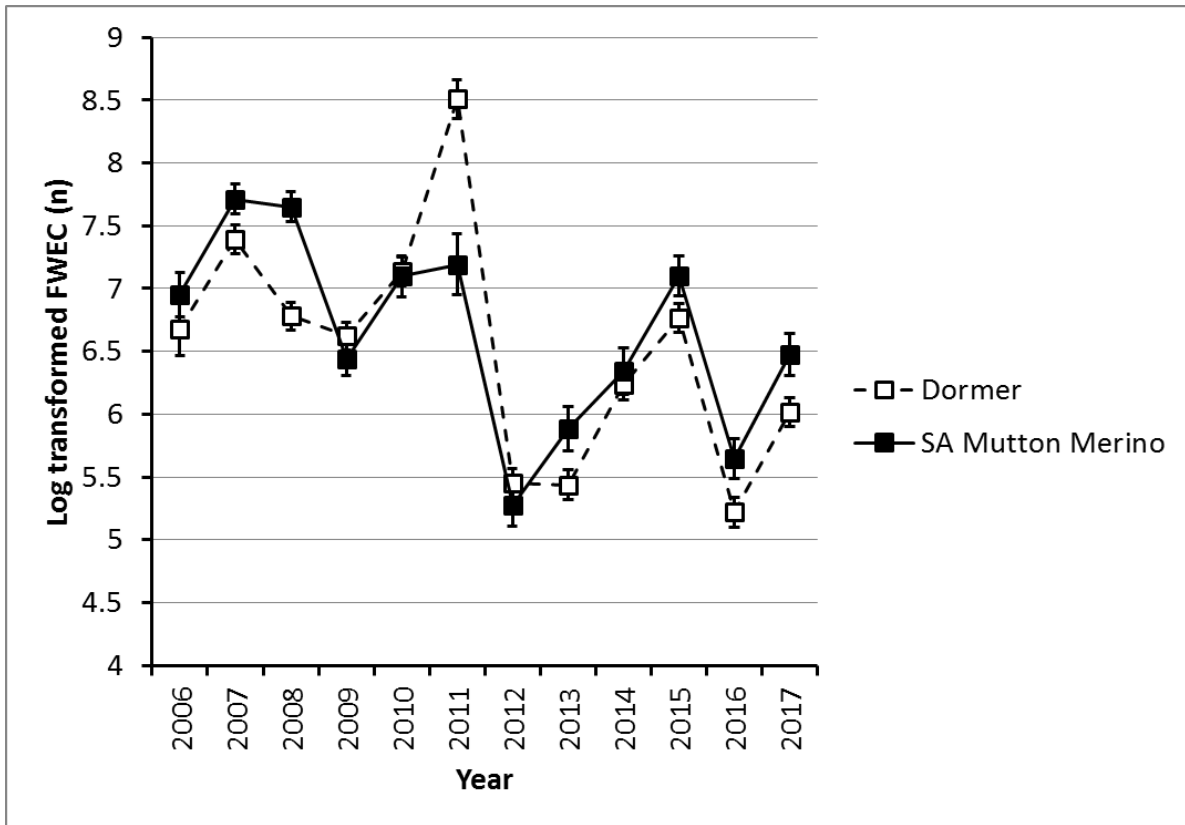
Figure 8.2Least-squares means depicting the interaction of breed with lambing year for the natural log of of faecal worm egg count (FWEC) in mature Dormer and SA Mutton Merino ewes used in the study
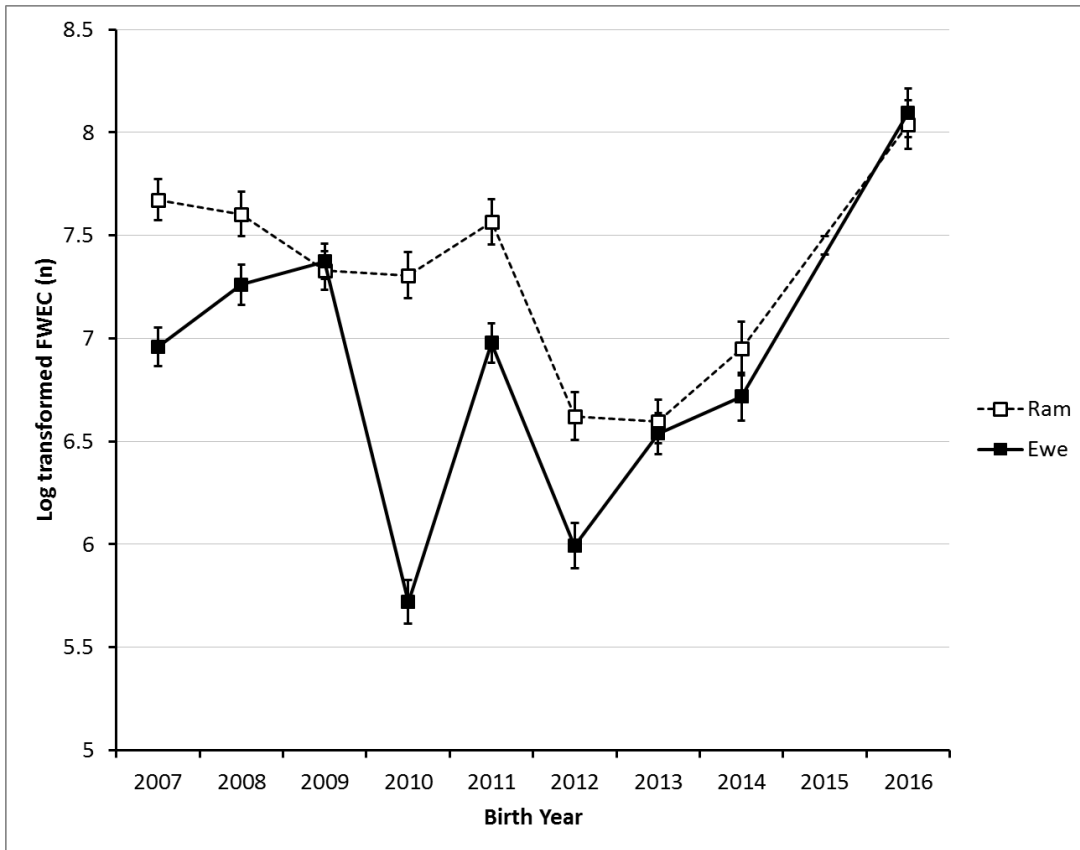
Figure 8.3Least-squares means depicting the interaction of sex with birth year for the natural log of of faecal worm egg count (FWEC) in Dormer and SA Mutton Merino lambs

Table 8.1 Descriptive statistics for the faecal worm egg count data (n=1860) on Dormer and SA Mutton Merino lambs used in the study

Statistic	Trait	
	Raw FWEC	Log transformed FWEC + 100
Mean	1960	6.97
Standard deviation	2599	1.25
Coefficient of variation (%)	133.0	17.9
Skewness	4.029	-0.318
Kurtosis	29.781	-0.581
Range	0 – 34000	4.61 – 10.44

Table 0.2 Descriptive statistics for the faecal worm egg count data (n=2003) on mature Dormer and SA Mutton Merino ewes used in the study

Statistic	Trait	
	Raw FWEC	Log transformed FWEC + 100
Mean	1899	6.58
Standard deviation	3400	1.46
Coefficient of variation (%)	179	22.2
Skewness	3.708	0.230
Kurtosis	20.151	-0.914
Range	0 – 39600	4.61 – 10.59

Table 0.3 Least-squares means (±SE) depicting the effects of breed, sex and birth type on log transformed FWEC in Dormer and SA Mutton Merino lambs

Effect and level	Number of observations	Log transformed FWEC + 100	Back-transformed mean
Breed		**	
Dormer	1202	6.94 ± 0.03	934
SA Mutton Merino	658	7.21 ± 0.05	1247
Sex		**	
Ram	851	7.30 ± 0.04	1378
Ewe	1009	6.85 ± 0.04	842
Birth type		0.83	
Single	582	7.08 ± 0.05	1087
Multiple	1278	7.07 ± 0.03	1073
FWEC	Total count	Zero count	Percentage (%)
Ewe	2003	414	20.7
Lamb	1860	192	10.3

* - P < 0.05; ** - P < 0.01; Actual significance for P > 0.05

150

Table 0.4 Least-squares means (±SE) depicting the effects of breed and ewe age on log transformed FWEC in mature Dormer and SA Mutton Merino ewes

Effect and level	Number of observations	Log transformed FWEC + 100	Back-transformed mean
Breed		**	
Dormer	1260	6.52 ± 0.04	579
SA Mutton Merino	741	6.65 ± 0.05	671
Ewe age (year)		*	
2	434	6.67 ± 0.06	685
3	553	6.57 ± 0.06	611
4	450	6.53 ± 0.06	588
5	358	6.51 ± 0.07	571
6	206	6.64 ± 0.09	667

* - P < 0.05; ** - P < 0.01

CHAPTER 9: GENETIC PARAMETERS INVOLVING SUBJECTIVE FAMACHA© SCORES AND FAECAL WORM EGG COUNTS ON TWO FARMS IN THE MEDITERRANEAN REGION OF SOUTH AFRICA

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9.1 Abstract

Data from two research farms, Elsenburg and Tygerhoek, were used to study genetic parameters for traits measured as part of the FAMACHA© system, as well as for the natural logarithm of faecal worm egg count + 100 (FWEC). The traits assessed subjectively as part of the FAMACHA© system were eye score (ES), rib fat score (FSR), loin fat score (FSL) and dag score (DS). The study used between 1701 and 1815 records of Dormer and SA Mutton Merino weaner lambs at Elsenburg and between 1531 and 2219 Merino hoggets at Tygerhoek. Direct heritability estimates at respectively Elsenburg and Tygerhoek amounted to 0.13 and 0.12 for ES, 0.12 and 0.38 for FSR, 0.17 and 0.30 for FSL, 0.31 and 0.31 for DS as well as 0.12 and 0.14 for FWEC. The genetic correlation between ES and FWEC was significant at 0.66 at Elsenburg. This correlation suggests that selection for low eye score would result in a change in FWEC. This correlation suggests that animals with anaemic eye scores would also have higher values for FWEC. Negative genetic correlations (ranging from -0.45 to -0.82) among traits indicated that animals with a higher ES (i.e. higher levels of anaemia) would have lower fat scores (i.e. they were leaner) both at Elsenburg and Tygerhoek. Fat scores (FSR and FSL) were genetically highly correlated at both localities (0.92 at Elsenburg and 0.80 at Tygerhoek), suggesting that they were genetically very similar traits. Genetic correlations involving DS in hoggets and FWEC were mostly low, variable in sign and magnitude and not significant. The practical implications of these results were discussed.

