Genomics as part of an integrated study of smallholder sheep farming systems in the Western Cape, South Africa

by
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Declaration

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Abstract

The aim of this study was to evaluate the productivity of smallholder sheep farming systems in the Western Cape, South Africa, using an interdisciplinary approach, combining socio-economic factors and genomics. The objectives were firstly to investigate sheep breeding practices followed in smallholder sheep farming systems and to determine socio-economic factors that influence offtake rate of flocks in the Western Cape, South Africa. Secondly, to compare genetic diversity and population structure of smallholder sheep flocks to Western Cape resource flocks. Thirdly, to identify single nucleotide polymorphisms associated with causal variants for the wet-dry phenotype using the ovine 50K SNP bead chip. The final objective was to determine selection signatures within South African sheep populations. To achieve the first objective interviews were conducted with 72 smallholder farmers in three districts of the Western Cape, namely the West Coast, Karoo and Eden. Phenotypic measurements of body weight, body condition score and reproduction (wet and dry phenotype) were obtained from a sample of ewes from the West Coast district from 2011 until 2014. Range condition scores were estimated for two farms in the Karoo and four farms in West Coast district. SURVEYMEANS and SURVEYFREQ in SAS were used to obtain means and frequencies for qualitative data. The production systems were largely small-scale (43-85%) and communal (10-57%). Sheep were mainly kept for consumption purposes. The Dorper was the prominent breed used in all the farming systems and selection emphasis was different for farming systems. Traits selected for by communal farmers included temperament, control of flies, meat taste, growth rate, fertility and foraging ability; whereas small-scale farmers selected for conformation, mothering ability, disease tolerance, heat tolerance and temperament. Lucerne was the predominant source of feed in addition to natural grazing of rangeland. The major constraints mentioned were land availability, drought and water availability. Average range condition scores were low for both districts and grazed *vs*. rested camps, implicating overgrazing. Carrying capacity was higher than the recommended carrying capacity in the Eden district (both communal and small-scale farmers, 0.26 and 18.5 ha/LSU respectively) and in West Coast for small-scale farmers. The flock structure showed variation

between farming systems with mature ewes (39-86%) and young replacement ewes (0.41-46%), young rams (0.41-15%), rams (0-5%) and lambs (0-2%). The wet-dry phenotype was recorded as a measurement of reproductive success over the three year period. The chi-square test indicated significant differences between reproductive performances over the different years with a repeatability of 0.399. Information on the socio-economic status of the farmers, their production system and reason for keeping sheep was obtained. Information on the average numbers of lambs sold and offtake rate was obtained as an economic indicator. A general linear model was fitted on average number of lambs sold and offtake with district, sources of income, participation in government programs and flock size as fixed effects. The majority of smallholder farmers were above 40 years of age and only 32% ranked their wealth status as poor. The smallholder sheep farming systems in the Western Cape were male dominated. District significantly influenced average number of lambs sold and offtake rate. The Karoo district sold a higher average number of lambs per year (41 ± 8.8), with West Coast and Eden selling the same average number of lambs per year at 7 ± 2.2 and 7 ± 2.6, respectively. Offtake rate for the respective districts were not significantly different and were 17 ± 17% for Eden, 48 ± 20% for the Karoo and 46 ± 20% for West Coast. To achieve the second objective blood samples were obtained from 295 sheep of which 172 had been identified as smallholder Dorpers, 4 smallholder White Dorpers, 46 purebred Dorpers, 26 purebred South African Mutton Merinos and 47 purebred Namaqua Afrikaners. Genetic diversity was estimated using allelic richness (Ar), observed heterozygosity (Ho), expected heterozygosity (He) and inbreeding coefficient (F). Population structure analysis was performed using fastSTRUCTURE to determine the breed composition of each genotyped individual. The Namaqua Afrikaner had the lowest He of 0.280 ± 0.18 while the He of smallholder Dorper, Dorper and South African Mutton Merino did not differ and were respectively 0.364 ± 0.13, 0.332 ± 0.16 and 0.329 ± 0.17. The inbreeding coefficient was highest for the pure breeds, Namaqua Afrikaner, Dorper and South African Mutton Merino compared to the average inbreeding coefficient for the smallholder Dorper population. There was evidence of introgression with Namaqua Afrikaner, South African Mutton Merino and White Dorpers in the

smallholder Dorper population. Similarly, the latter population was more genetically diverse than the purebred Dorper, South African Mutton Merino and Namaqua Afrikaner breeds from the resource flock. To achieve the third objective wet-dry records were obtained from smallholder farmers (n = 176) and the Nortier Research Farm (n = 131) for the 2014 breeding season. A logistic regression model was fitted to adjust the data for the fixed effects of farm, breed, and age of the ewe and mating weight as a covariate. Linkage disequilibrium (LD) and inbreeding coefficient were estimated using PLINK. Association analysis was performed using the genome-wide efficient mixed-model association package (GEMMA) to determine whether any significant SNPs were associated with the wet-dry reproductive trait. The wet-dry phenotype differed significantly between the smallholder (0.63 ± 0.04) and research farm flocks (0.79 ± 0.04). Genome-wide linkage disequilibrium (LD) across all populations amounted to $r^2 = 0.36$. Dorpers from the smallholder flock exhibited rapid LD decay versus the resource ovine populations. Inbreeding levels were also lower for the smallholder flock ($4 \pm 0.003\%$) versus the research flock ($13 \pm 0.008\%$). No significant SNPs were identified after correction for false discovery rate. The heritability estimate for the wet-dry trait, using SNP information, was 0.24. To achieve the last objective a study was done to obtain selection signatures in the three purebred sheep breeds using HAPFLK and Bayescan methods. Selection signatures obtained from HAPFLK included 26 significant SNP loci which were associated with genes that play a role in the physiological pathways of the immune system, nervous system and pigmentation. Using Bayescan, 92 SNP loci were under selection and some were associated with genes influencing the immune system and polledness. Candidate genes obtained from this study included genes that play a role in the immune system, the nervous system, reproduction (GNRH1), pigmentation (MREG, KITLG), muscle growth (GDF11) and heat shock protein (DNAJC28). Smallholder sheep farming systems on a socio-economic scale were unsustainable. However, on an environmental scale using genetic diversity as an indicator, smallholder sheep were more sustainable. Selection signatures linked to fitness and robustness may to contribute to literature investigating the adaptation of South African ovine genetic resources to variability in ambient temperature.

Opsomming

Die doel van hierdie studie was om die produktiwiteit van klein-skaapboerderystelsels in die Wes-Kaap, Suid-Afrika, te evalueer deur 'n interdissiplinêre benadering te gebruik deur sosio-ekonomie en genomika te kombineer. Die doelwitte was eerstens om skaap teelpraktyke te ondersoek wat gevolg word in klein-skaapboerderystelsels en om sosio-ekonomiese faktore te bepaal wat die produksie van skaapkuddes in die Wes-Kaap, Suid-Afrika beïnvloed. Tweedens, was die genetiese diversiteit en populasie struktuur van klein-skaapkuddes met Wes-Kaapse Department van Landbou se navorsing kuddes vergelyk. Derdens was enkel nukleotied polimorfismes identifiseer wat verband hou met oorsaaklike variante vir die nat-droog fenotipe met behulp van die '50K SNP beadchip'. Die finale doel was om seleksie patrone binne Suid-Afrikaanse skaap populasies te bepaal. Om die eerste doelwit te behaal, is onderhoude met 72 kleinboere in drie distrikte van die Wes-Kaap, naamlik die Weskus, Karoo en Eden, uitgevoer. Fenotipiese metings van liggaamsgewig, liggaamskondisie telling en reproduksie (nat en droog fenotipe) is van 2011 tot 2014 verkry uit ooie van die Weskus distrik. Veld kondisie beramings is gedoen vir twee plase in die Karoo en vier plase in die Weskus. 'SURVEYMEANS' en 'SURVEYFREQ' in SAS is gebruik om gemiddeldes en frekwensies vir kwalitatiewe data te verkry. Die produksiestelsels was grootliks kleinskaals (43-85%) en kommunale (10-57%). Skape is hoofsaaklik vir verbruiksdoeleindes gehou. Die Dorper was die prominente ras wat in al die boerderystelsels gebruik is en die seleksie keuse het verskil vir boerderystelsels. Eienskappe wat deur kommunale boere geselekteer is, sluit in temperament, beheer van vlieë, vleis smaak, groei tempo, vrugbaarheid en weidingsvermoë; terwyl kleinskaalse boere geselekteer het vir konformasie, moederskapvermoë, siekteverdraagsaamheid, hitteverdraagsaamheid en temperament. Lusern was die oorheersende bron van voer, bo en behalwe natuurlike weiding van land. Die belangrikste beperkings was die beskikbaarheid van grond, droogte en water beskikbaarheid. Gemiddelde veld kondisie was laag vir beide distrikte en wat impliseer oorbeweiding. Die dravermoë was hoër as die aanbevole dravermoë in die Eden-distrik (beide kommunale en kleinboere, onderskeidelik 0.26 en 18.5 ha / LSU) en in die Weskus vir kleinskaalse boere. Die kudde-struktuur

het variasie getoon vir die verskillende boerderystelsels met volwasse ooie (39-86%) en jong vervangings ooie (0,41-46%), jong ramme (0,41-15%), ramme (0-5%) en lammers (0-2 %). Die nat-droog fenotipe is aangeteken as 'n meting van reproduksiesukses oor drie jaar. Die chi-kwadraat toets dui op beduidende verskille tussen reproduktiewe prestasie oor die verskillende jare met 'n herhaalbaarheid van 0.399. Inligting oor die sosio-ekonomiese status van die boere, hul produksiestelsel en rede om skape te behou, is verkry. Inligting oor die gemiddelde aantal lammers wat verkoop is en die afkoopkoers is as 'n ekonomiese aanwyser verkry. 'n Algemene lineêre model is toegepas vir gemiddelde aantal lammers verkoop met distrik, inkomstebronne, deelname aan regeringsprogramme en kuddegrootte as vaste effekte in die model. Die meerderheid kleinboere was bo 40 jaar en slegs 32% het hul rykdomstatus as arm beskou. Die klein -skaapboerdery stelsels in die Wes-Kaap was deur die manlike geslag oorheers. Distrik het 'n aansienlike invloed gehad op die gemiddelde aantal lammers wat verkoop is en die afkoopkoers. Die Karoo-distrik het 'n hoër gemiddelde aantal lammers per jaar (41 ± 8.8) verkoop, met Weskus en Eden wat dieselfde gemiddelde aantal lammers per jaar teen onderskeidelik 7 ± 2,2 en 7 ± 2,6 verkoop. Afkoopkoers vir die onderskeie distrikte was nie beduidend anders nie en was 17 ± 17% vir Eden, 48 ± 20% vir die Karoo en 46 ± 20% vir die Weskus. Om die tweede doelwit te bereik, is bloedmonsters verkry van 295 skape waarvan 172 geïdentifiseer is as kleinboere Dorpers, 4 kleinboere Witdorpers, 46 suiwer Dorpers, 26 suiwer Suid-Afrikaanse Vleis Merinos en 47 suiwer Namakwa-Afrikaners. Genetiese diversiteit is beraam deur gebruik te maak van alleliese rykdom (Ar), waargenome heterosigotisiteit (Ho), verwagte heterosigotisiteit (He) en intelings koëffisiënt (F). Populasie struktuuranalise is uitgevoer met behulp van fastSTRUCTURE om die rassamestelling van elke genotipeerde individu te bepaal. Die Namakwa-Afrikaner het die laagste He van 0.280 ± 0.18 gehad terwyl die He van kleinboer Dorper, Dorper en Suid-Afrikaanse Vleis Merino nie verskil het nie en was onderskeidelik 0.364 ± 0.13, 0.332 ± 0.16 en 0.329 ± 0.17. Die intelingskoëffisiënt was die hoogste vir die suiwer rasse, Namakwa-Afrikaner, Dorper en Suid-Afrikaanse Vleis Merino in vergelyking met die gemiddelde intelingskoëffisiënt vir die kleinboer Dorper-bevolking. Daar was bewyse van