Keywords: parasite burden, resistance, eye score, fat score, helminth control, subjective scores

9.2 Introduction

There is general consensus that the continued treatment of gastro-intestinal parasites with drenches as the first line of defence has become unsustainable (Kelly *et al.*, 2010). Gastro-intestinal nematodes has shown the ability to become resistant to the all active compounds in major drenches, leading to farming with sheep becoming unsustainable in areas where widespread resistance occurs.

Because of this, alternative measures need to be exploited to manage gastro-intestinal parasites in a sustainable manner (Kelly *et al.*, 2010). An important component in almost all integrated pest management (IPM) programmes involves the issue of host resistance. It has been proven that selection based on faecal worm egg counts in sheep has resulted in marked responses in host resistance to infestation by gastro-intestinal helminths (Woolaston & Piper, 1996; Karlsson & Greeff, 2006; Morris, 2009). Such selection has led to a marked reduction in the contamination of pastures by worm eggs, resulting in a reduced need for drenching, and resultant economic gains (Greeff *et al.*, 2006). It is therefore understandable that faecal worm egg counts are routinely recorded in sheep flocks in Australia, as part of national small stock improvement (Khusro *et al.*, 2004; Brown *et al.*, 2010). However, faecal worm egg counts may not always be a true reflection of the parasite burden of animals (Reinecke & Groeneveld, 1991), while infestation may be transient and seasonal. Moreover, despite being seen as potentially applicable to both smallholder and pastoral small stock production systems in Kenya (Gicheha *et al.*, 2007), the infrastructure to conduct faecal worm eggs counts on a routine basis may not always be available or affordable, especially in rural areas of developing countries. This situation requires that alternatives need to be sought to ensure sustainable small stock production under these conditions.

The FAMACHA© system has been proposed by Bath & Van Wyk (2009) as an alternative to enable sheep farmers to treat specific sheep in their flocks, in contrast to treating all sheep present. According to this system, strategic treatment of sheep may be based on the subjective scores of the conjunctivae of the eye of the sheep in cases where high burdens of haemotophageous nematodes, like *Haemonchus contortus*, are present. The application of this system reduced drenching costs without compromising production of sheep under South African (Leask *et al.*, 2013) and Brazilian (Molento *et al.*, 2009) conditions. Such scores have been shown to be variable and heritable in sheep, while favourable genetic correlations with haematocrit and faecal worm egg counts were also reported (Riley & Van Wyk, 2009).

153

However, the principle does not apply to circumstances where non-haemotophageous nematodes form the bulk of the gastro-intestinal parasite challenge. For such conditions, Bath & Van Wyk (2009) recommended that eye conjunctivae scores be supplemented with condition scores and dag scores. These scores were seen as practical by both commercial and resource-poor communal farmers in South Africa, while the system has also been considered elsewhere in the world, including Brazil (Sotomaior *et al.*, 2012; Vilela *et al.*, 2012; Maia *et al.*, 2014; 2015; Pereira *et al.*, 2016), the United Kingdom (Olah *et al.*, 2015), Malaysia (Mohammed *et al.*, 2016) and India (Thomas & Syamala, 2016). However, research in Mediterranean regions (where non-haematophageous helminth species such as *Teladorsagia* spp, *Trichostrongylus* spp and *Nematodirus* spp predominate) like Italy (Di Loria *et al.*, 2009) and Greece (Papadopoulos *et al.*, 2013) reported that FAMACHA© eye scores did not always accurately predict anaemia in small ruminants. Similar reasoning applied to temperate regions like Germany (Moors & Gauly, 2009). The latter authors made out a case for a more objective assessment of the colour of small ruminant eye conjunctivae, for instance by using a colour meter.

Against this background, genetic parameters were estimated for scores recommended as part of the FAMACHA© system (Bath & Van Wyk, 2009), as well as for faecal worm egg counts, on two properties in the Mediterranean region of South Africa. Based on the aetiology of gastro-intestinal helminth infestations on intensive irrigated pastures compared to dryland pastures (Reinecke, 1994), the properties were chosen to represent a situation where dryland pastures were supplemented with irrigated pastures, as compared to dryland pastures exclusively.

9.3 Material and Methods

9.3.1 Locations and experimental animals

The study was conducted at two locations, namely Elsenburg and Tygerhoek. Elsenburg is situated about 10 km north of Stellenbosch in the Western Cape province of South Africa at 33°51' S and 18°50' E, at an elevation of 177m. The climate is Mediterranean, with 77% of the total average annual precipitation of 606 mm being recorded from April to September. Tygerhoek is situated adjacent to the Town Riviersonderend in the Southern Cape at 34°08' S and 21°11' E and at an elevation of 425m. The total annual precipitation averages 425 mm, 60% of which is recorded during winter. The 43% higher rainfall recorded at the Elsenburg environment, as well as well-developed mountain catchment areas, allows for adequate

154

storage of water to allow for the irrigation of > 40 ha primarily used as pastures for the sheep flocks on the farm. These irrigated paddocks are supplemented with adequate dryland pastures, used mostly during winter and spring. Irrigated pastures at Tygerhoek are scarce, and the animals mostly rely on dryland pastures and crop residues throughout the year.

Data were obtained of weaner lambs born from 2007 to 2014 in the Elsenburg Dormer flock (Van Wyk *et al.*, 2003) and the Elsenburg South African (SA) Mutton Merino flock (Cloete *et al.*, 2004b). All these lambs were maintained in two separate flocks, separated on sex. These lambs mostly grazed dryland and irrigated lucerne (*Medicago sativa*) paddocks, as well as irrigated paddocks with the tropical grass kikuyu (*Pennisetum clandestinum*). According to Reinecke *et al.* (1987), irrigated kikuyu paddocks are considered to be a "paradise for all nematode species". It can thus be contended that the incorporation of irrigated kikuyu paddocks in the grazing management of flocks at Elsenburg arguably contributed to the parasite burden of these animals.

Two-tooth Merino hoggets born from 2006 to 2012 formed the basis of the experiment at Tygerhoek. These animals were the progeny of three selection lines (the Fleece weight+ line, the fine wool line, and an unselected Control line) as described by Cloete *et al.* (2007). All three lines were present for the period from 2006 to 2009. However, the Fleece weight+ and Control lines were phased out in 2010, meaning that only the fine wool line was retained. The pastures used to maintain the animals at Tygerhoek were predominantly dryland lucerne, supplemented with oat (Avena sativa) fodder crops during winter and spring as well as wheaten stubble lands being used after harvest in the summer. It is of interest to note that stubble lands are generally considered to be free from the eggs of gastro-intestinal nematode parasites and safe for utilisation by sheep without fear of infestation (Reinecke & Louw, 1989). As a matter of fact, larvae excreted by infested weaners on stubble lands failed to re-infest the animals. This was attributed to the unfavourable environment for larvae survival on stubble lands in the latter study.

No intentional selection against helminth infestation or any potential related trait was practiced at either locality. However, the impact of potential indirect genetic changes stemming from the selection regimes in place in the respective flocks is dealt with in the Discussion.

9.3.2 Recordings

Data that were recorded at both localities included the following subjective linear scores using the FAMACHA© system (Bath & Van Wyk, 2009):

- Eye colour score (ES): Score based on the colour of the conjunctivae of the eye of the sheep, with 1 – pink (not anaemic) to 5 – pale (very anaemic)
- Body conditions score in the rib and loin regions (respectively rib fat score – RFS and loin fat score – LFS): The fat score of animals, with 1 – very thin fat covering to 5 – very thick fat covering
- Dag score (DS): Score based on the faecal soiling of the breech of animals, with 1 – no dags to 5 – excessive breech soiling with large dags

The FAMACHA© system also recommends a score of the nasal discharge of animals, as well as a score for oedema of the jaw. However, no jaw oedema was observed, while the vast majority of animals had no nasal discharge. The latter score is mostly aimed at the nasal bot, *Oestrus ovis*. Infestation of tracer sheep with *Oestrus ovis* was sporadic during the winter in the study of Reineke (1994), with most infestations occurring from November to April. Against this background, the latter scores were not considered further.

Grab samples of faeces were obtained directly from the rectums of individual animals, after drenching was withheld for at least 10 weeks. At Elsenburg, this procedure initially took place in early spring (end of August) during 2007, when the lambs were approximately 5 to 6 months of age. In subsequent years, the procedure took place later in the year (between late October and early December) when the animals were > 7 months of age. All scores were recorded and faecal samples were taken within a space of two days at all occasions. At Tygerhoek, sampling mostly took place during August, when the animals were 16 to 17 months of age. Exceptions were during 2008, when only dag scores were recorded at the end of August for 2007 progeny, with FAMACHA© scores and faecal grab sample only being obtained during the last week of September. Ram hoggets born in 2009 were similarly scored according to the FAMACHA© system and grab-sampled during the last week of July in 2010.   Within gender groups, all actions were mostly planned for within a 3-day interval. Exceptions were during 2008, when the 2007 progeny were scored for dags about a month before the other records were taken, 2008 when dag scores for 2007 ewe progeny were recorded 12 days before the other traits and 2010, when dag scores were taken 9 days after the other traits in rams, and 6 days after the other traits in ewes. Scoring regime is unlikely to affect the outcome

156

of analyses at Elsenburg, where all data were recorded over a short period of about two days. At Tygerhoek, in contrast, scoring events were sometimes interspersed over longer periods. The lack of synchrony among scoring events is unlikely to affect the genetic variances estimated, but it needs to be conceded that the possible effect of this regimen on correlations among traits not scored simultaneously is unknown and could only be speculated about.

The total number of nematode eggs (faecal egg count – FEC) per sample was counted at the Western Cape Provincial Veterinary Laboratory. Initially, nematode eggs were identified according to species, with the substantially larger eggs of *Nematodirus* spp being discerned from those of other strongyles. However, the vast majority of faeces samples had zero counts for *Nematodirus* spp eggs (87% at Elsenburg and 97% at Tygerhoek). It was thus decided to only use FEC in further analyses, as based on the across-species sum of eggs from *Nematodirus* spp and from the other strongyles. The McMaster technique was used at a sensitivity of 100 eggs per gram (epg) of wet faeces (Van Schalkwyk *et al*., 1994).   A higher accuracy than 100 epg of wet faeces would obviously have been preferable. Unfortunately constraints in terms of manpower and time prevented the more accurate assessment of parasite burdens.