introgressie met Namakwa-Afrikaner, Suid-Afrikaanse Vleis Merino en Witdorpers in die kleinboer Dorper-populasie. Net so, was die laasgenoemde populasie meer geneties diverse as die suiwer Dorper, Suid-Afrikaanse Vleis Merino en Namakwa-Afrikaner rasse van die hulpbron-kudde. Om die derde doelwit te bereik, is nat-droog rekords van kleinboere (n = 176) en die Nortier-navorsingsplaas (n = 131) vir die 2014-teelseisoen verkry. 'n Logistieke regressiemodel is toegepas om die data vir die vaste effekte van plaas, ras en ouderdom van die ooi en paringsgewig as 'n kovariaat aan te pas. Koppeling onewewigtigheid (LD) en intelingskoëffisiënt is beraam deur gebruik te maak van PLINK. Assosiasie analise is uitgevoer met behulp van die genoom-wye doeltreffende gemengde-model assosiasie pakket om te bepaal of enige beduidende SNP's geassosieer word met die nat droog reproduksie eienskap. Die nat-droog fenotipe het beduidend verskil tussen die kleinboer (0.63 ± 0.04) en die navorsingsplaaskudde (0.79 ± 0.04). Genoom-wye koppeling-onewewigtigheid oor alle populasies beloop r2 = 0.36. Dorpers van die kleinboer kudde het vinnige LD-verval teenoor die navorsings kudde getoon. Intelings vlakke was laer vir die kleinboer kudde (4 ± 0,003%) teenoor die navorsings kudde (13 ± 0,008%). Geen beduidende SNP's is geïdentifiseer na regstelling vir vals ontdekkingskoers nie. Die oorerflikheidsberaming vir die nat-droog eienskap, met behulp van SNP-inligting, was 0,24. Om die laaste doelwit te bereik, is 'n studie gedoen om seleksie patrone in die drie suiwer skaaprasse te verkry met behulp van HAPFLK- en Bayescan-metodes. Seleksie patrone wat van HAPFLK verkry is, het 26 belangrike SNP lokusse ingesluit wat geassosieer was met gene wat 'n rol speel in die fisiologiese weë van die reproduksie, teenwoordigheid van horing en pigmentasie. Met behulp van Bayescan was 92 SNP loci onder seleksie en sommige is geassosieer met gene wat die immuunstelsel beïnvloed en die teenwoordigheid van horings. Kandidaatgene wat uit hierdie studie verkry is, sluit in gene wat 'n rol speel in die reproduksie (GNRH1), pigmentasie (MREG, KITGL), spiergroei (GDF11) en hitte skok proteïene (DNAJC28). Klein-skaapboerdery stelsels was op 'n sosio-ekonomiese skaal onvolhoubaar. Op 'n omgewingsskaal wat genetiese diversiteit as 'n aanwyser gebruik, was kleinboere egter volhoubaar. Seleksie patrone wat gekoppel

is aan fiksheid en robuustheid, mag bydra tot literatuur wat die aanpassing van Suid-Afrikaanse skape

genetiese bronne aan veranderlikes in omgewings temperatuur ondersoek.

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List of Abbreviations

AFLP – Amplified Fragment Length Polymorphism

BEE –Black Economic Empowerment

BLUP - Best linear unbiased prediction

CH_4 - Methane

CO_2 –Carbon dioxide

CASP – Comprehensive Agricultural Support Program

DNA – Deoxyribonucleic Acid

FEC – Faecal Egg Counts

FecB – Booroola gene mutation

GBLUP – Genomic Best Linear unbiased prediction

GDF9 – Growth Differentiation Factor

GEBV – Genomic Estimated Breeding Value

GWAS – Genome Wide Association Study

h^2 – Heritability

ICT – Information and communication technologies

KIF16B- kinesin family member 16B

KRTCAP3 – Keratinocyte associated protein 3

LD – Linkage Disequilibrium

LRAD –Land Redistribution for Agricultural Development

Ne – effective population size

NSIS - National Smallstock Improvement Scheme

PCR – Polymerase chain reaction

PO – Posterior Odds

QTL – Quantitative Trait Loci

RAPD – Random Amplified Polymorphic DNA

RFLP – Restriction Fragment Length Polymorphism

SAMM – South African Mutton Merino

SNP – Single nucleotide polymorphism

TSPEAR – thrombospondin-type laminin G domain and EAR repeat

Chapter 1

General introduction

1.1 Background

Sustainable agriculture infers to natural systems that can be sustained over the long term, and achieve optimal production with using low inputs, the profitability of a farming unit, ensuring food security, and provision for the demands and necessities of households and communities. To have a sustainable and efficient farming operation, three dimensions i.e. economic, social and environmental should be considered. To incorporate all of these dimensions into finding solutions for unsustainability requires an interdisciplinary approach. An interdisciplinary approach is defined by Rosenfield (1992) as "researchers that work jointly but still form disciplinary–specific basis to address a common problem". This study will integrate two disciplines i.e. social sciences and agricultural sciences, to address the problem of low production performance of smallholder sheep farms in South Africa.

It important to look at the improvement of smallholder sheep farming systems in South Africa because livestock production is one of the major role players in providing food security, particularly for protein foods. Small stock is mainly kept for socio-economic benefits like household food security, capital, direct income as well as the spreading of risk (Moyo & Swanepoel, 2010). Smallholder farmers are not necessarily able to exploit the full potential of their livestock because of constraints such as a lack of education, a lack of infrastructure, poor management, inadequate resources, as well as inadequate strategies for genetic improvement (Rege *et al.,* 2011). Added to the aforementioned challenges for smallholder farmers are the effects of climate change. Smallholder livestock production systems must be investigated economically, environmentally, and socially. This calls for adaptation in farming systems and

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strategies by using an interdisciplinary approach to address this problem. For the context of this study, the issue will be addressed on two levels, socio-economically and environmentally. Socio-economic sciences will be linked to the offtake rate and environmental sciences will be linked to genetic diversity of the animal genetic resources.

Offtake rate is defined as the percentage of sold or slaughtered animals at the end or during a production cycle to the initial stock (Otte &Chilonde). It can also be linked to the number of lambs marketed per year expressed relative to the breeding flock maintained. Smallholder cattle farming systems have low offtake rates (Musemwa *et al.,* 2010) and low lamb marketing percentages have been reported in sheep smallholder systems (Grobler, 2008, Spies & Cloete, 2013). This can be linked to the social-context of the farmers, having little or limited financial resources, land available for farming and whether they are participating in land reform projects or not. Lamb marketing percentage is also influenced by the breed (genetics), nutrition, management practices and environmental factors like extreme droughts.

The environmental concern for smallholder farmers is the ability of animals to adapt and produce in changing and challenging environments. Environmental sustainability can be assessed by determining the genetic structure of the animal resources used by smallholders. Obtaining information on animal performance mainly through phenotypic information is important and allows linkage of quantitative production traits to genetics. It is assumed that a genetically diverse population will contain a combination of alleles able to adapt to the changing environment (Frankham, 2005). It is important to determine the levels of genetic diversity, since high levels of homozygosity (can lead to inbreeding) compromises economically important traits such as reproduction and fertility (Erkanbrack & Knight, 1991). Genomic tools can be used to determine genetic diversity as well as to identify causal variants for quantitative traits related to robustness through employing genome wide association studies (GWAS) (Kijas *et al.,* 2012; Demars *et al.,* 2013; Qwabe *et al.,* 2013). The most common

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molecular markers used in genetic diversity studies include microsatellites and single nucleotide polymorphisms (SNP's). Microsatellites have been used to genetically characterise sheep breeds in South Africa (Soma *et al.,* 2012). This work has been primarily on breeds important for commercial sheep enterprises and there is no information on genetic diversity within and between sheep populations managed by smallholder farmers. In the absence of formal recordkeeping in smallholder farming systems, it may be more efficient to obtain genetic information using molecular markers compared to traditional performance records. However, a suitable reference population with extended phenotypes as well as genomic information is needed to predict accurate genomic breeding in such populations (Daetwyler *et al.,* 2012; Legarra *et al.,* 2014).

1.2 Problem statement

The central and western parts of South Africa, as predominantly a semi-arid area, are more suitable for small stock farming than alternative land-use systems. Enhanced production performance in commercial sheep flocks has been achieved by manipulating genetic diversity of the breeding flock using various breeding techniques. However, low production performance and offtake rates are observed in smallholder sheep farming systems (Grobler, 2008; Spies & Cloete, 2013). Literature indicates that there have been several breeding strategies implemented to improve production of smallholder production systems which included: i) selection between breeds, ii) crossbreeding iii) selection within breeds, iv) marker assisted introgression (Kosgey *et al.,* 2006; Marshall *et al.,* 2011). Selection between breeds has led to breed substitution in smallholder production systems. Several studies have been published, where exotic breeds with high performance levels (under adequate environment) have been introduced in smallholder flocks where inadequate nutrition and management are prevalent (Madalena *et al.,* 1990; Workneth *et al.,* 2002). These exotic breeds are likely to underperform and struggle to adapt to different temperatures and exposure to parasites and diseases. Genotype and environment

interaction is where a breed performs well under optimal conditions (receiving optimal nutrition and efficient management practices) but when located under extreme conditions where limited nutrition and management is available that breed exhibits mediocre performance or similar performance to that of the indigenous breed (Okeyo & Baker, 2005).