9.3.3 Statistical analysis

Prior to the genetic analysis, data at both farms were subjected to least-squares analyses to allow operational models to be identified. Data were analysed with ASREML software (Gilmour *et al*., 2009) testing the fixed effects of selection line (Tygerhoek) or breed (Elsenburg), birth year, sex, age of dam and birth type, as well as two-factor interactions between these fixed effects. Results so derived were used for modeling to estimate genetic parameters, as described below.

Five-trait animal linear-threshold models were then fitted with the subjective eye score, fat score at two locations and dag score as well as feacal worm egg counts as the dependent variables. The latter trait was extremely variable, and was transformed to natural logarithms prior to analysis, after 100 has been added to account for zero counts. For analysis, the subjective traits were treated as threshold traits. The five-point score card was not fully utilised for all traits, as eye scores only ranged from 1 to 4 at both localities while rib fat score at Tygerhoek also only ranged from 1 to 4. The natural log of (feacal worm egg count + 100) was defined as a linear trait. Based on previous analyses, the systematic effects included contemporary group (a concatenation of year, genetic group and sex), dam age (2 to 6+ years)

157

and birth type (singles and multiples at Tygerhoek and singles, twins and triplets at Elsenburg). Genetic groups involved breed at Elsenburg and selection line at Tygerhoek. The five-trait model could be described by the following equation:

$$y_{ijklm} = f_{ij} + a_{ik} + e_{ijkl} \qquad\qquad (1)$$

In this model, y was a vector of observations for the respective subjective scores and the natural log of (FEC + 100); i was indicative of the respective traits (i=5), 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, and e was the vector of randomly distributed residual effects.

The data were analysed by using THRGIBBS1F90 software (Misztal *et al.*, 2002; Misztal, 2008). This software allows the estimation of variance components and genetic parameters in animal mixed models for any combination of threshold and linear traits (Cloete *et al.*, 2009). Following THRGIBBS1F90 analysis, Post Gibbs analysis was conducted with the programme POSTGIBBSF90 (Misztal *et al.*, 2002; Misztal, 2008). The software allows for the prediction of solutions for fixed and random effects.

The analyses involved the running of a single chain of 300000 cycles. The first 50000 cycles were used as the burn-in period. POSTGIBBSF90 provides sample values for each iteration. These values were plotted against the iterations. Every 10th sample was stored after 50000 iterations, giving a total of 25000 samples. These values were used for the computation of posterior means, standard deviations as well as 95% highest posterior density (HPD) confidence intervals. Point estimates representing variance components were considered as the posterior mean of the specific variance component, using the results from the final 25000 samples as set out above.   Direct genetic, phenotypic and environmental (residual) correlations were derived from these analyses.

9.4 Results

9.4.1 Descriptive statistics

Overall means for the respective traits recorded at the two experimental sites were fairly similar, as were the corresponding standard deviations (Table 9.1). Coefficients of variation were also fairly similar, amounting to 37 – 40% for eye score, 19 – 26% for rib fat score, 26 – 27% for loin fat score, 55% in both instances for dag score and 18 – 20% for the natural logarithm of (FEC+100). Untransformed values for the natural logarithm of (FEC+100) were

158

extremely variable ranging from 0 – 34100 epg of wet faeces at Elsenburg and from 0 to 32700 epg of wet faeces at Tygerhoek.

9.4.2 Fixed effect solutions

At Elsenburg, Dormers had higher overall fat scores but lower eye scores than their SAMM contemporaries (Table 9.2). Ewe lambs had a deeper subjective fat cover, less dags and lower feacal worm egg counts. Fat scores increased from the progeny of 2-year-old ewes to lambs borne to 4-year-old dams. In contrast, eye colour scores declined (i.e. became less anaemic) as dam age increased to 4-year-old ewes. Subsequently there a suggestion for eye colour score to become more anaemic with an increased dam age. Log-transformed faecal worm egg counts were unaffected by dam age. Multiple lambs, and particularly triplets, were leaner with higher eye colour scores than singles. Dag score and faecal worm egg count were unaffected by birth type.

Most two-factor interactions between sex and birth year as well as between breed and birth year were significant (P < 0.05). Eye scores for Dormer lambs were between 17 and 25% lower (i.e. less anaemic) compared to SAMM lambs for 2007 to 2013. The absolute difference for 2014 was in the same direction but not significant (P > 0.05) at 5.7%. In contrast, means for rib fat scores were between 8 and 34% higher in Dormers for 2007 to 2013, with the 5.5% difference in 2014 not reaching significance (P > 0.05). Accordingly, annual means for rump fat score was between 8 and 32% higher in Dormers than in SAMM lambs (P < 0.05). However, in the case of log-transformed faecal worm egg count there was some reranking between breeds (Figure 9.1). For this trait, SAMM lambs had higher means than Dormers for most of the years, namely for 2008 and 2009 as well as from 2011 to 2014. During 2007, in contrast, SAMM lambs had a markedly lower mean for faecal worm egg count than Dormers, while the absolute difference in favour of Dormer lambs did not reach significance in 2010.

Pertaining to the significant birth year x sex interaction observed for most traits, it is noted that lambs are separated on sex at weaning. Therefore it is very difficult to provide the same conditions to both sexes at that stage, as confirmed in literature cited in the Discussion section. Detailed results of this interaction will therefore not be provided here.

At Tygerhoek, the interaction between selection line, sex and birth year were significant in most analyses. This interaction is presented in Figure 9.2 for dag score during the period from 2006 to 2009 when all three lines were maintained in a single flock. It is evident that it is very

difficult to derive clear and meaningful conclusions from the graph, as a considerable amount of crossing over occurred among lines. Most traits at Tygerhoek were independent of the age of the dam and birth type (P > 0.14). The exception in the case of dam age was rump fat score, where least squares means ranged from 2.80 ± 0.02 for the progeny of 2-year-old dams to 2.99 ± 0.02 for the progeny of 7-year-old dams (P < 0.05). Singles also had higher (P < 0.05) fat scores than multiples, averaging 3.04 ± 0.02 and 2.97 ± 0.02 for the rib fat score of singles and multiples respectively. Corresponding means for rump fat score were 2.91 ± 0.02 and 2.84 ± 0.02.

9.4.3 Variance components and thresholds

Figure 9.3 depicts a plot of residual and additive variance components for dag score in the Elsenburg flocks as an example of derived plots that were available for all traits at both localities. A plot demonstrating the third and fourth thresholds for the same trait is presented in Figure 9.4. The first and second thresholds are set to respectively 0 and 1. Posterior means (± posterior standard deviations) amounted to 1.814 ± 0.058 for the third threshold and 2.729 ± 0.105 for the fourth threshold. Corresponding 95% confidence intervals were respectively 1.70 – 1.93 and 2.52 – 2.93. Posterior distributions for three traits, namely rib fat score score, dag score and the natural logarithm of faecal worm egg count at Elsenburg are provided in Figure 5.

9.4.3 Genetic parameters

The two data sets yielded heritability (h²) estimates that were quite similar for the animals maintained at Elsenburg (Table 9.3) and Tygerhoek (Table 9.4). All h² estimates differed (P < 0.05) from zero, being mostly appreciably higher than double the corresponding standard error. The ratios derived ranged from 0.12 – 0.13 for eye score, 0.12 – 0.38 for rib fat score, 0.17 – 0.30 for loin fat score, 0.31 for dag score, and 0.12 to 0.14 for the natural logarithm of worm egg count.

Negative genetic correlations between eye scores and fat scores were observed in both data sets (Tables 9.3 and 9.4 respectively). These results suggest that animals with anaemia were likely to be leaner in both data sets. Fat scores on the ribs and loin were moderately and positively correlated on the genetic level, suggesting that a genetic increase in fat score on the ribs would also increase loint fat score. The genetic correlations of dag scores with eye and fat scores were generally lower, and mostly smaller than the corresponding standard

160

errors. A positive relationship between eye score and natural logarithm of worm egg count was observed at Elsenburg, suggesting that animals with anaemic eye scores would also have high values for faecal worm egg count. No other significant genetic correlations involving the natural logarithm of worm egg count were found. The relative magnitude of correlations of the natural logarithm of worm egg count with the fat scores was comparatively small in all instances and not significant. Environmental correlations were mostly similar in direction, but smaller in magnitude when compared with the corresponding significant genetic correlations.

9.5 Discussion

9.5.1 Descriptive statistics

From the mean values in Table 9.1 it is clear that scores for eye colour and dags were clearly below a median value of three, which would be expected when scores are normally distributed around a median value of three on a 5-point subjective scale. Riley & Van Wyk (2009) reported means (coefficients of variation in brackets) of respectively 1.23 (33%), 1.40 (43%) and 1.90 (42%) for eye scores under conditions of low, moderate and peak nematode challenge. Their eye scores thus only exceeded those recorded in the present study under peak challenge conditions. In another study, Riley & Van Wyk (2011) reported a mean of 1.92 with a coefficient of variation of 43% for eye score in a Merino flock they studied, which is also somewhat higher than the means derived in the present study. It is also notable that the scale were not fully utilised for eye score on both localities and for dag score at Tygerhoek. There were notable low average values for eye score at both sites, suggesting that most of the animals used in this study were not anaemic (anaemic eye scores would be 4 and 5). The study by Riley & Van Wyk (2011) pertaining to eye scores utilized the full range from 1 – 5 for another South African Merino flock. Means of just above 2 for both flocks were consistent with a mean of 1.8 (sd = 1.1) reported for dag score in Australian Merinos by Brown *et al.* (2010). Corresponding dag score means reported by Greeff *et al.* (2014) ranged from as low as 1.3 after weaner classing, to as high as 3.56 during spring. The latter score could be related to hypersensitivity scouring, as discussed in Chapter 2. The averages of fat score ranged from 2.92 to 3.29 with standard deviations ranging from 0.55 to 0.73 at the 13th rib and loin across both locations. These scores were closer to the average score of 3 with generally smaller coefficients of variation, suggesting either a closer-to normal distribution or higher levels of kurtosis. The distribution of the scored traits, however, did not matter since threshold models were applied. Large variation is expected in untransformed feacal worm egg data. Ranges

that were encountered were from respectively 0 – 51895 and 0 – 53583 in yearling and hogget Merinos participating in 37 flocks recorded by Merino Genetic Services in Australia (Khusro *et al.*, 2004). The previous range reported for untransformed faecal worm egg data in the same Merino flock at Tygerhoek was from 0 – 13667 (Cloete *et al.*, 2007) while it ranged from 0 – 27600 in a Merino flock at Elsenburg, as reported in chapter 3.