The use of crossbreeding has been both successful (Metawi *et al.,* 1999) and unsuccessful in smallholder flocks (Ayalew *et al.,* 2003). A study done by Metawi *et al.,* (1999) in Egypt, compared two different farming systems, namely a transhuman herding system (THS) and mixed crop/livestock farming system (MCLFS) to monitor ewe productivity and lamb production. The MCLFS had higher ewe productivity and a higher number of lambs born than the THS even though the THS had a lower feed input cost and had advantage in the feed costs/kg of lamb weaned in comparison to MCLFS farmers. The THS had a lower mortality rate than the MCLFS. They concluded that low pre-weaning average daily gain and high lamb losses were the main limiting factors that affected flock productivity under the THS and MCLFS respectively. It can be seen from this study, when comparing feed input cost, that the THS sheep were more profitable to their owners than the sheep in the MCLFS system, even though the latter system resulted in a higher productivity. The breeds used by Metawi *et al.* (1999) were crossbred Egyptian breeds which were adapted to their environment and were able to be profitable to their producers although receiving inadequate nutrition in the THS system. The study by Ayalew *et al.* (2003) indicated that net benefits obtained from using indigenous goats were higher in comparison to using crossbreds. The latter study included both tangible value (benefits derived from meat, manure and milk) and intangible value (benefits derived from saved interest/premium on credit/insurance) of goats in the calculation of net benefits.

Kosgey *et al.* (2006) pointed out that constraints to selection within breeds are due to limitations in flock sizes, single sire flocks, inadequate animal identification and recording of pedigree, as well as low level of literacy. Successful marker-assisted introgression of the FecB

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mutation in smallholder sheep flocks in India have been reported which resulted in increased number of live born lambs and lamb survival (Nimbkar *et al.,* 2003).

Marshall *et al.* (2011) indicated that most breeding programmes fail due to insufficient attention given to system requirements such as infrastructure, external funding, organisation at farming level and recognition by stakeholders. The latter authors argued that the use of genomics could only be successful if all the system requirements are met. The use of genomics does have limitations in terms of the lack of availability of phenotypic data. Obtaining reliable records for traits of economic relevance of an appropriate reference population needs to be addressed. Efforts should be concerted in the development of breeding schemes that allows the recording of traits important for both tangible and intangible benefits. Another limitation with the use of genomics is the genotyping costs involved. Genotyping costs per individual using the 50K SNP chip are 73 Euro (Geneseek, 2015). However, these costs have been predicted to decrease in the future (Cloete *et al.*, 2014). Genomics can play a role in obtaining pedigree information for smallholder flocks and decreasing generation interval. However, when designing a breeding plan a holistic approach should be taken that will address socio-economic issues as well as production issues of smallholder farmers.

Limited interdisciplinary studies are available for the evaluation of productivity of smallholder sheep farming systems in the Western Cape, South Africa. Multi-disciplinary studies have been done in Kwa-Zulu Natal (Mahlobo, 2016) and in the Eastern Cape (Marandure *et al.,* 2016) regions of South Africa. Neither of the two studies had a particular focus on productivity of smallholder sheep production system. The former focused on the sustainability of the overall smallholder farming systems in communities that did not keep sheep; while the latter assessed the sustainability of smallholder beef production systems. Livestock offtake rates and animal genetic diversity were not explicitly considered as indicators in either study. Interdisciplinary approaches have been done in Spain (Ripoll-Bosch *et al.,* 2012) where the Framework for

Assessing the Sustainability of Natural Resource Management Systems (MESMIS) was used to evaluate the sustainability of different sheep farming systems. The study observed trade-offs between economic and environmental pillars, thus the higher the economic sustainability the lower the environmental sustainability.

As the production systems and constraints to production efficiency of Western Cape smallholder farmers have not been quantified adequately, further research on this topic is needed. It is anticipated that smallholder sheep farmers in South Africa will be experiencing similar problems as smallholder farmers in other developing countries (Rege *et al.,* 2011). It is therefore necessary to conduct a study to investigate smallholder sheep farming systems in South Africa and to apply an integrated approach to managerial strategies that will include socio-economics and genomics to aid in the overall enhancement of production and economic viability of smallholder farmers.

1.3 Justification

Sheep production in the smallholder sector contributes significantly to the livelihoods of many farmers in the Western Cape. It is therefore important to elucidate factors that influence offtake rates and genetic diversity of the sheep farming systems. Once these are mapped they can be used to improve the productivity of smallholder sheep farming systems. The study will focus on socio-economic factors and flock size as determinants of the offtake rate of smallholder sheep farmers in the Western Cape, South Africa. This is important since smallholder sheep farmers in this sector have been reported to have low offtake rates compared to commercial farmers (Grobler, 2008, Spies & Cloete, 2013). The latter could be linked to their management of animal genetic resources, as well as to other factors, which include social or political constraints. No previous studies have focused on biodiversity on a gene level in sheep and its impact on production and reproduction traits. Genetic diversity of smallholder sheep

populations in South Africa is poorly described and indigenous breeds utilized by smallholder farmers are mostly uncharacterized in terms of their production and reproduction performance. An interdisciplinary approach will thus be taken to determine the social-economic constraints of smallholder sheep farmers, to determine their offtake rate, and to study the genetic structure of their animal resources (sheep) used.

The aim of this study was to evaluate the production performance of smallholder sheep farming systems in the Western Cape, South Africa, using an interdisciplinary approach. The socio-economic aspects encompassed the reasons why smallholders farm with small stock, their constraints and the influence thereof on offtake rate. The environmental aspect investigated the animal genetic resources utilised in smallholder sheep farming systems, quantifying genetic diversity and identifying selection signatures for robustness traits.

1.4 Objectives of the study

The specific objectives of the study were to:

i) Ascertain sheep farming characteristics and breeding practices utilised by smallholder sheep farmers and determine growth and reproduction of smallholder ewes.

ii) Investigate different socio-economic factors that influence offtake rate of smallholder sheep flocks in the Western Cape, South Africa.

iii) Determine genetic diversity and population structure of smallholder sheep flocks in comparison to resource population flocks in the Western Cape, South Africa.

iv) Identify single nucleotide polymorphisms associated with causal variants for the wet-dry phenotype using the ovine 50K SNP bead chip.

v) Determine selection signatures within South African sheep populations using different methods, namely Bayescan and HAPFLK.

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1.5 Thesis overview and layout

The aim of this study was to investigate the production performance of smallholder sheep farming systems in the Western Cape, South Africa, using an interdisciplinary approach. This was achieved through a socio-economic and genomic approach. The thesis is divided into eight chapters consisting of the general introduction, literature review, five research chapters and a conclusion. Each chapter, except chapters 1 and 8, is structured as a manuscript for publication, complete with abstract and list of references.

Chapter 1 is the general introduction and provides a background and motivation for the study.

Chapter 2 is the literature review and discusses issues of sheep farming systems in South Africa, and the role of genomics in addressing some of these limitations. This manuscript has been published in *Sustainability (07/07/2017)*.

Chapter 3 is a research chapter investigating sheep breeding systems of smallholder sheep farmers in the Western Cape. This manuscript is in preparation for submission to *Small Ruminant Research.*

Chapter 4 is a research chapter investigating socio-economic factors influencing offtake rate. This manuscript is in preparation for submission to *Small Ruminant Research*.

Chapter 5 investigated the population structure and genetic diversity of smallholder sheep flocks and pure breed Dorper, Namaqua Afrikaner and South African Mutton Merino obtained from a governmental resource farm. This manuscript has been published in *Tropical Animal Health and Production* 49, 1771-1777.

Chapter 6 is a preliminary genome wide association study using the ovine 50K SNP bead chip to identify single nucleotide polymorphisms associated with the wet-dry phenotype in sheep.

This manuscript was published in the *South African Journal of Animal Science 2017, 47, 327-331*.

Chapter 7 explored selection signatures in smallholder and resource sheep flocks using two different methods, Bayescan and HAPFLK. This manuscript is in preparation for publication in the *South African Journal of Science*.

Chapter 8 concludes the thesis and presents further comments and recommendations.

References

Ayalew, W., Rischkowsky, B., King, J.M. & Bruns, E., 2003. Crossbreds did not generate more net benefits than indigenous goats in Ethiopian smallholdings. Agric. Sys. 76, 1137-1156.

Demars, J., S. Fabre, J. Sarry, R. Rossetti, H. Gilbert, L. Persani, G. Tosser-Klopp, et al. 2013. Genome-Wide Association Studies Identify Two Novel BMP15 Mutations Responsible for an Atypical Hyperprolificacy Phenotype in Sheep. PLoS Genetics 9, no. 4.

Daetwyler, H.D., Bolormaa, S., Brown, D.J., Van der Werf, J.H.J. & Hayes, B.J. 2012. A Genomic Prediction Cross-Validation Approach Combining Ewe Repeated Phenotypes and Ram Daughter Trait Deviations. In: Proc. Assoc. Advmt. Anim. Breed. Genet. 360–363.

Ercanbrack, S.K. & Knight, A.D., 1991. Effects of inbreeding on reproduction and wool production of Rambouillet, Targhee, and Columbian ewes. J. Anim. Sci. 69, 4734-4744.

Frankham R., 2005. Genetics and extinction. Biol. Conserv. 126, 131–140.

Grobler, H.J.F., 2008. How are our LRAD farmers doing? Agriprobe 5, pp. 4-5.

Grobler, H.J.F., 2010. Evaluation survey at extensive farms in the Central Karoo 2009. Agriprobe June, pp. 6-9.

Heaton M.P., Leymaster K.A., Kalbfleisch T.S., Kijas J.W., Clarke S.M., McEwan J., Maddox J.F., Basnayake V., Petrik D.T., Simpson B., Smith T.P.L., Chitko-McKown C.G. & the International Sheep Genomics Consortium, 2014. SNPs for parentage testing and traceability in globally diverse breeds of sheep. Public Library of Science ONE: e94851

Kijas, J.W., Townley, D., Dalrymple, B.P., Heaton, M.P., Maddox, J.F., McGrath, A., Wilson, P., Ingersoll, R.G., McCulloch, R., McWilliam, S., Tang, D., McEwan, J., Cockett, N., Oddy, V.H., Nicholas, F.W. & Raadsma, H., 2009. A Genome wide survey of SNP variation reveals the genetic structure of sheep breeds. PLoS ONE 4, e4668, doi: 10.1371/journal.pone.0004668

Kijas, J.W., Lenstra, J.A., Hayes, B., Boitard, S., Porto Neto, L.R, San Cristobal, M., Servin, B., McCulloch, R., Whan, V., Gietzen, K., Paiva, S., Barendse, W., Ciani, E., Raadsma, H., McEwan, J., Dalrymple, B. & the International Sheep Genomics Consortium Members. 2012. Genome-wide analysis of the world's sheep breeds reveals high levels of historic mixture and strong recent selection. PLoS Biol 10, e1001258.

Kosgey, I.S., Baker, R.L., Udo, H.M.J. & Van Arendonk, J.A.M., 2006. Successes and failures of small ruminant breeding programmes in the tropics: a review. Small Rumin. Res. 61, 12-28.

Legarra, A., Baloche, G., Barillet, F., Astruc, J.M., Soulas, C., Aguerre, X., Arrese, F., et al. 2014. Within- and across-Breed Genomic Predictions and Genomic Relationships for Western Pyrenees Dairy Sheep Breeds Latxa, Manech, and Basco-Béarnaise. J. Dairy Sci. 97, 3200–3212. http://www.ncbi.nlm.nih.gov/pubmed/24630656.

Madalena, F.E., Lemos, A.M., Teodoro, R.L., Barbosa, R.T. & Monteiro, J.B.N. 1990. Dairy production and reproduction in Holstein-Freisan and Guzura crosses. J. Dairy Sci. 73, 1872-1886.

Mahlobo, B.T., 2016. Multi-criteria livestock assessment of sustainability of smallholder farms in Kwa-Zulu Natal. M.Sc thesis, Stellenbosch University.

Marais, P.G., King, B.R. & Stannard, C.G., 2006. Evaluation of the genetic potential for growth and wool production of sheep in the communal areas of the Eastern Cape. Research report of the Grootfontein Agricultural Development Institute, 2007. Private Bag X529, Middelburg 5900, South Africa. pp. 33-34.

Marandure, T., Mapiye, C., Makombe, G. & Dzama, K., 2016. Indicator-based sustainability assessment of the smallholder beef cattle production in South Africa. Agroecol. Sust. Food Syst. DOI: 10.1080/216835652016:1231152.

Marshall, K., Quiros-Lompos, C., van der Werf, J.H.J. & Kinghorn, B., 2011. Marker-based selection within smallholder production systems in developing countries. Livest. Sci. 136, 45-54.

Metawi, H.R., Kandil, H.M. & El Shear, H.M., 1999. Sheep productivity under extensive and semi-intensive production systems in Egypt. In: Systems of sheep and goat production: Organization of husbandry and role of extension services. Eds. Rubino, R. & Mohrand-Fehr, P. CIHEAM IAMZ, 239-243.

Moyo, S. & Swanepoel, F.J.C., 2010. Multifunctionality of livestock in developing communities. In: The role of livestock in developing communities: enhancing multifunctionality. Eds. Swanepoel, F.J.C., Stroebel, A., Moyo, S. publ. UFS & CTA. pp. 1-12.

Musemwa, L., Mushunje, A., Chimonyo, M. & Mapiye, C., 2010. Low cattle market offtake rates in communal production systems of South Africa: Causes and migration strategies. J. Sustain. Dev. Africa, 12, 209–226.

Nimbkar, C., Ghalsasi, P.M., Maddox, J.F., Pardeshi, V.C., Sainani, M.N., Gupta, V., & Walkden-Brown, S.W., 2003. Expression of the FecB gene in the Garole and crossbred ewes in Maharashtra, India. Proc. Assoc. Advmnt. Anim. Breed. Genet. 15, 111-114

Okeyo, A.M. & Baker, R.L., 2005. Methodological illustration of genotype x environment interaction (GXE) phenomenom and its implications: A comparative productivity performance study on Red Massai and Dorper sheep breeds under contrasting environments in Kenya. Training module, published by the ILRI in the CGIAR database. http://hdl.handle.net/10568/3597

Otte, M.J. & Chilonde, P., 2002. 'Cattle and small ruminant production systems in Sub-Saharan Africa. A systematic review', FAO publishing Rome.

Rege, J.E.O., Marshall, K., Notenbeart, A., Ojango, J.M.K. & Okeyo, A.M., 2011. Pro-poor animal improvement and breeding – What can science do? Livest. Sci. 136, 15-28.

Ripoll-Bosch, R., Diez-Unquera, B., Ruiz, R., Villalba, D., Molina, E., Joy, M., Olaizila, A. & Bernues, A. 2012. An integrated sustainability assessment of mediterranean sheep farm with different degrees of intensificiation. Agricul. Sys. 105, 46-56.

Rosenfield, P.L., 1992. The potential of transdisciplinary research for sustaining and extending linkages between the health and social sciences. Sos. Sci. Med. 35, 1343-1357.

Soma, P., Kotze, A., Grobler, J.P. & Van Wyk, J.B., 2012. South African sheep breeds: Population genetic structure and conservation implications. Small Rumin. Res. 103, 112–119.

Spies, D.C. & Cloete, P.C., 2013. Performance and marketing options for red meat in the formal and informal value chains in the Free State Province. 19th International Farm Management Congress, SGGW, Warsaw, Poland.

Chapter 2

Literature review

2.1. Introduction

Smallholder livestock production plays a pivotal role in the economies of developing countries. Smallholder farmers are the primary producers of food and account for 80% of all the farms in sub-Saharan Africa (World Resources Institute [WRI], 2014). Livestock are important for income generation and supplying basic animal protein products; however, poor reproduction and growth performance are a common feature of these production systems. Most of the surface area in South Africa is semi-arid which makes it unsuitable for anything but extensive ruminant livestock farming (Cloete *et al.*, 2014). In South Africa the sheep industry is divided into commercial, emerging (i.e. farms transitioning from small-scale or communal to commercial farms), small-scale farmers and communal farmers (a group of farmers farming on communal land). There are an estimated 28.8 million sheep in South Africa, of which 21.4 million are owned by commercial farmers (Directorate Statistics and Economic analysis, 2013). The industry is dominated by the commercial sheep sector that supplies meat products locally and wool products for export. The emerging and small-scale sheep farmers supply meat and wool products to the informal and formal market, whereas the communal farmers are supplying meat for informal markets. Sheep also fulfil multiple socio-economic roles to small-scale and communal farmers, including the production of meat for consumption, wool, income, manure, draught power and for religious and cultural rituals. The Dohne Merino, Merino and Dorper breeds are the most prominent breeds of sheep in South Africa. Other sheep breeds found in the South African sheep industry include Dormer, Ile de France, Meatmaster, Namaqua Afrikaner, Afrino, Merino Landsheep and South African Mutton Merino (Cloete *et al.*, 2014). The number of sheep owned by smallholder farmers is inadequately documented. Sheep raised

by most communal farmers in South Africa include the Nguni, Damara, Pedi, Namaqua Afrikaner and the Dorper. However, the Dorper is the breed of choice for farmers in the semi-arid and arid environments of South Africa, because of its ability to grow and reproduce in harsh environments. Some of these breeds are indigenous to South Africa and have characteristics that make them well-adapted to local conditions (Kunene *et al.,* 2007; Almeida, 2011; Snyman *et al.,* 2013; Zishiri *et al.*, 2013). Commercial farmers achieve high production due to selection of these breeds for improved growth, reproduction, meat and wool traits in exotic breeds (Schoeman *et al.,* 2010). Minimal or no selection took place in the abovementioned traits in smallholder sheep production systems resulting in low production performance (Grobler, 2010). Indigenous breeds used in smallholder systems such as the Damara (Almeida, 2011) and Namaqua Afrikaner (Cloete *et al.,* 2013), however, outperform commercial breeds for fitness traits, survival and tick resistance. Fitness traits can be described as a group of traits enabling animals to adapt and include several reproduction and survival traits (Goddard, 2009). Selection in commercial flocks has been achieved using traditional breeding methods. However, with the advent of genomics it is possible to accelerate genetic progress for traits important in smallholder production through more accurate selection, by including molecular markers into traditional breeding values and obtaining genomic breeding values for individuals (Van der Werf, 2009).

Sustainable agriculture implies long-term maintenance of natural systems, to produce in harmony with the available resources without over exploitation, adequate income per farming unit, fulfilment of basic food needs, as well as provision for both existing and emerging demands and necessities of rural families and communities (Brown *et al.,* 1987). The ability of smallholder farmers to exploit the full potential of their livestock is limited by infrastructure, limitations in management, inadequate feed resources, as well as inadequate strategies for genetic improvement of their livestock (Rege *et al.*, 2011). These constraints are further

aggravated by issues like climate change and its impact on the future availability of natural resources like water, land, plant and animal species integral to the survival of future generations (World Resources Institute [WRI], 2014). It is therefore necessary to have livestock farming systems that are resilient to the effects of climate change. Resilience focuses on the adaptive capacity of an ecosystem (Anderies *et al.*, 2013) and therefore the focus of this review will be to discuss robustness at animal level.

This calls for adaptation in farming systems and strategies using interdisciplinary and participatory approaches to address the constraints for sustainable production of smallholder farmers. One such approach is to investigate productivity on three different dimensions namely, socially, economically and environmentally (Oudshoorn *et al.*, 2012). Interdisciplinary studies addressing the constraints of smallholder livestock farming systems in South Africa are limited. Studies done have covered all three dimensions of sustainability, but they have rather focused on sustainability indicators in relation to specific environments and production systems (Mahlobo, 2016; Marandure *et al.*, 2016). Indicators covered in such studies include education levels, gender roles, cost-benefit analyses, market access, rangeland condition as well as the influence of crop rotation on soil quality (Mahlobo, 2016; Marandure *et al.*, 2016). Environmental indicators in other literature mainly focus on water derived from precipitation, ground water pollution, CH_4 and CO_2 emissions, eutrophication, acidification, change in land use patterns as well as soil erosion (Van Calker *et al.*, 2008; Lebacq *et al.,* 2013). Even though biodiversity is mentioned as an indicator, no studies have been done focusing on how to measure biodiversity on the gene level in animals (which will be further referred to as genetic diversity) and its impact on production and reproduction traits. Genetic diversity serves as the raw material to ensure optimum production and reproduction in livestock. The genetic diversity of smallholder sheep populations in Africa is generally unknown, but is directly related to their potential for genetic improvement, and indigenous breeds utilized by smallholder farmers are

mostly uncharacterized in terms of their production and reproduction performance. This is due to the absence of recordkeeping and formal breeding strategies in smallholder farming systems. Genetic improvement using traditional breeding strategies thus has limited application and the use of genomic tools can aid in obtaining pedigree information for smallholder sheep flocks. Genomic tools can also be used to determine genetic diversity as well as to identify causal variants for traits related to robustness and important for sustainability through employing genome wide association analyses (GWAS) (Kijas *et al.*, 2012; Demars *et al.*, 2013; Qwabe *et al.,* 2013).

The objective of this review is to give a brief overview of the indicators important for sustainable production in ovine resources maintained by smallholder farmers in South Africa and the constraints to sustainable sheep farming in smallholder production systems. The review also provides an overview of the genetic traits important for productivity, the role of genomics in improving these traits and the linkage of these genetic traits to different farming systems in South Africa.

2.2. Indicators of sustainable productivity of sheep farmers in South Africa

Most sustainability assessment methods follow a hierarchy where dimensions are at the highest level. These dimensions can be classified as social, economic and environmental (Oudshoorn *et al.*, 2012) and indicators can be used to measure them. Sustainability indicators are defined as variables that provides information on another less accessible variable (Zahm *et al.*, 2007).