9.5.2 Fixed effect solutions

Dormers had higher fat scores, but lower eye scores at Elsenburg (Table 9.2). Dormers also had lower transformed faecal worm egg counts than SAMM lambs in most years (Figure 9.1), suggesting that they could adapt better to the parasite challenge at Elsenburg. No literature could be sourced on the relative ability of these specific breeds to withstand the natural challenge posed by gastro-intestinal nematodes under conditions where irrigated pastures contribute to the feed on offer. Moors & Gauly (2009), however, reported significant differences in FAMACHA© eye scores as well as objective colour measurements between the Black Head Mutton and Leine sheep breeds in Germany. However, there was no difference in log-transformed of worm egg counts or packed cell volume between these breeds (P > 0.86). There was also some evidence that indigenous Xhosa goats coped better with experimentally induced haemonchosis than commercial Boer goats (Marume *et al.*, 2011). Further research on possible breed differences to gastrointestinal nematode challenge is thus indicated.

Year (or contemporary group) x sex interactions commonly occur in animal breeding studies conducted after weaning owing to lambs usually reared in separate-sex flocks and is often accommodated statistically by concatenating sex with contemporary group, as was also done in this study (Cloete *et al.*, 2007; Brown *et al.*, 2010; Riley & van Wyk, 2011; Greeff *et al.*, 2014; Brown *et al.*, 2015). Since this principle is well established no further discussion will be presented here for the effects of birth year and sex as well as the interaction between these traits.

At Elsenburg, fat scores increased from the progeny of 2-year-old ewes to lambs borne to 4-year-old dams. In contrast, eye scores declined (i.e. became less anaemic) for the progeny of 4-year-old dams. After the 4-year-old ewe age group, fat and eye scores tended to divert back to 2-year-old performance. No specific literature to confirm or refute these findings was found, but it is mentionable that the general pattern accorded with the well-established ewe age effect

upon weaning weight (Cloete & de Villiers, 1987). Such trends are often explained by the conflict between own growth and lamb growth in still-growing 2-year-old dams as well as older dams starting to decline in their maternal ability as they age. It is reasonable to assume that the better care provided by dams in the intermediate age classes would also transfer to fatness scores and the ability of lambs to withstand parasite challenge, as reflected by eye scores. The contrast between the Elsenburg and Tygerhoek results may well be attributed to the fact that assessment at Elsenburg was at a substantially younger age than at Tygerhoek and more likely to be effected by residual dam age affects. Faecal worm egg count was not affected by dam age at either of the localities, a result that was consistent with Chapter 3 in the Elsenburg resource flock.

Single lambs had generally higher fat scores than twins and particularly triplets at Elsenburg. The same trend was seen in singles and multiples at Tygerhoek, but the magnitude of differences was smaller. Once again these results can be compared to the well-known fact that birth type has a marked effect on early weights of lambs (Cloete & de Villiers, 1987). The difference in size of this effect between the Elsenburg and Tygerhoek sites can once again be attributed to the age difference in the animals studied between locations. Faecal worm egg count was independent of birth type at both localities, as was also reported in Chapter 3.

9.5.3 Variance components and thresholds

Figure 3 indicates that a stationary state was indeed reached during when samples for the estimation of posterior means and posterior standard deviations were taken, as suggested by Cloete *et al.* (2009). A similar trend was seen when other traits at both localities were considered. It is important to note that the third and fourth thresholds in Figure 4 were slightly below the theoretical values of 2 and 3, and that the derived 95% confidence intervals excluded the desired value in both instances. These results suggest that the intention of using a linear scale with equal intervals between thresholds was not quite reached, although the scorers came quite close to achieving this. The posterior distributions for the traits: rib fat score, dag score and the natural logarithm of (FWEC) were all slightly skewed, as indicated by Figure 5. Accounting for this slightly skewed distributions by substituting the posterior mean for each trait with the equivalent median value only had a marginal effect on the parameters estimated and did not influence any of the conclusions derived from the study.

9.5.4 Genetic parameters

Heritability (h²) estimates for eye score ranged from $0.12 \pm 0.05 - 0.13 \pm 0.05$ in the present study (Tables 9. 2 and 9. 3). The comparable values reported by Riley & Van Wyk (2009; 2011) ranged from 0.08 to 0.24, depending on the level of challenge and whether animals treated with anthelmintics were excluded from the data, or included with a penalty. Although the present estimates are well within the range of these values, it needs to be pointed out that Riley & Van Wyk (2009; 2011) used linear models and assumed normality in their study. In theory, the threshold models (eye scores were treated as a threshold trait in both data sets) used in the present study should hold advantages above linear modelling, as was conceded by the latter authors. Results from the present study also suggested that subjective fat depth could be scored fairly accurately, with fairly good statistical properties as well as usable levels of genetic variation (h² estimates of 0.12 – 0.38). Comparable estimates ranged from 0.17 to 0.33 in the study of Riley & Van Wyk, 2009), which is fairly consistent with those reported here. Repeated eye scores were used effectively to identify Suffolk ewes resistant/resilient or susceptible to artificial *H. contortus* challenge in the study of Pereira *et al.* (2016).

Direct h² estimates obtained in this study for dag score were 0.31 ± 0.07 in both data sets. Recent studies accordingly reported variable results for dag score, with h² estimates ranging from 0.09 to 0.63 (Smith *et al.*, 2009; Greeff & Karlsson, 2009; Brown *et al.*, 2010; Pickering *et al.*, 2010; Scholtz *et al.*, 2011). In a study by Smith *et al.* (2009), the heritability estimates for dag score in Merinos was low at 0.09. However, in studies by Brown *et al.* (2010), Pickering *et al.* (2010) and Scholtz *et al.* (2011), moderate heritability estimates of 0.25 to 0.28, 0.31 and 0.24 were reported respectively. Greeff & Karlsson (2009) and on the other hand, reported high (0.55) heritability estimates of dag score. The present heritability estimates obtained in this study suggest genetic differences for this trait at both localities and that genetic progress should accrue if purposeful selection is applied.

The present study also showed moderate heritability estimates for the natural logarithm of worm egg count, ranging from 0.12 ± 0.04 to 0.14 ± 0.04. Although these estimates are different in magnitude, it is clear that significant genetic variation was present in the natural logarithm of worm egg count at both localities. Therefore, the additive genetic variation of this trait would allow genetic progress should selection of this trait be of choice. These estimates are somewhat lower than an estimate of 0.27 derived from 16 literature values surveyed for the comprehensive review of h² estimates in the sheep literature by Safari *et al.* (2005) but

164

marginally higher than estimates of 0.09 to 0.10 for transformed faecal worm egg count was derivedin chapter 3). Previous h² estimates in the Tygerhoek flock ranged from 0.14 for untransformed data to 0.18 for data transformed to natural logarithms, which is in good agreement with the present estimates (Cloete *et al.,* 2007; Matebesi-Ranthimo *et al.,* 2014). Brown *et al.* (2015) accordingly reported heritability estimates ranging from 0.14 to 0.16 for cube root transformed faecal worm egg count of Australian meat sheep, depending on the models fitted. Riley & Van Wyk (2009) also reported h² estimates of 0.19 to 0.23 for log-transformed worm egg count under high challenge conditions when animals treated with anthelminthics were either excluded from the data, or included with a penalty. Khusro *et al.* (2004) used data obtained from Merino Genetic Services in Australia to estimate the h² of yearling cube root transformed worm egg count at 0.21 (n = 16669) and that of hogget cube root transformed worm egg count at 0.38 (n = 5110).   In a subsequent analysis on the same resource, Brown *et al.* (2010) used 5880 records for yearling worm egg count and 10991 records for hogget worm egg count to estimate h² at respectively 0.29 to 0.38 and 0.29 to 0.41 in Australian Merinos, depending on the modelling used. The fact that the present estimates for the h² of the natural logarithm of worm egg count are on the lower end of the range of literature estimates may be related to the fact that samples were assessed at an accuracy of 100 epg of wet faeces. A study by Notter *et al.* (2003) reported moderate heritability estimates for faecal worm egg count, ranging from 0.22-0.42 in sheep after artificially infecting them with *H. contortus*. In their study, the faecal grab samples were assessed at a sensitivity of 50 epg.

Negative genetic correlations between eye scores and fat scores, ranging from -0.45 to -0.82 were observed in both datasets (Tables 9.3 and 9.4). Riley & Van Wyk (2009) accordingly reported that genetic correlations of FAMACHA© eye scores with body condition score ranged from -0.39 to -0.55, depending on the level of parasite challenge and whether the records of treated animals were excluded, or included with a penalty. It stands to reason that animals with a higher level of anaemia (high FAMACHA© eye scores) will have less fat cover than animals without anaemia, so these results are not entirely unexpected. A high positive genetic correlation between fat scores on the ribs and loin at two localities were observed in both data sets, and not different (P < 0.05) from unity. These results are not surprising, as it is reasonable to assume that these traits would be genetically very similar (i.e. that largely the same genes would result in fat deposition at the two localities). Riley & Van Wyk (2009) correspondingly reported that body condition score and live weight were highly correlated on a genetic level.