2.2.1. Social indicators

The social dimension is often ranked lower than environmental and economic dimensions in sustainability assessment operations (Omann & Spangenberg, 2002). This could be due the lack of conceptual clarification of social indicators and how to measure it. Omann and

Spangenberg, (2002) reported that "social scientists had bad experiences in the 1960's receiving limited public resonance and been rejected as ideological strait jackets. "The social dimension also poses questions to the current European development model which is fordistic in nature (Omann & Spangenberg, 2002). The social dimension however is included as a framework for more effective environmental strategies (Omann & Spangenberg, 2002). This dimension has to be considered on the same footing as the other dimensions to avoid bias in assessments. To date, no consensus exists on what constitutes social sustainability. Various studies have derived different social sustainability indicators as based on their research questions. Examples of indicators used to reflect social sustainability in previous studies include; education level, working conditions and quality of life (Lebacq *et al.,* 2013). Social sustainability indicators relevant to South Africa's smallholder livestock production are not known and warrant investigation. The geo-location of most smallholder farmers was influenced by the colonial apartheid regime while, their current socio-economic conditions are a result of policies of both the apartheid government and the new democratic government (Cousins, 2010). Therefore, historic and current events markedly influence the social status of smallholder farmers. Indicators such as food access, family health status, education level, access to information and gender equality in decision making were used to assess the sustainability of the smallholder cattle production system in the Eastern Cape Province of South Africa (Marandure *et al.*, 2016). It was concluded that the social dimension of the system was partially sustainable. Other indicators relevant to the social dimension of sustainability include household well-being, access to clean water and sanitation, participation and belonging in social organizations and animal welfare among other indicators (Vandamme *et al.,* 2010). Certain social indicators will only be applicable to specific farming systems, for instance access to clean water and sanitation might not be a priority in commercial farming systems as this hurdle is already overcome in these systems. In contrast, such indicators would be of greater

importance for smallholder farming systems in rural communities. It is thus important to first characterize the farming system before deciding which social indicators are suitable to measure sustainability.

2.2.2 Economic indicators

Economics refers to the short and long term profitability of a farming system. Indicators used for this includes net farm income, resource use efficiency and productivity (Lebacq *et al.,* 2013). Other studies also used total agricultural offtake as an economic indicator (Atanga *et al.,* 2013). The role of livestock as a direct income source is overridden by socio-cultural roles for most subsistence farmers (Musemwa *et al.,* 2010). For example, to most resource poor subsistence farmers without access to formal financial institutions, livestock are maintained as a form of capital, providing them with savings and offering opportunities for farmers to accumulate wealth (Coetzee *et al.,* 2005). Swanepoel *et al.* (2008) also stated that livestock guarantees financial security and help to finance planned and unplanned expenditure of smallholder farmers. The latter is more applicable for smallholder cattle farmers, whereas for smallholder sheep farmers, profit derived from sheep plays an important role. This is true for the situation in Eastern Cape, Kwa-Zulu Natal and Lesotho where smallholder sheep farmers mainly farm with Merino type sheep for financial income (Mkhabela, 2013). In the Western Cape sheep are kept for the production of meat for consumption and for income. Sustainability indicators based on input-output systems or cost-benefit analyses may thus not directly reflect subsistence livestock production systems as they do in the profit oriented commercial livestock sector (Hoffmann, 2011).

2.2.3 Environmental indicators

Indicators used to measure environmental sustainability include CH_4 and CO_2 emissions, eutrophication, acidification, groundwater pollution, dehydration of soil and biodiversity, and

the extent of rangeland degradation (Van Calker *et al.*, 2008; Lebacq *et al.,* 2013). These indicators are widely covered in literature and will not be explicitly covered in this review. In the literature, biodiversity is used in the broad sense and includes all components of biological diversity: the variation between animals, plants and micro-organisms including those hosted by livestock species. South Africa's landscapes have a diverse biomes including grasslands, Nama-Karoo and Karoo vegetation types, which are suitable for livestock grazing. However, these landscape have been reported as overgrazed (Scholtz *et al.*, 2008). Overgrazing results in a decline in biodiversity of the plant species. This resulted in the grazing of all the palatable plant species by livestock and the domination of unpalatable plant species(Herrero *et al.*, 2009; Mahlobo, 2016). A reduction in palatable grass species will compromise the production of livestock. Low livestock production is linked to reduced income and thus the livelihood of farmers are compromised.

The biodiversity of livestock breeds are under question as 8% of livestock breeds are extinct and 21% of livestock breeds are classified as being at risk of extinction (Hoffman, 2011). Studies on livestock biodiversity as an indicator of sustainability are limited (Hoffmann, 2011). Attaining genetic diversity within and between livestock species are essential for the sustainability of life on earth. Considering the potential economic role that indigenous breeds may have in the future as well as their current cultural value it is crucial to characterise their genetic diversity. A number of studies have, however, mapped the genetic diversity of major livestock species in South Africa using molecular markers, including work by Halimani *et al.* (2012) on pigs, Mtileni *et al.* (2011) on poultry and Soma *et al.* (2012) on sheep. High levels of genetic diversity have been observed for indigenous sheep genetic resources in South Africa (Kunene *et al.,* 2007; Hlophe, 2011), thus implicating the potential to use these breeds to develop sustainable breeding programs for smallholders using genomic tools.

The three dimensions of sustainability are closely interlinked. The environmental dimension, in this context animal genetic diversity, will influence animal production and thus the economic dimension. The economic dimension will in turn influence the social dimension. If reproduction and production is high, income obtained from sheep will be high. This will positively affect the social dimension of sustainability; where an increased income from livestock will lead to increased food security and well-being of the farmer. There could however be negative trade-offs between the dimensions, improved animal production through intensification can lead to negative impact on the environment as seen in commercial livestock practices (Vitousek *et al.*, 1997). It is necessary to describe the different sheep farming systems in South Africa. The suitable indicators for each system to measure sustainability should also be described. These farming systems have unique problems of sustainability that need to be addressed.

2.3. Limitations for productivity of sheep farming systems in South Africa

The limitations to productivity for sheep farming systems are driven by the climate, vegetation, topography and husbandry practices and the political dispensation in which it is found, i.e. socialism, communism, capitalism or free-market. In South Africa smallholder farmers were excluded from supplying food to the market prior to 1980 under the Marketing act 1968 (Dzivakwi, 2010). This has led to commercial farmers dominating the market. Often the influence of the social dimension on the outcome of the farming system is overlooked (Boogaard *et al.*, 2011).

Due to the political history of South Africa there are different types of smallholder farming enterprises. Prior to the colonial administration in the 19th century most of the land in South Africa belonged to black people, this changed in 1913 when 87% of the land were redistributed to white people and only 13% to black people staying in the homelands (Percival & Homer-

Dixon, 1995). This had a dramatic effect on agriculture in South Africa, which consists of a relatively small number of commercial farms (though with high output), co-existing with large numbers of smallholder farms (Organisation for economic co-operation and development [OECD], 2006). This system has led to many smallholder farmers ending up with marginal land and resources to farm.

After the 1994 election, black economic empowerment (BEE) actions have been implemented to further support employment equity. Since then, programs like the Land Redistribution for Agricultural Development (LRAD) and the Comprehensive Agricultural Support Program (CASP) have been initiated by the Department of Agriculture, Forestry and Fisheries to assist in the agricultural development of underprivileged communities. These programs have been successful in settling 61% of land claims. However, problems have occurred in the land redistribution process. These problems are linked to farmers receiving land without adequate training in livestock production, institutional capacity, financial resources and a lack of agricultural support services to allow these farmers to start up viable farming enterprises.

The socio-political situation in South Africa led to the development of the following farming systems: 1. Commercial sheep farming system, 2. Emerging sheep farming systems, 3. Smallholder (small-scale and communal) sheep farming systems. The different farming systems and their constraints are described in Figure 2.1. To determine the productivity of smallholder sheep farmers in South Africa, it is necessary to determine which indicators are relevant to the specific farming system to address these constraints.

Problems of intensive commercial sheep farming systems are related to the effects of intensification. For commercial farmers the economic dimension is determined by their profitability which depends on income, efficiency and productivity (Lebacq *et al.,* 2013). To achieve high profitability, high input and thus high output system is necessary. Sheep breeds selected for this production system are important, as breeds are required that have high
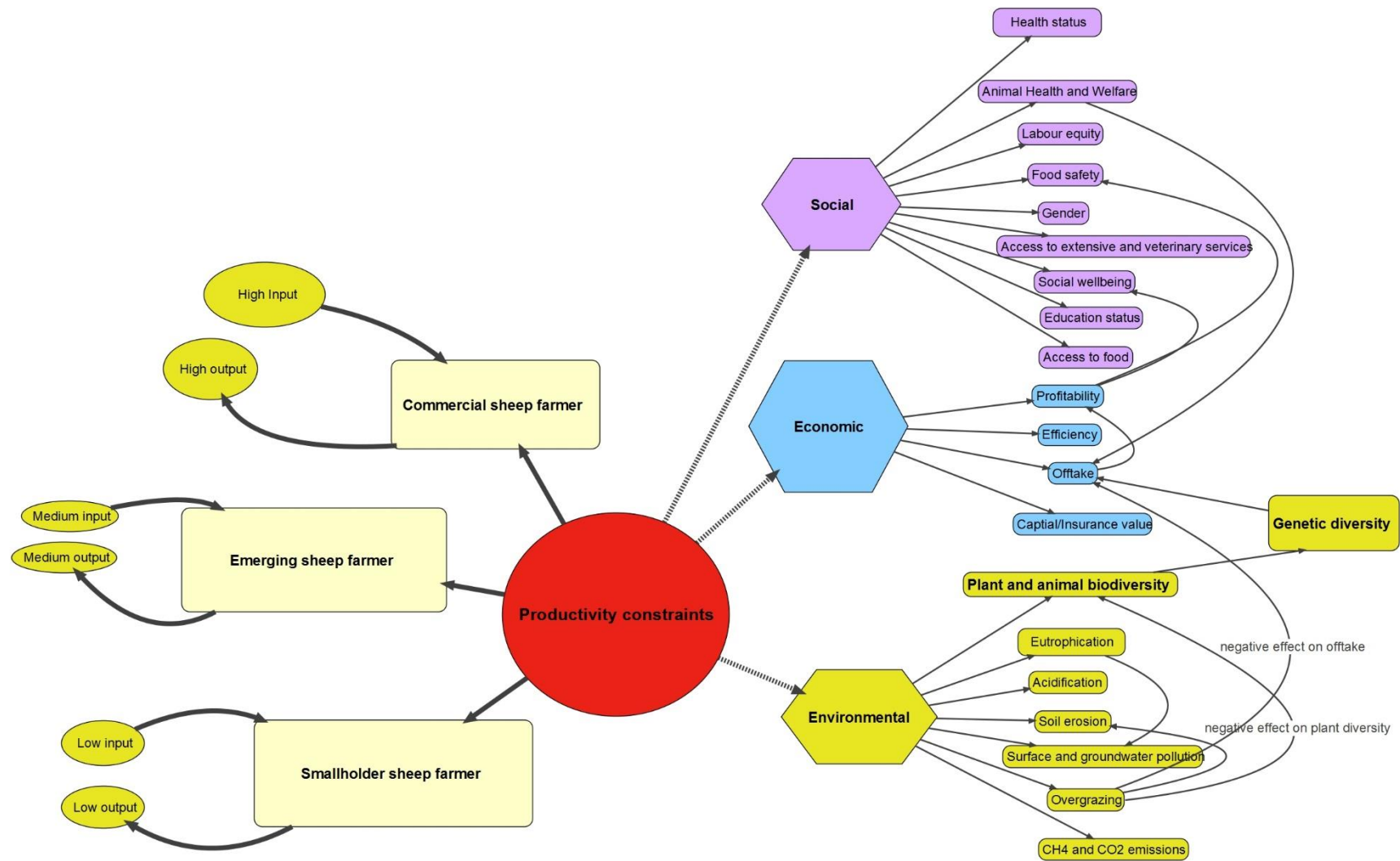
Figure 2.1 Different sheep farming systems in South Africa and productivity constraints