On a genetic level, eye score and natural logarithm of worm egg count were moderately positively related with each other at Elsenburg, where the presence of a Haemonchus challenge is more likely (see below). The genetic correlation of eye score with FWEC (albeit significant) was associated with quite a large standard error and thus a wide confidence interval. Further research is required to unequivocally show that selection for a high eye score would lead to an increased FWEC or vice versa. Similar results were found by Burke *et al.* (2007). In their study, eye scores and faecal worm egg count showed a positive relationship of 0.44 with each other. However, in the present study the opposite trend was evident at Tygerhoek, indicating no relationship between eye score and FWEC. No comparable results were found in literature to support the direction of this correlation but a low correlation between eye score and faecal worm egg counts were reported by Gauly *et al.* (2004), suggesting that situations where there is low parasite challenge may limit the usefulness of the FAMACHA© system. Unfortunately, the nature of the present study did not allow detailed knowledge pertaining parasite species composition of nematode challenge present at either locality. However, these trends may be associated with the more general availability of irrigated pastures at Elsenburg compared to Tygerhoek. In his review of a decade of studies on internal parasites in the Mediterranean area of South Africa, Reinecke (1994) reported that haematophagous parasites like *Haemonchus contortus* are numerically important on irrigated pastures in the Western Cape province of South Africa. The latter author also reported that a mixed challenge of *Teladorsagia* spp, *Trichostrongylus* spp and *Nematodirus* spp was more likely at dryland properties. In fact, although the other species were present, *Teledorsagia* spp were by far the dominant contributor to worm burdens of Merino ewes sampled during late winter and early spring (when the data at Tygerhoek were recorded) on a nearby property in the review of Reinecke (1994). Infestation with *Haemonchus contortus* was particularly severe on intensive properties during autumn. Although sheep at Elsenburg commonly graze safer dryland pastures (Cloete *et al.*, 2009), irrigated paddocks are also used frequently. In contrast, production at Tygerhoek was based solely on dryland pastures, with cereal stubbles commonly being available during summer (Cloete *et al.*, 2004a). Reinecke (1994) reported that grain stubble paddocks are largely free of eggs from gastro-intestinal nematodes. Although the specific parasites infesting the sheep at the respective localities were not explicitly known in the present study, the work of Reinecke (1994) suggests that sheep at Elsenburg were more likely to be infested with haematophagous nematodes than at Tygerhoek. In a stud by Nolan (2006) the fecundity of adult females for *Haemonchus contortus*

166

ranged from 5000 to 10000 eggs/day. Therefore, it can be deduced that the composition of the nematode challenge at the respective localities could arguably have contributed to the observed variation in the results observed at the respective localities. On the same note, Bath & van Wyk (2009) reported that the FAMACHA© eye score are more likely to be of value at localities with predominantly haematophagous nematodes, while fat scores as well as dag score would be more relevant where non-haematophagous helminths dominate. The former contention is supported by the work of Riley & Van Wyk (2009) and the results at Elsenburg in the present study. According to the latter study, genetic correlations of eye score with log transformed faecal worm egg count amounted to 0.85 when treated animals were excluded from the data set and to 0.73 when they were penalised under peak *Haemonchus contortus* challenge conditions. Although the present genetic correlation of 0.66 is somewhat smaller in magnitude than those reported by Riley & Van Wyk (2009), the direction is similar. The correspondence in the absolute sign of the genetic correlations may suggest that it is feasible that the mechanisms underlying the gastro-intestinal parasite challenge may be comparable across studies.

In contrast, the contention that fat scores would be more relevant for predicting FWEC where non-haematophagous helminths are expected to dominate (based on the work of Reinecke, 1994), do not seem to be supported by the present data in the absence of any significant genetic correlation of FWEC with fat scores. Genetic correlations of fat scores with the natural logarithm of faecal worm egg count were mostly close to zero on both locations. The absolute direction of the correlations at Tygerhoek, where non-haematophagous helminths are likely to dominate (Reinecke, 1994), also suggested that recorded sheep with high values for fat score would also have higher values for the natural logarithm of faecal worm egg count. No literature findings to support or refute these results could be found for subjective fat scores and the natural logarithm of faecal worm egg count. However, Brown & Swan (2015) reported a genetic correlation of -0.18 between ultrasound-scanned yearling fat depth and cube root transformed faecal worm egg count. A comparable genetic correlation of -0.43 was reported between carcass fat depth and faecal worm egg count in the study of Pollot & Greeff (2004a). In another study, Pollot & Greeff (2004b) found that the genetic correlation of ultrasound fat depth with FWEC varied according to the standardised mean of contemporary groups for FWEC. It seemed that resistant animals would have higher means for fat depth under conditions of high parasite challenge. It thus seems that the genetic correlation of FWEC with fat depth or fat score may vary according to parasitic challenge.

FWEC and dag scores were not related on either the genetic or environmental level at both farms.The 95% confidence intervals for these correlations were very wide, and would include zero in both instances. Part of the available literature supported a negative direction for this genetic correlation (Pocock *et al.*, 1995; Larsen *et al.*, 1999; Bisset *et al.*, 2001b). However, other references also reported either no or positive relationships (Woolaston and Ward, 1999; Greeff *et al.*, 1999; Greeff & Karlsson, 1999). Bisset *et al.* (2001a) accordingly suggested that the genetic relationship of dag score with faecal worm egg count is not straightforward. Brown *et al.* (2010) recently reported genetic correlations ranging from -0.07 to 0.20 between dag score and cube root transformed faecal worm egg count on a large data set involving ~28000 dag score records and ~17000 faecal worm egg count records. It is thus evident that the correlation of FWEC with dag scores is relatively complicated, presumably because of the expression of dags resulting from either hypersensitivity scouring or scouring resulting from high parasite loads (Karlsson *et al.*, 1995; Karlsson & Greeff, 1996). Presumably, this relationship could depend upon the climate, pastures, husbandry practices as well as reactions from individual animals, making it difficult to predict. More research is thus needed to understand the complex interactions between animals, gastro-intestinal nematodes and the environment as far as the formation of dags is considered. The complexity of such genotype x environment effects was highlighted by Karlsson *et al.* (2004), who contended that selection should be focused both on FEC and dag score. Apart from dags being an important source of wool contamination (Scobie *et al.*, 1997), dag scores are also genetically correlated with breech blowfly strike (Greeff & Karlsson, 2009), as well as with traits considered as indicators of breech strike (Greeff & Karlsson, 2009; Brown *et al.*, 2010; Pickering *et al.,* 2010; Scholtz *et al.*, 2011).

It is noted that part of the philosophy with the FAMACHA© system is to be able to identify animals that are resistant and/or tolerant to challenge by gastrointestinal nematodes (Riley & van Wyk, 2011). Such animals are supposedly better able to cope with parasite challenge in the current flock, while they may also be able to produce offspring that will exhibit similar performance in the future generation. The system may allow breeders to select both for resistance and resilience to helminthic nematodes, as discussed in detail by Bisset *et al.* (2001a). The latter authors produced evidence of both these approaches yielding selection gains, as manifested by genetic trends in selected populations. The FAMACHA© system may play a role in this respect if applied in a correct and responsible manner.

Finally, it was stated in the Material and Methods section that no intentional selection for faecal worm egg counts or any related trait took place during the study. However, the possibility remains that unintentional correlated responses might have followed from selection strategies implemented in the resource flocks studied. Indeed, Van Wyk *et al.* (1993) reported moderate genetic gains in weaning weight and preweaning weight gain in the Elsenburg Dormer flock, amounting to respectively 0.2 and 0.3% of the overall phenotypic means. The Elsenburg SA Mutton Merino flock also realised small to moderate genetic gains in weaning weight, yearling live weight, clean fleece weight and clean yield (Zemuy, 2002). Genetic change in the other resource flocks were more substantial in the traits selected for when expressed relative to the overall phenotypic means, namely 0.97% for clean fleece weight in the Fleece weight+ line (Cloete *et al.*, 1998) and -1.01% for fibre diameter in the Fine Wool line (Cloete *et al.*, 2013). However, when genetic correlations of these selected traits with faecal worm egg counts (Khusro *et al.*, 2004; Cloete *et al.*, 2007; Matebesi-Ranthimo *et al.*, 2014; Brown & Swan, 2015) are considered, such effects appear to be quite unlikely. Also, if the genetic trends for faecal worm egg count at Tygerhoek for the period from 1995 to 2005 were considered (Cloete *et al.,* 2007), it was clear that the selection applied did not lead to correlated genetic changes in the lines maintained there. However, further research on genetic correlations of the FAMACHA© traits with other traits of economic importance are warranted, since no such values could be sourced from the literature.

9.6 Conclusions

All traits considered in this study would respond to purposeful selection, should genetic progress therein be desired. While selection against anaemic eye scores would result in a correlated response in fatness scores at both sites, selection for low FWEC would not affect dag scores in both farms. A positive relationship between eye score and the natural logarithm of faecal worm egg count was observed at Elsenburg. This relationship suggested that selection for lower eye scores would possibly reduce FWEC, although the 95% confidence interval for the correlation was wide and the outcome might be quite unpredictable. Fatness was not strongly related to either dag scores or the natural logarithm of faecal worm egg count at either site. Selection based on FAMACHA© eye scores thus will possibly lead to an increased fatness as a correlated response. The genetic correlations of dag scores with the natural logarithm of faecal worm egg count were variable between localities and inconclusive.

Further research is required to establish protocols for the improvement of robustness of sheep in the Mediterranean regions of South Africa with regard to internal parasite control.

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9.8 Annexes of Figures and Tables
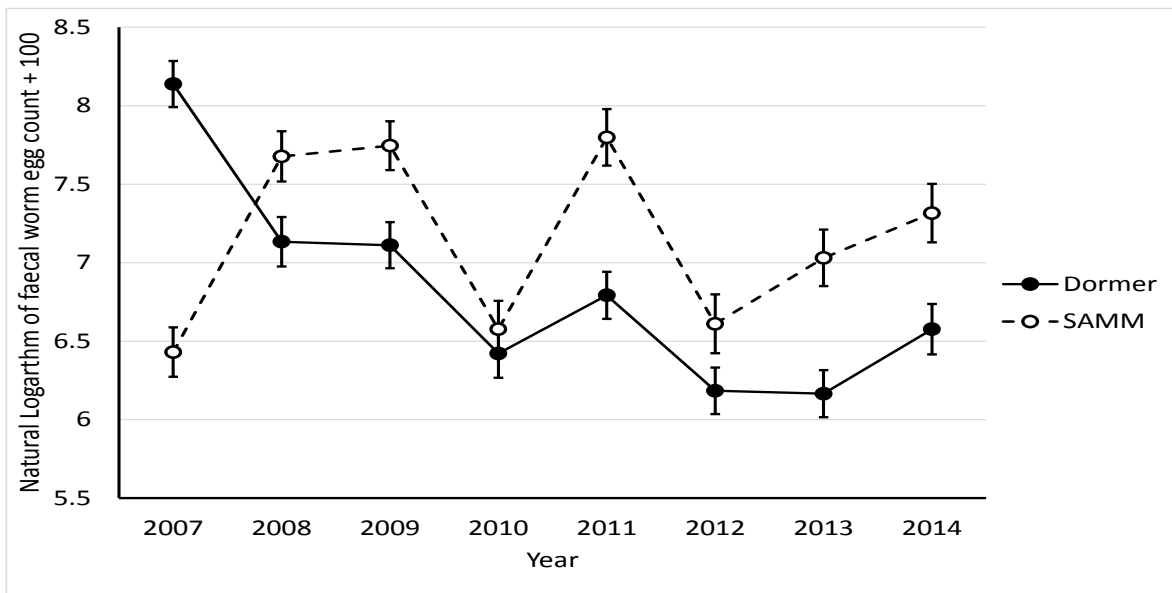
Figure 9.1 Least squares means depicting the interaction between breed and birth year at Elsenburg for log transformed faecal worm egg count fom data that was collected from 2007 to 2014. Vertical bars about means reflect standard errors
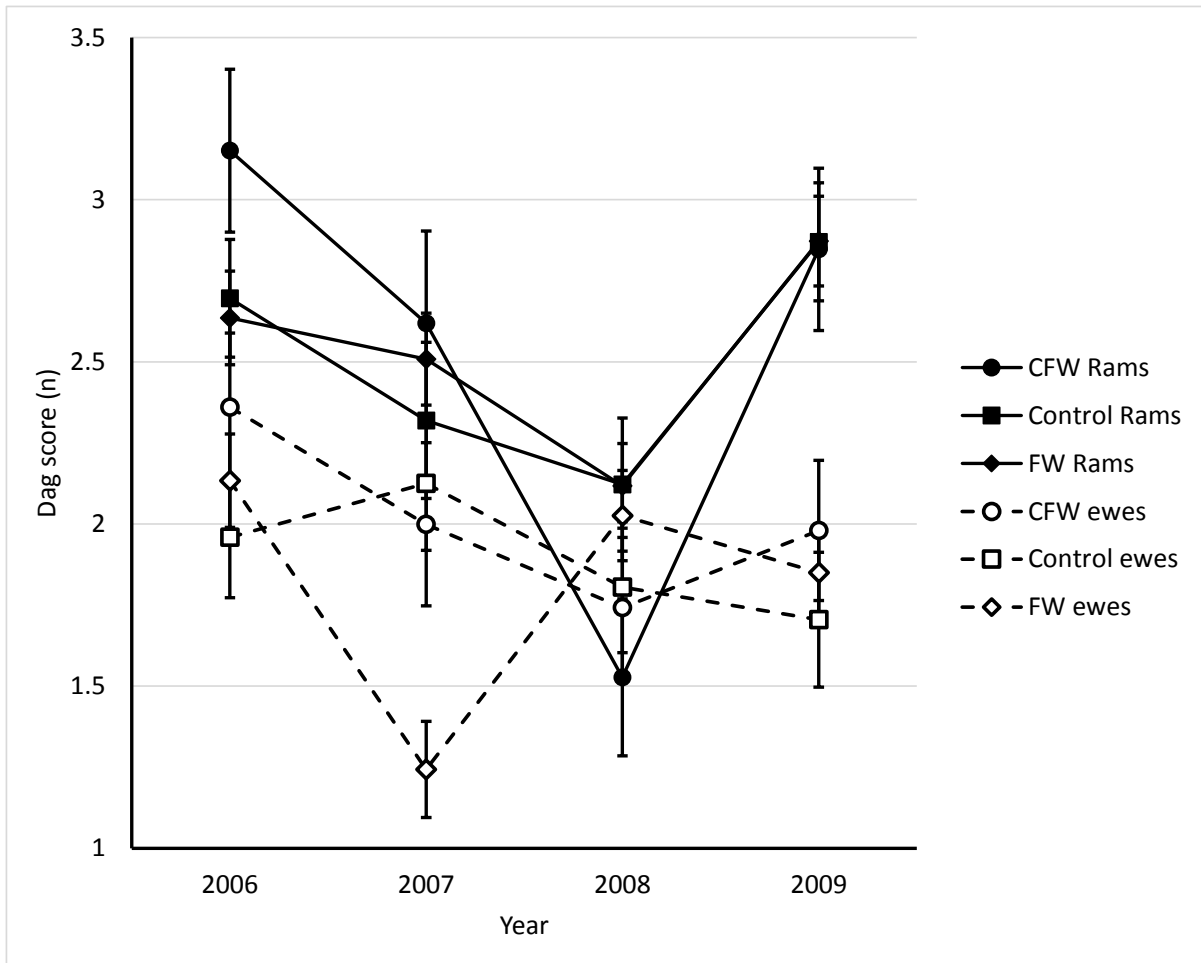
Figure 9.2 Least squares means depicting the interaction between selection line (CFW – Fleece weight+; FW – Fine wool), birth year and sex at Tygerhoek for dag score. Vertical bars about means reflect standard errors
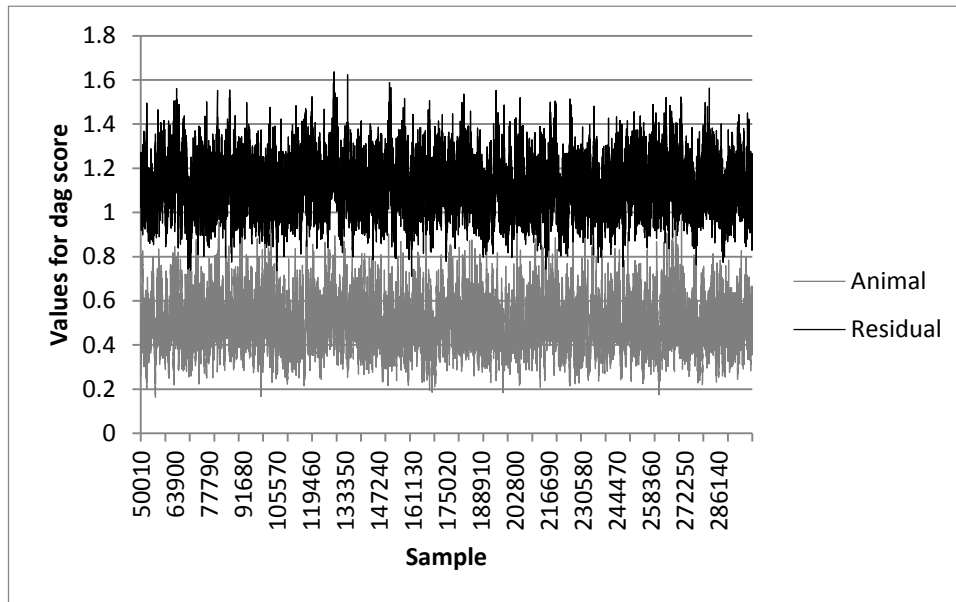
Figure 9.3 Direct additive (Animal) and residual variance components plotted against the sequence numbers for 25000 samples used to derived posterior means and posterior standard deviations for dag scores at Elsenburg. Every 10th sample was saved of 200000 samples in the chain between samples 50010 to 300000. The 25000 saved samples were numbered from 5001 to 30000 in the graph

Figure 9.4 Estimated third and fourth thresholds for dag score at Elsenburg plotted against the sequence numbers for 25000 samples used to derived posterior means and posterior standard deviations for these thresholds. Every 10th sample was saved of 250000 samples the chain between samples 50010 to 300000. The 25000 saved samples were numbered from 5001 to 30000 in the graph

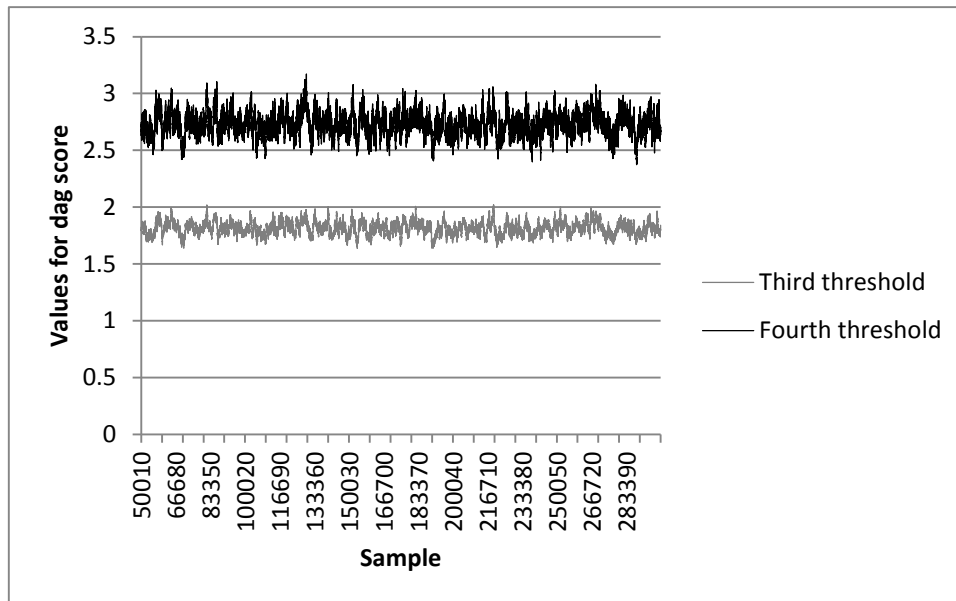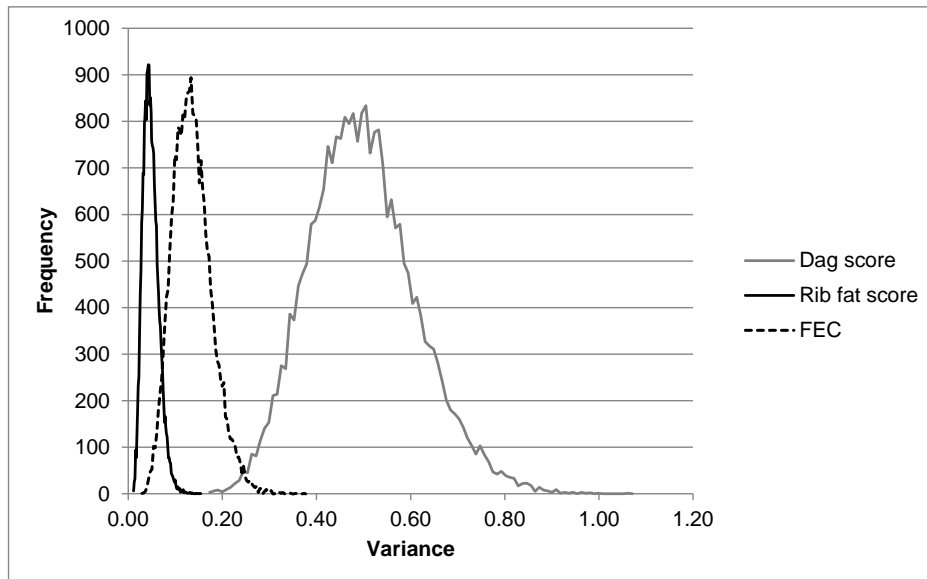Figure 9.5 Histograms depicting the posterior distributions for direct, additive animal effects for rib fat scores, dag scores and faecal worm egg counts (FWEC)