reproduction performance and fast growth rate. Exotic breeds like the Merino type breeds (Merino, Dohne Merino, South African Mutton Merino and Merino Landsheep) are commonly used in these systems due to their high prolificacy (Cloete *et al.,* 2003; Cloete *et al.*, 2014). High stocking rates are maintained to achieve high production levels and have resulted in overgrazing of land thus resulting in a decrease of plant and animal biodiversity (Vitousek *et al.*, 1997). The planting of irrigated pastures has led to the use of pesticides and fertilizers which has affected chemical and physical soil quality as well as added to eutrophication and acidification of soil and water bodies (Vitousek *et al.*, 1997). Social aspects of commercial farming systems can be divided into internal social aspects and external social aspects (Lebacq *et al.,* 2013). The internal social aspects includes gender equality and labour inequity, whereas the external social aspects include animal health and welfare. For extensive commercial sheep farmers the economic and social sustainability problems will be similar to those of intensive sheep enterprises. The environmental problems will be different in terms of the effects of eutrophication and acidification which will be less in extensive systems due to the use of natural grazing with little additional planted crops or pastures. The problem of overgrazing and resultant decrease in plant biodiversity is, however, more applicable to extensive commercial and smallholder communal sheep farming systems.

Smallholder sheep farmers in South Africa depend on low-input systems. Smallholder-commercial farmers are in a transition phase between subsistence and commercial farming operations and are commonly referred to as emerging farmers in South Africa. The economic problems for communal (smallholder subsistence) farmers include offtake rate and income derived from offtake. Offtake rate can be defined as the proportion of animals sold or consumed within a year (Otte & Chilonde, 2002). Smallholder farmers also depend on the capital value/insurance value of their sheep as well as on offtake. Therefore owning a large flock of mainly adult sheep may serve as an indicator of wealth and liquid asset for use to meet family

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emergencies. Offtake rate for smallholder farmers has been reported to be low (Motiang & Webb, 2016). Low offtake rate can be linked to the low production performance (Grobler, 2010). Internal social issues are for smallholder farmers includes social wellbeing, education levels, health status (which can be compromised through contact with zoonotic diseases), gender equity, access to food, food safety and access to information, extension and veterinary services. Environmental problems include water resources and land available for grazing, sheep resources used (animal biodiversity) and plant biodiversity. Smallholder sheep farmers have sheep genetic resources that are highly genetically diverse (Hlophe, 2011; Soma *et al.*, 2012). These resources, however, exhibit low production performance levels.

Enhancing production performance in commercial sheep flocks has been achieved by altering genetic diversity of the breeding flock using various breeding techniques, including linebreeding (decreasing genetic diversity in a flock) and crossbreeding (increasing genetic diversity in a flock) as well as selection for traits of economic importance. Formulation of feeds that have a high feed conversion ratio to improve growth rate has also been used to enhance production. The use of vaccinations and antibiotics to treat diseases, as well as the use of reproductive technology such as synchronisation of ewes and superovulation to increase number of lambs born per ewe. Low production performance of sheep kept by smallholder farmers in low input farming systems can be improved using similar genetic strategies as in the commercial set-up. It is, however, important to ensure that the accumulation of deleterious loci through the effect of genetic erosion and inbreeding is limited.

2.4. The importance of genetic diversity for sustainable genetic improvement

2.4.1. Genetic variability for adaptability and robustness

Genetic diversity can be defined as the genetic variation at neutral or adaptive loci of a population or species (Holderegger *et al.,* 2006). Neutral genetic diversity is gene variants detected that do not have a direct effect on fitness. This is measured by molecular techniques using neutral markers for instance random amplified polymorphic DNA (RAPDs), amplified fragment length polymorphism (AFLP) and microsatellites to estimate parameters such as heterozygosity and homozygosity (Holderegger *et al.,* 2006). Adaptive genetic diversity refers to genes that have an effect on fitness; this can be measured using quantitative genetic experiments to estimate parameters such as heritability (h^2) and genetic variance. In the context of this study genetic diversity studied will focus on using neutral genetic variation in combination with adaptive genetic diversity at breed level.

Genetic diversity within a gene pool is linked to the robustness of the animals (Goddard, 2009; Bijlsma & Loeschcke, 2012). Robustness can be defined as the ability of an animal to adapt to challenging environmental conditions (Goddard, 2009). This entails the ability of the animal to survive, reproduce and maintain homeostasis without losing body condition when exposed to adverse conditions (Knap, 2005; Star *et al.*, 2008). Robustness encompass a group of traits enabling animals to adapt and includes several reproduction and survival traits such as disease and parasite resistance, heat tolerance and drought tolerance (Knap, 2005). Reproduction and survival traits in livestock are known to be lowly heritable and in spite of this genetic progress have been possible over 20 years of selection in South African sheep flocks (Schoeman *et al.,* 2010). This indicates the possibility of using adaptive genetic variation to improve robustness traits in South African sheep flocks.

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2.4.2. Genetic diversity of indigenous breeds

Smallholder subsistence farmers make use of indigenous breeds that are more hardy or robust (Snyman *et al.,* 2005; Cloete *et al.,* 2013; Cloete *et al.,* 2016). Indigenous breeds are sometimes crossed randomly without prior knowledge of pedigree or selection for specific traits. Indigenous Nguni sheep breeds have been shown to have a higher genetic diversity than Merinos using RAPD markers (Hlophe, 2011). Studies done on the indigenous Namaqua Afrikaner proves them more tick resistant than the South African Mutton Merino (SAMM) and Dorper (Cloete *et al.,* 2013). The indigenous Namaqua Afrikaner achieved higher survival from birth to weaning (91%) in comparison to the Dorper (88%) (Snyman *et al.,* 2005). A recent study reported that the number of lambs weaned was highest for indigenous Namaqua Afrikaner compared to the Dorper and South African Mutton Merino (Cloete *et al.,* 2016). These results imply robustness in terms of survival, reproduction and disease/parasite resistance of indigenous breeds. The trade-off with indigenous breeds are that their carcass yield is inferior to those of commercial breeds. This was proven true for the indigenous Namaqua Afrikaner breed (Burger *et al.,* 2013). Genetic diversity studies have reported low heterozygosity levels within the indigenous Namaqua Afrikaner breed (Sandenbergh *et al.,* 2016). The low levels of heterozygosity for this breed could be linked to its small effective population size (Ne). Effective population size can be defined as the number of individuals who contribute to the next generation. Low levels of heterozygosity have also been reported in other indigenous fat rumped sheep (Black headed Persian and Red head Speckled Persian) whereas other indigenous fat tailed sheep (Pedi, Swazi and Zulu) sheep obtained higher levels of genetic diversity (Soma *et al.,* 2012). The reason for these higher levels of diversity could be resultant of some level of crossbreeding in these populations. It is, however, interesting to note that even though the Namaqua Afrikaner have high inbreeding levels their robustness

traits have not been negatively affected. This could be due to the impact of natural selection on adaptation traits.

2.4.3. Genetic diversity of commercial breeds in South Africa

Commercial sheep enterprises utilize exotic and synthetic breeds that have been purebred and selected for certain phenotypic traits, like colour and size, for example, in the Dorper breed (Olivier & Cloete, 2006). These purebreds may accumulate homozygous loci for deleterious genes over time and become inbred, which can result in reduced fitness, poor survival and low reproduction (Goddard, 2009). Commercial breeds are known to have a lower genetic diversity than smallholder populations. Inbreeding in the Danish Texel population has led to a reduction in birthweight, average daily gain and litter size (Norberg & Sørensen, 2007). The use of artificial insemination or the use of one ram of high genetic merit, resulted in a reduced effective population size (Ne), leading to higher inbreeding rates and resulted in a loss of genetic diversity and reproductive fitness. A decrease of genetic diversity through linebreeding and artificial selection has, however, resulted in increased growth and production traits in exotic sheep breeds (Swanepoel *et al.*, 2007; Van Wyk *et al.,* 2009). Inbreeding percentage should be kept below 20-25% in sheep flocks to prevent inbreeding depression. Higher inbreeding rates have led to economic losses of $17 per ewe and where inbreeding approached 50% up to $36 per ewe (Erkanbrack & Knight, 1991).

2.4.4. Is fitness always good if genetic diversity is high?

The fact that the Namaqua Afrikaner, Black headed Persian and Red head Speckled Persian have low genetic diversity and still are more robust than exotic breeds (Soma *et al.*, 2012) is a paradox to the notion that higher levels of genetic diversity are linked to robustness and fitness (Goddard, 2009). The reason for this paradox is unclear and leaves us with the question: 'Is fitness always good if genetic diversity is high?' Reed & Frankham (2003) postulated that

selection can purge a population of deleterious recessive alleles and in theory can create inbred populations with a higher fitness. This phenomena of the Namaqua Afrikaner sheep breed could also be explained by the fact that the neutral genetic diversity measures were used to estimate heterozygosity levels within these breeds and thus only refer to gene variants that do not have a direct effect on fitness.

Characterization of traits relevant for sustainability of the specific sheep farming systems is the next step.

2.5. Genetic traits important for sustainable production performance

Traits of importance to ensure enhanced production includes reproduction, survival and production traits (Table 2.1). Reproduction is a composite traits and can be measured by component traits such as number of lambs born per ewe's lifetime, or number of lambs weaned per ewe lifetime, litter size, conception rate, lamb survival and mothering ability (Zishiri *et al.*, 2013). The wet-dry phenotype (Fourie & Cloete, 1993) is recorded from an udder examination performed during the marking of recently born lambs or at the weaning of lambs. Wet-dry refers to whether a ewe is lactating or not, and can be used as an indicator of reproductive performance of ewes in low-input farming systems. Heritabilities estimated in Australian Merino flocks ranged from 0.09 to 0.17 for wet-dry at weaning and 0.04 to 0.11 when at lamb marking (Lee *et al.,* 2010). The wet-dry phenotype is a composite trait and includes both conception rate and mothering ability. Heritability estimates for the component trait conception rate ranges from 0.01 to 0.30 (Iniguez *et al.,* 1986; Tosh *et al.,* 2002; Piwczyński & Kowaliszyn, 2013). Estimates for number of lambs born and number of lambs weaned were 0.05 to 0.10 and 0.05 to 0.07, respectively (Safari *et al.,* 2005; Safari *et al.,* 2007). Survival traits in sheep can be measured by survival from birth to weaning. Heritability estimates reported for lamb survival were 0.03 to 0.07 (Safari et al., 2005; Bunter & Brown, 2015).