Table 9.1 Descriptive statistics for subjective Famacha© scores, involving eye score (ES), fat score at the 13th rib (FSR), fat score at the loin (FSL), dag score (DS), as well as the natural logarithm of Faecal worm egg count + 100 (LFWEC) in two flocks

Flock and parameter	Traits				
	ES	FSR	FSL	DS	FWEC
Elsenburg Dormer and SA Mutton Merino flocks					
Number of observations	1815	1815	1815	1813	1701
Mean (SD)	1.54 (0.59)	3.27 (0.73)	3.10 (0.73)	2.08 (1.14)	6.87 (1.24)
Range	1 – 4	1 – 5	1 – 5	1 – 5	4.6 – 10.4
Tygerhoek Merino flock					
Number of observations	2093	1531	1533	2207	2219
Mean (SD)	1.56 (0.59)	3.07 (0.55)	2.92 (0.67)	2.17 (1.18)	5.65 (1.09)
Range	1 – 4	1 – 4	1 – 5	1 – 5	4.6 – 10.4
	Total count	Zero count	Percentage (%)		
FWEC Elsenburg	1201	192	11.3		
FWEC Tygerhoek	2219	682	30.7		

Table 0.2 Least squares means depicting the fixed effects of year, breed, sex, dam age and birth type on the traits assessed using the FAMACHA© system in the Elsenburg Dormer and SAMM flocks

Effect and level	Trait				
	ES	FSR	FSL	DS	FWEC
Year	**	**	**	**	**
Breed	**	**	**	0.68	0.14
Dormer	1.48 ± 0.06	3.40 ± 0.07	3.26 ± 0.08	1.94 ± 0.14	6.82 ± 0.12
SAMM	1.86 ± 0.06	3.87 ± 0.07	2.76 ± 0.07	2.11 ± 0.14	7.14 ± 0.12
Sex	0.25	**	**	**	**
Ram	1.66 ± 0.06	3.05 ± 0.07	2.96 ± 0.07	2.21 ± 0.13	7.24 ± 0.12
Ewe	1.67 ± 0.06	3.22 ± 0.07	3.07 ± 0.07	1.85 ± 0.13	6.73 ± 0.11
Age of dam	**	**	**	*	0.40
2 years	1.77 ± 0.06	2.99 ± 0.08	2.87 ± 0.08	1.97 ± 0.14	7.04 ± 0.12
3 years	1.62 ± 0.06	3.17 ± 0.07	3.04 ± 0.07	2.05 ± 0.13	7.01 ± 0.12
4 years	1.59 ± 0.06	3.22 ± 0.07	3.12 ± 0.07	1.89 ± 0.13	6.96 ± 0.12
5 years	1.65 ± 0.06	3.10 ± 0.07	3.01 ± 0.08	2.12 ± 0.13	6.89 ± 0.12
6+ years	1.71 ± 0.07	3.17 ± 0.07	3.02 ± 0.09	2.11 ± 0.15	7.00 ± 0.15
Birth type	**	**	**	0.37	0.73
Single	1.44 ± 0.03	3.48 ± 0.04	3.28 ± 0.04	2.12 ± 0.08	6.94 ± 0.06
Twin	1.66 ± 0.02	3.09 ± 0.03	2.91 ± 0.03	2.17 ± 0.07	6.91 ± 0.04
Triplet	1.91 ± 0.16	2.82 ± 0.20	2.85 ± 0.20	1.80 ± 0.34	7.09 ± 0.33

** - P < 0.01; * - P < 0.05; actual significance for P > 0.05

Table 9.3 Variance components, posterior standard deviations (PSD), heritability estimates as well as genetic and environmental correlations for subjective Famacha© scores, involving eye score (ES), fat score at the 13th rib (FSR), fat score at the loin (FSL), da dag score (DS) and the natural logarithm of Faecal worm egg count + 100 (FWEC) in progeny of the Elsenburg Dormer, SA Mutton Merino and Merino flocks

Elements and traits	Traits				
	ES	FSR	FSL	DS	FWEC
Variance components					
Genetic	0.0298	0.0474	0.0653	0.4934	0.1340
Phenotypic	0.2368	0.3828	0.3943	1.6124	1.0767
(Co)variance ratios (± s.e.)*					
ES	**0.13 ± 0.05**	-0.43 ± 0.06	-0.44 ± 0.06	0.16 ± 0.07	-0.03 ± 0.06
FSR	-0.45 ± 0.22	**0.12 ±0.04**	0.66 ± 0.07	-0.17 ± 0.06	-0.10 ± 0.05
FSL	-0.71 ± 0.27	0.92 ± 0.23	**0.17 ± 0.05**	-0.18 ± 0.06	-0.09 ± 0.05
DS	0.06 ± 0.22	0.12 ± 0.18	0.04 ± 0.18	**0.31 ± 0.07**	-0.03 ± 0.05
FWEC	0.66 ± 0.27	-0.19 ± 0.21	-0.25 ± 0.22	-0.19 ± 0.23	**0.12 ± 0.04**

*Heritability estimates (± s.e.) in bold on the diagonal, genetic correlations below the diagonal and environmental correlations above the diagonal. Estimates more than double the corresponding standard error are significant ($P < 0.05$).

Table 0.4 Variance components, posterior standard deviations (PSD), heritability estimates as well as genetic and environmental correlations for subjective Famacha© scores, involving eye score (ES), fat score at the 13th rib (FSR), fat score at the loin (FSL), dag score (DS) and the natural logarithm of Faecal worm egg count + 100 (FWEC) in progeny of the Tygerhoek Merino flock

Elements and traits	Traits				
	ES	FSR	FSL	DS	FWEC
Variance components					
Genetic	0.0343	0.3644	0.0930	0.5111	0.1470
Phenotypic	0.2940	0.9630	0.3125	1.6691	1.0397
(Co)variance ratios (± s.e.)*					
ES	**0.12 ± 0.05**	-0.26 ± 0.07	-0.26 ± 0.06	0.06 ± 0.06	-0.02 ± 0.05
FSR	-0.82 ± 0.23	**0.38 ± 0.13**	0.65 ± 0.06	-0.10 ± 0.06	-0.10 ± 0.05
FSL	-0.50 ± 0.18	0.80 ± 0.18	**0.30 ± 0.11**	-0.07 ± 0.07	-0.15 ± 0.06
DS	0.25 ± 0.22	-0.14 ± 0.27	-0.15 ± 0.22	**0.31 ± 0.08**	-0.07 ± 0.06
FWEC	0.29 ± 0.21	0.00 ± 0.22	0.23 ± 0.23	0.27 ± 0.27	**0.14 ± 0.05**

*Heritability estimates (± s.e.) in bold on the diagonal, genetic correlations above the diagonal and environmental correlations below the diagonal. Estimates more than double the corresponding standard error are significant (P < 0.05).

CHAPTER 10: CONCLUSIONS AND RECOMMENDATIONS

10.1 Background

This study was designed to propose practical ways in which the South African small stock can react to challenges imposed by infestation of sheep with gastrointestinal nematodes. The point of departure of the thesis was that these parasites are associated with reduced productivity and economic gains in livestock and small stock in particular. The study furthermore assumed that the genetic improvement of the resistance of host animals to these parasites will play a major role in the sustainable management of parasitism by roundworms by using an integrated approach. The current study was conducted to add to the existing knowledge required to design effective breeding programmes to add to the control of gastrointestinal nematode infestations in a sustainable manner.

Background information available at the onset of the study was that faecal worm egg count (FWEC) based on natural challenge as an indicator trait for host resistance in South African Merino sheep was heritable. However, Western Cape studies so far was limited to a single resource flock maintained at the Tygerhoek research farm. This study expanded research to other well-recorded resource flocks in the province to add to the existing knowledge. Specific objectives researched were the following:

10.2 To determine whether there are breed and line differences in FWEC

It is generally assumed that differences between genetic groups such as breeds, strains or breeding lines are indicative of a genetic basis for a trait of interest. In the absence of any history of selection for low FWEC in any of the breeds constituting the local ovine genetic resource, such differences were not expected. The commercial breeds used in the study were also not subjected to situations where natural selection imposed by underdrenching or responses associated with overdrenching were likely to result in genetic changes as far as FWEC is concerned.

This assumption proved to be true for two Merino lines divergently selected for reproduction where no line differences in FWEC were found, either on the phenotypic or genetic levels (Chapter 3 and Chapter 6). However, this outcome could have been resulted from the fact that both lines were managed under same conditions as one group for many years. Long term selection for production traits on the other hand could negatively impact the reproductive efficiency and health status of the animals. Since previous studies demonstrated marked

186

divergence in reproduction traits between the Elsenburg lines (also found in Chapter 6), this result also implied that reproduction and FWEC were unrelated at the genetic level as reported in Chapter 3, a contention supported by a limited number of studies in the international literature. Given the lack of additive genetic variation for FWEC in the ewes studied in Chapter 6, it is assumed that the estimation of genetic correlations with reproduction traits may still be problematic, prompting a cautious approach in interpreting these correlations. Also it is still unclear how these results may be related to resource allocation in the resource flock that was studied.

Surprisingly, additional studies indicated that the Dormer breed had a lower overall FWEC than SA Mutton Merino contemporaries maintained in the same flock (Chapter 8). This breed difference was not robust across production years, as SA Mutton Merinos did not differ from Dormers in some years, and even proved to be superior to Dormer in a single year from respectively 10 and 12 production years, both for yearling replacement animals and mature breeding ewes. Dormers, however, had significantly lower means than SA Mutton Merinos in 67% of production years for yearlings and 50% of lambing years for mature ewes. The fact that breed differences in favour of Dormers were found in overall analyses, as well as in the bulk of production years adds some robustness to the contention that Dormers generally have lower FWECs than SA Mutton Merinos. However, the mechanisms in place to achieve this, as well as proof of an increased robustness of Dormers under challenge conditions, have not yet been established. Although that is the case, it can be speculated that natural selection has possibly had a greater effect on S.A. Mutton Merino's compared to Dormers resulting in increased environmental sensitivity that could be expressed as an increased susceptibility to nematodes. Further studies in this respect are evidently needed.

10.3 To derive genetic parameters for FWEC and other traits of economic importance

Low to moderate heritability estimates were derived in different breeds and classes on sheep in this study with ranges from 0.03 in mature Merino Elsenburg ewes (Chapter 6) to 0.19 in Tygerhoek Merino hoggets sampled in the spring (Chapter 4). Initial low heritability estimates of 0.09 – 0.10 for Elsenburg Merino progeny sampled for FWEC in autumn prompted a study on the heritability of FWEC in different seasons, using historic data at Tygerhoek (Chapter 4). This study suggested low levels of genetic variation in autumn under Mediterranean conditions, with increased heritability estimates based on winter and spring samples. Similar to the present study, results from Rylington Merino flock in Australia under similar environmental conditions

also reported the lowest heritabilities for FWEC in autumn/summer and highest FWEC in winter coinciding with the growth of pastures from rains. This finding led to a recommendation that grab samples for the determination of FWEC under natural challenge should preferably be collected after the break of the season (in winter and spring) in the Mediterranean region of South Africa.

The heritability of FWEC in Dormer and SAMM yearlings amounted to from 0.12 to 0.14 in Elsenburg and Tygerhoek farm, respectively (Chapter 9). Linked to acceptable levels of phenotypic variation, most of these estimates suggested that genetic progress would indeed be achievable in South African sheep. With that said, our results suggest that it is best to select for low FWEC when the animals reach an age of at least a year old.

There is currently no direct selection for low FWEC in South Affrica. For the industry, focus should be in young rams (to allow the storage of semen and ultimately increase genetic gains across flocks). So, a database with accurate records of FWEC from rams should be a priority.

A first across-flock genetic analysis for South Africa was conducted by combining data from Tygerhoek and Elsenburg in a single analysis. There seemed to be adequate genetic variation to estimate breeding values to improve FWEC across flocks, should it be desired. With a sire x site/season variance ratio of below 2%, the likelihood of extreme reranking of sires in different environments appeared to be small. Across-flock studies should be continued, with the eventual aim of making it part of the formal recording scheme in South Africa.

If selection for a lower FWEC is practiced in South Africa, it is important to know how other traits of economic importance will be affected. Genetic correlations of FWEC with traits in the live weight, wool, conformation and reproduction complexes were thus considered in Chapters 5 and 6. No conclusive favourable or unfavourable genetic correlations of FWEC with any of the wool or live weight traits were found although the direction of correlations with traits like staple strength, standard deviation of fibre diameter and testis dimensions were favourable. In contrast to the genetic and phenotypic trends in those lines divergently selected for reproduction, a study on the genetic correlations of reproduction traits in mature Merino ewes at Elsenburg with FWEC revealed fairly sizable favourable genetic correlations (Chapter 6). However, as these correlations were derived with a low heritability for FWEC, they were accompanied by high standard errors. Clearly further research is needed on this topic.

10.4 To study the application of the FAMACHA© system under Mediterranean conditions

The FAMACHA© system was designed to improve the resistance/resilience of sheep under conditions where haematophageous parasites predominate. The system was propoagated to be easy to apply, both by commercial and small-scale farmers. Since it is suggested to reduce drenching costs, it also may be appropriate for resource-poor farmers in South Africa. The system uses subjective assessments of eye score (using bright pink to pale colour as an indication of anemia) as well as condition score and dag score (to also consider non-haematophageous parasites). The system was applied to Merinos at Tygerhoek and Dormers and SA Mutton Merinos at Elsenburg. All FAMACA© traits as well as FWEC were heritable at both sites, estimates ranging from 0.12 for eye score at Tygerhoek and rib fat score at Elsenburg to 0.38 for rib fat score at Tygerhoek. Genetic correlations indicated that selection for low eye score (i.e. no anaemia) would result in a reduction in FWEC, although 95% confidence intervals for the correlation were quite wide. The two condition scores were also highly correlated, suggesting that rib and loin fat scores were genetically quite similar. However, the experimental sites differed appreciably for the direction of the genetic correlation of eye score with FWEC. It was favourable and moderate to high at Elsenburg, where the likelihood of haematophageous parasites to occur on irrigated pastures was high. In contrast, this correlation was not significant at Tygerhoek, where non-haematophageous were likely to predominate on dryland pastures. It was concluded that the FAMACHA© system may play a role in parasite control where irrigated pastures are used under Mediterranean conditions. However, it did not seem to be as applicable under dryland conditions.

10.5 Recommendations

This study is by no means a complete solution to parasitism by gastrointestinal helminths. A number of recommendations for further research can be made from the study:

- The breed difference for FWEC in favour of Dormers relative to SA Mutton Merinos is difficult to explain, seeing that no intentional selection for or against FWEC has been practiced in either breed. There was some evidence that Dormers were fatter that SA Mutton Merinos (Chapter 9). It is not sure if this breed difference in fatness may be associated with the means for FWEC, given results in the literature. However, there is ample scope for further studies to better understand the underlying mechanisms involved in the lower means for FWEC in Dormers, and how it could be related to a putative

increased robustness in the breed. The fact that Dormers were not superior to SA Mutton Merinos in a minority of years and putative drivers for this inconsistency should also be studied. Genetic correlations of FWEC with other traits of economic importance in these breeds are also indicated, to allow for the formulation of a selection objective and a selection index based on economic considerations.

- The genetic parameters derived in this study suggested that, although it is feasible, genetic progress in a trait like FWEC could take some time to achieve the desired effect on the industry at large. The importation of germplasm from genetic resources already showing resistance to gastrointestinal helminths may play an important role to complement the measures proposed here. One of these flocks, i.e. the Rylington Merino flock, was developed under largely similar climatic conditions in Western Australia when compared to the climate experienced by the animals in the present study. Serious consideration should be given to import semen from this flock for assessment under local conditions.

- Further across-flock and, eventually, even across-breed analyses of input traits like FWEC should be seriously considered. Prerequisites for such studies will include the usage of common sires to create linkage among the flocks, as well as a standardized data collection protocol. This protocol should include FWEC as well as other traits of economic importance. Across-flock analyses will also assist to provide clarity on those genetic correlations that cannot be estimated at a desired accuracy at present. It is also the way forward to eventually include input traits like FWEC in the national sheep recording system.

- One of the biggest limitations of this study was that FWEC was calculated at an accuracy of 100 epg which is a bit low. An accuracy of 50 epg is desired. For a workable recording system in South Africa, It is recommended to monitor the animals under challenge for a minimum of 6 – 8 weeks. FWEC must then be calculated at an accuracy of 50 epg. Data from the seasonal experiment in Chapter 4 were used to simulate the utility of data recorded with a higher precision. To achieve this, all animals with records in all three seasons were selected and a mean FWEC across seasons were calculated (i.e. yielding counts with an accuracy of 33 epg). Running a single trait model on these data similar to Chapter 4 yielded a heritability estimate (± SE) of 0.20 ± 0.06. This figure compares favourably to within-season heritability estimates ranging from 0.07 (autumn)

190

to 0.19 (spring). This result seems to suggest that the genetic assessment of FWEC is likely to benefit from being counted at a higher accuracy. Further research is warranted.

- In addition, the proportion of zero counts must also be calculated to give an indication of the intensity of challenge along with the mean FWEC. It important to arrive at a standard operation protocol for assessing FWEC in South Africa if inclusion in a formal national test is considered.

- Species identification of the nematodes is also recommended in studies of this nature. Different nematodes have different fecundity levels and some parasites are prevalent in other seasons than the others. So, species identification of the nematodes especially for *Haemonchus contortus* is recommended. A larval culture or differentiation test for the proportion of the nematodes present could be used. Depending on the prevalence of infestation, a selective *Haemonchus* drench along with FWEC (at drenching) and FWEC 14 days post drenching could be compared. Therefore, FWEC records should be collected before selective drench, during and 14 days post drench.

- Hypersensitivity, also known as low FWEC scouring has been poorly described in South Africa. Based on Australian results, it usually occurs a few months after winter, in sheep that are 14 to 15 months old. Scouring needs to be addressed since dagginess are also linked to a high risk of blowfly strike. To treat hypersensitivity a chemical drenching of the sheep once scouring starts is recommended.

- Future local studies should consider the reason for scouring in South African sheep. Based on results in the literature, poor immune-competence could be the cause of high dag scores in the weaners at Elsenburg (Chapter 9), while hypersensitivity could be implicated in the Tygerhoek hoggets. Inconclusive genetic correlations of dag scores with FWEC, however, complicated reasoning as to potential underlying causes of high dag scores. Futher research on this topic is warranted.

- The present results suggested that the FAMACHA© system may have a role to play under conditions where irrigated pastures are used in the Mediterranean region of South Africa (Chapter 9). However, no conclusive advantages could be demonstrated on dryland pastures where non-haematophageous parasites are expected to predominate. More research should be conducted to clarify the utility of FAMACHA© under a variety of Mediterranean conditions. Genetic correlations of the subjectively scored FAMACHA© traits with other traits of economic importance is also indicted.

- Finally, it is hoped that this research will set in motion a series of events that will eventually allow the routine application of genomic principles to the local ovine genetic resource. As an increasing number of genotypes of resource flock and industry animals become readily available it will become possible to conduct a genome wide association scan for putative loci that could be involved in the expression of resistance to gastrointestinal nematodes and other pathogens as well as in other hard-to-measure traits of economic importance. With extended phenotypes being recorded in the resource flocks studied, these flocks are also well-placed to act as part of a reference population for the prediction of genomic breeding values in South African sheep. Fortunately, most South African resource flocks are, to an extent, already linked among each other, and also to the industry genetic resource. Effort should be put in obtaining more genotypes of influential animals with extended genotypes, while linkage with industry flocks should be maintained and expanded where feasible. This research will have to include representation of a range of industry and institutional human and monetary resources, as the financial burden as well as appropriate human capital is unlikely to be present in a single organization. Linkages with reputable overseas academic partners are also foreseen to contribute to the success of projects of this nature, as all expertise needed is unlikely to come from within South Africa. Sustainable sheep production in the face of global challenges such as climate change, a rapid population growth and declining research funding could be achieved in this way.