Weaning of lambs occurs at approximately 100 days of age in commercial intensive sheep farming systems. Survival in exotic breeds under harsh conditions are known to be lower than in indigenous breeds. Disease and pathogen resistance are other important traits to consider for sustainability. Studies reported on traits linked to disease resistance in sheep include faecal egg worm count (FEC) as an indicator for resistance to helminth nematodes (Safari *et al.,* 2005; Huisman & Brown, 2009), resilience to nematodes, foot rot and pneumonia (Morris, 2009) as well as tick resistance (Cloete *et al.,* 2016). Heritability estimates for FEC were in the range of 0.25-0.28 (Huisman & Brown, 2009) and ranged between 0.07-0.59 for tick resistance (Grova *et al.,* 2014; Cloete *et al.,* 2016). Estimates depended on the model used to estimate heritability as well as the body location from which ticks were sampled.

Important growth related traits to select for include birth weight, weaning weight, body condition score (BCS), average daily gain, feed conversion efficiency and adult weight (Safari *et al.,* 2005) as well as carcass traits such as fat depth and eye muscle depth (Huisman & Brown, 2009). Heritability estimates for growth and carcass traits are moderate to high, with estimates of 0.30-0.41 for adult weight and 0.20 for carcass traits (Huisman & Brown, 2009). Heritability estimates for BCS ranged from 0.16 for BCS during mid-pregnancy and 0.18 for BCS two weeks before lambing (Everett-Hincks & Dodds, 2008). Early growth traits like birth weight and whether or not a lamb was born as single, twin or multiple are important for survival and future growth of an animal, as they are correlated to survival and post-weaning growth performance (Matika *et al.*, 2003). Research has shown that birth weight affects survival of lambs, where low birth weight (<3kg) leads to high mortalities because of starvation and exposure (Everett-Hincks & Dodds, 2008) and high birth weight (>6kg) leads to high mortalities because of dystocia (Brand *et al.,* 1985). Dystocia is defined as difficulty in giving birth due to a large fetus. To obtain maximal survival of lambs, optimum birth weights should be targeted, ranging between 3 and 6 kg. The abovementioned research was done on

Coopworth, Romney and Texel sheep breeds and indicated that birth weight for lambs born as twins or multiples will be lower than for single born lambs (0.70kg and 1,69kg, respectively) (Everett-Hincks & Dodds, 2008). Feed conversion efficiency is the amount of feed consumed in relation to growth. Feed conversion ratio is highly heritable at 0.26 (Snowder & Vleck, 2003). Measuring feed intake is difficult in practice and using highly correlated traits like post weaning weight or yearling weight with feed conversion rate (r^2=0.98) can be an indication of feed conversion efficiency (Snowder & Vleck, 2003). This is important where feed scarcity occurs, so the animal will need to convert low quality feed into growth and production. Growth traits are positively correlated with reproduction traits (Safari *et al.,* 2005; Huisman & Brown, 2009). Selection for growth can thus have an influence on reproduction traits. This is in contrast to the dairy and poultry industry where selection for production traits like increased milk yield, growth and egg production are negatively correlated with fitness traits (Star *et al.*, 2008; Nielsen *et al.*, 2011).

Table 2.1 Heritability estimates for traits important for enhanced productivity

Trait	Heritability estimate	References
Reproduction		
Wet-dry	0.04-0.17	(Lee *et al.,* 2010)
Conception rate	0.01 – 0.30	(Iniguez *et al.,* 1986; Tosh, *et al.,* 2002; Piwczyński & Kowaliszyn, 2013)
Number of lambs born / ewe joined	0.05-0.10	Safari *et al.,* 2005; Safari *et al.,* 2007
Number of lambs weaned / ewe joined	0.05-0.07	Safari *et al.,* 2005; Safari *et al.,* 2007
Lamb survival	0.03	Safari *et al.,* 2005
Disease and pathogen resistance		
Feacal egg count	0.27	Safari *et al.,* 2005
Tick Resistance	0.07-0.59	(Grova *et al.,* 2014; Cloete *et al.,* 2016)
Growth traits		
Birth weight	0.18-0.41	Safari *et al.,* 2005; Safari *et al.,* 2007
Adult weight	0.30-0.41	Safari *et al.,* 2005
Feed conversion ratio	0.15-0.33	(Snowder & Vleck, 2003)
Carcass weight	0.20	Safari *et al.,* 2005

Quantifying and measuring fitness traits in smallholder production systems can be challenging due to lack of recordkeeping. It is therefore necessary to measure indicator traits that involve minimal recordkeeping and input costs for example "wet and dry" phenotype as in indicator of reproduction in smallholder sheep farming systems. Smallholder farmers can also implement body condition scoring as a management tool to improve ovulation rate and hence reproduction performance in flocks. However, all of the abovementioned traits are important for sustainable sheep production for both smallholder and commercial producers and emphasis of selection for traits to include in the breeding objective would need to be different for different farming systems. Emphasis could be placed according to the input-output of the farming system, as well as the geographical location of the farm. For high input-high output farming systems located in high rainfall geographical regions of South Africa; growth, carcass and reproduction traits could be the main emphasis. In low input- low output farming systems located in drier arid regions of South Africa; survival, disease/pathogen resistance, reproduction and adaptability could be of higher importance. Farmers should include traits for sustainability applicable to their sheep farming system in their breeding objectives to enable genetic improvement. Gizaw *et al.,* (2010) used a desired-gain selection index to derive relative weights for traits resulting in gains desired by subsistence sheep farmers in Ethiopia. Another means of prioritizing traits of importance could be by adding non market value to the market value of traits (Nielsen & Christensen, 2006). Non market value entails a value given to a trait that is not reflected in the current market economy or that is partly transferred by the market (Nielsen & Christensen, 2006). No studies have been done in South Africa to identify traits of preference for smallholder sheep farmers to include in breeding objectives. The first step will be to start with identifying traits of sustainability for smallholder farmers, and secondly to set up a recordkeeping system for these traits. Once phenotyping has been established the use of genomics can be combined

with traditional selection and crossbreeding strategies to increase genetic gain. The contribution of indigenous breeds in smallholder sheep farming systems also need to be investigated.

2.6. Indigenous breeds in smallholder sheep farming systems

Using indigenous breeds in smallholder sheep farming systems can decrease the costs of input related to additional feed or medicine. Meat output and thus income received per kg will be less because of their inferior growth and carcass traits. The trade-offs between robustness and carcass traits of indigenous breeds needs to be considered when suggesting these breeds to improve economic sustainability of the smallholder sheep farming systems. Structured breeding programs can be developed where indigenous breeds are crossed with exotic breeds to improve genetic diversity. Examples of this being achieved include composites like the Meatmaster and Van Rooy which were derived from crosses between the indigenous breeds like the Damara / Ronderib Afrikaner and exotic breeds like the Ile de France, Dorper, and SA Mutton Merino (Peters *et al.*, 2010; Soma *et al.*, 2012). A terminal crossbreeding system can be an option, where all the F1 offspring are sold as slaughter lamb (Cloete *et al.,* 2003). The benefits of a terminal crossbreeding arise through the effects of F1 hybrid vigour and complementarity, which can lead to an immediate improvement in the desired growth and reproduction traits (Roux, 1992). Sexual dimorphism is when large offspring is obtained from small breeding animals (Roux, 1992). This could be of benefit to the smallholder farmer as more carcass yield can be obtained from F1 offspring. This can thus add value in ensuring a higher income to the farmer. Studies of crossbreeding Red Massai (indigenous breed to Kenya) with a Dorper has shown the possible effects of improving resistance to gastro-intestinal parasites (Baker *et al.,* 2003). Another option to improve production performance of indigenous breeds would be increase selection for desired traits using genomic selection. Selection for improved robustness or production traits will reduce genetic diversity in a population.

However, the reduction in diversity will be gradual over a number of generations (Schoeman *et al.,* 2010). This is due to the additive effect of genes using traditional selection methods, where the effect will be cumulative. Crossbreeding on the other hand is using non-additive genetic effects to produce immediate desirable results in terms of production performance.

2.7. Applying genomics to improve traits important for sustainable farming systems

2.7.1. Identifying causal variants

2.7.1.1 Genome-wide association analysis

Before the advent of high throughput technology, marker assisted selection were explored with the study of markers and their linkage to specific quantitative trait loci (QTL) responsible for phenotypic expression (Williams, 2005). These markers were used to construct genetic and physical maps of genomes of livestock species (Williams, 2005). Different genetic markers were used for marker assisted selection; includes RAPD, AFLP, restriction fragment length polymorphism (RFLP), microsatellites and single nucleotide polymorphism (SNP). Single nucleotide polymorphisms have become the marker of choice for genotyping and genotyping platforms are available for ovine species. This includes the 12K SNP chip for parentage determination (Heaton *et al.,* 2014) and genotyping replacements at a low cost, 50K SNP chip (Kijas *et al.,* 2009, Kijas *et al.,* 2012) and recently the 600K SNP chip (Anderson *et al.,* 2014). The heritability estimates for reproduction and survival traits range from low to medium, whereas estimates for production traits range from medium to high. The use of genomics will be of benefit to the traits that are lowly heritable and expressed later in an animal's life (Kijas *et al.,* 2012). This will enable the ability to predict a ram/ewes performance for a specific trait at an early age and so increase genetic gain (Kijas *et al.,* 2012). Genomic tools can help to further elucidate differences between indigenous breeds and exotic breeds in term of

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reproduction and production traits. This can be done using different methods, for example, studying the genetic diversity and population structure of sheep. This serves as a backbone for genome wide association studies (GWAS) that can be used to associate phenotypes with causal variants (Liandris *et al.*, 2012; Demars *et al.*, 2013). Causal variants have been identified for various traits important for sustainability including reproduction (Demars *et al.*, 2013), gastrointestinal parasite resistance (Riggio *et al.*, 2013), growth and meat production (Zhang *et al.*, 2013, 2016), wool traits (Wang *et al.*, 2014) and adaptation in extreme environments (Yang *et al.*, 2016) (Table 2.2). Causal variants linked to litter size (prolificacy) were growth differential factor (GDF9), bone morphogenetic protein 15 (BMP15), bone morphogenetic protein receptor 1B (BMPR1B) (FecB allele) and beta-1,4-N-acetyl-galactosaminyl-transferase 2 (B4GALNT2) (Abdoli *et al.,* 2016). GDF 9 is an autosomal gene and is located on chromosome 5 and BMP15 is located on the X-chromosome. BMPR1B is located on chromosome 6 and have six different mutations for this gene, whereas B4GALNT2 is located on chromosome 11. Faecal egg count (FEC) is used to measure resistance to gastrointestinal parasites in sheep, and the causal variants for FEC using a genome wide association study were found on chromosome 14 (linked to *Nematodrius* average animal effect) and chromosome 6 (*Strongyles* FEC at 16 weeks) (Riggio *et al.*, 2013). Various other genes have been linked to host resistance to different gastrointestinal parasites (*Haemonchos contortus*, *Teladorsagia circumcinta* and *Trichostrongylus colubriformis*) (Benavides *et al.,* 2016). These genes were found on chromosomes, 1, 3, 6 and 20 and were linked to the immune system, mucosal protection and haemostasis. Genes that have been reported to influence carcass traits, include callipage, myostatin and carwell (Cockett *et al.,* 2005; Miar *et al.,* 2014). Another study using three different sheep breeds to determine causal variants for growth and meat traits observed significant loci within chromosome 3, 5 and 9 linked to post weaning gain (Zhang *et al.*, 2013) (Table 2). Causal variants TSPEAR (thrombospondin-type laminin G domain and EAR repeat),

KRTCAP3 (expressed in the skin keratinocytes) and KIF16B (kinesin family member 16B) influencing wool traits such as fiber diameter, fiber diameter CV and fineness dispersion were confirmed in Chinese Merino sheep breeds (Wang *et al.*, 2014). Whole genome sequencing has been used to identify genes related to adaptation traits in sheep adapted to different environments in Tibetan plateau and Taklimakan desert region in Asia (Yang *et al.*, 2016). The abovementioned causal variants are only examples of the abundances of genes already identified in literature.

Sheep can be screened for causal variants using assays consisting of primers of genes related to specific traits of interest. This was done in the study of Liandris *et al.* (2012) using PCR-RFLP to verify the presence of the GDF9 and FecB within two Greek sheep breeds. Following screening for causal variants, introgression of individuals carrying favorable loci into sheep flocks lacking these loci can occur. Successful introgression of the FecB mutation in smallholder sheep flocks in India has been reported which resulted in increased number of live born lambs and lamb survival (Nimbkar *et al.,* 2003).

The issue to bear in mind with GWAS studies is that quantitative traits are more likely to be influenced by many loci of small to medium effect acting on the expression of one trait, than few loci of major effect. Another issue is that the SNPs included on a chip for GWAS are not the causal variants for the phenotype but are associated with the phenotype because they are in linkage disequilibrium (LD) with the causal variant (Wray *et al.*, 2013). Thus the variation explained by causal variants is not completely explained by the genotyped SNPs. Causal variants identified will be different in terms of breeds studied and their environment they have adapted to, as seen in a recent study in South African Merino where the major genes for reproduction (GDF9, BMP15, BMPR1B and B4GALNT2) have not been confirmed. Therefore in attempt to create SNP panels for genetic improvement in smallholder sheep flocks it is important to first verify the presence of the causal variants for relevant traits within that flock.

Different SNP panels will have to be designed specifically to the farming system and goal of the farmer.

Table 2.2 Examples of causal variants for traits important for productivity as determined using genomics

Traits	Causal variants	Method used	References
	Production traits		
Post weaning gain	MEF2B, RFXANK, CAMKMT, TRHDE & RIPK2	GWAS	(Zhang *et al.*, 2016)
Preweaning gain	PFKFB4, PLA3G6	GWAS	(Zhang *et al.*, 2013)
Body weight	LAP3, NCAPG, LCORL	GWAS	(Al-Mamun *et al.*, 2015)
Carcass quality (Hypertrophy)	Myostatin, Callipyge and Carwell		Cockett *et al.*, 2005; Miar *et al.*, 2014
Shin circumference	ADK & SHISHA9	GWAS	(Zhang *et al.*, 2013)
Fiber diameter	TSPEAR, PIK3R4, KRTCAP3 & YWHAZ	GWAS	(Wang *et al.*, 2014)
Fiber diameter CV	KIF16B	GWAS	(Wang *et al.*, 2014)
Fineness dispersion	KIF16B	GWAS	(Wang *et al.*, 2014)
Crimp	PTPN3, TCF9, GPRC5A, DDX47, EPHA5, TPTE2, NBEA	GWAS	(Wang *et al.*, 2014)
	Disease/pathogen resistance		
Nematodrius average animal effect	S29550.1	GWAS	(Riggio *et al.*, 2013)
Strongyles FEC at 16 weeks	OAR6_40496374.1 SSP1	GWAS	(Riggio *et al.*, 2013)
Gastrointestinal parasite resistance	IFNG, TLR1, TLR6, DYA, TAP1, MUC21, IL18RAP, IL18R1, TAL1, LRP8, PPAP2B		Benavides *et al.,* 2016
	Adaptation traits		
Adaptation in plateau environments	IFNGR2, MAPK4, NOX4, SLCZA4, PDK1	Whole Genome sequencing	(Yang *et al.*, 2016)
Adaptation in desert environments	ANXA6, GPX3, GPX7, PTGS2	Whole Genome sequencing	(Yang *et al.*, 2016)
Adaptation in arid environments	AKR1A1, RAB11FIP2, CPVL & MFSD6	Whole Genome sequencing	(Yang *et al.*, 2016)
	Reproduction traits		
Litter size	GDF9, BMP15, BMPR1B/FecB and B4GALNT2	PCR-RFLP	(Liandris *et al.*, 2012; Abdoli *et al.,* 2016)

2.7.1.2. Selection sweeps

Another approach to identify causal variants for phenotypes is the technique selections signatures. Selection signatures are used to determine selection patterns in populations. It is a backward approach inferring selected mutations with their associated phenotypes (Ross-Ibarra *et al.,* 2007). Different methods are used to detect selection signatures in populations, which includes the Fst and more recently FLK approach (Fariello *et al.,* 2013). Kijas *et al.,* 2012 used the Fst approach to determine selection signatures in sheep populations and found 31 genomic regions under selection. These regions were associated with coat pigmentation, skeletal morphology, body size, growth and reproduction. A study using HAPFLK using the same HAPMAP dataset observed 41 selection signatures with only 10 regions overlapping with the study of Kijas *et al.,* 2012 (Fariello *et al.,* 2014). Selection signature studies are thus important to determine selection for traits of economic importance in livestock. It has also been widely used in several studies to determine regions under selection in different livestock species including beef, goats and pigs (Ramey *et al.,* 2013; Ai *et al.,* 2013; Ma *et al.,* 2015; Kim *et al.,* 2016).

2.7.2. Genomic selection

Genomic selection is another tool that can be used to improve genetic gain in sheep flocks. The inclusion of genotypic data based on genetic markers and specifically SNP's can allow the estimation of genomically enhanced estimated breeding values (GEBV's). Genomic selection involves the use of phenotypic and genotype records to derive GEBV's for traits of economic importance. Studies have shown that using genomic best linear unbiased prediction (GBLUP) for the number of lambs weaned in sheep is more accurate than only using best linear unbiased prediction (BLUP) (Daetwyler *et al.*, 2012). For this to be possible an appropriate reference population must be established (Daetwyler *et al.*, 2012). A reference population must be fully phenotyped, genotyped, and representative of the population herds/flocks to be predicted.

Genomic prediction can be advantageous over pedigree selection when individuals are less related as well as if multi-breed populations are used as reference populations (Daetwyler *et al.*, 2012). It was established recently that the use of a multi-breed reference population results in less accurate GEBV's than using smaller single-breed populations (Legarra *et al.*, 2014). Studies on genomic selection in sheep indicated molecular markers can be used to improve selection accuracy (Van der Werf, 2009; Duchemin *et al.*, 2012). Thus, combining traditional animal breeding and genomics may increase productivity, sustainability and economic viability achieved by animal improvement. There is scope to apply genomic selection to smallholder conditions, where no pedigree information is available and where reference populations are small. Phenotypic information on the trait of economic importance, whether it be reproduction or growth traits is necessary to successfully achieve this. This could enable the estimation of SNP heritabilities for traits related to sustainability for smallholder farmers such as number of lambs weaned, disease/pathogen resistance, survival, feed conversion efficiency and growth. SNP heritabilities have been estimated for "wet-dry" trait for smallholder sheep farmers in South Africa. The challenges of implementing this approach for genetic improvement in smallholder systems is the availability of phenotypic data. Obtaining reliable records for traits of economic relevance of an appropriate reference population needs to be addressed. Efforts should be concerted in the development of breeding schemes that allows the recording of traits important for sustainability. Another challenge would be the genotyping costs involved. Genotyping costs per individual using the 50K SNP chip are 73 Euro (Geneseek, 2015). However, these costs have been predicted to decrease in the future (Cloete *et al.*, 2014).

2.7.3. Willingness and means for recording of phenotypes

Recording of phenotypes to include in selection indices and genomic selection is of importance for genetic improvement. This is one of the major challenges for smallholder and even commercial sheep farmers in South Africa due to the extensive nature of sheep farming

systems. The availability of the national small stock improvement scheme (NSIS) makes it possible for registered stud farmers and commercial sheep farmers to participate in genetic improvement programs (Schoeman *et al.,* 2010; Cloete *et al.*, 2014). The question, however, is how do we encourage the smallholder farmer to participate in recordkeeping? A study done in Malawi indicated that smallholder farmers' main three reasons for not participating in record keeping were, 'busy with other activities', 'lack of knowledge' and 'lack of education' (Chagunda *et al.,* 2006). The study also indicated that recordkeeping were influenced by recording equipment available and herd/flock size. This could be circumvented by the wide availability and usage of smartphones to use as recording equipment. A recent study done in Limpopo, South Africa, indicated that smallholder farmers regularly use smart phones to share information and that a recording application could be developed for use on smart phones (Mapiye, 2017). Recordkeeping systems have been developed using information and communication (ICT) technologies in Kenya (Irungu *et al.,* 2015).

2.8. Summary

Addressing sustainability issues of smallholder sheep systems is complex and indicators should be chosen based on the farming goals and the intensity of input-output in the system. A system sustainable for a subsistence smallholder farmer may not be equally sustainable for a commercial smallholder sheep farmer. The type of genetic resources used in a farming system plays an important role in sustainability. Maintaining genetic diversity while selecting for genetic improvement in smallholder flocks is, however, crucial. Indigenous breeds as an important genetic resource is poorly benchmarked for growth and reproduction performance against commercial breeds thus requiring further research. Choosing the relevant fitness traits to select for is dependent on the geographical location and farming system. Breeding objectives can be developed based on farmers' preference for traits using it as weight to add non market value in the selection index. It is possible to use genomics to improve genetic traits important

for sustainability. For commercial sheep farmers emphasis will be on improving adaptation traits of exotic breeds, whereas for smallholder subsistence farmers the emphasis would be to improve production traits. This can, in theory, be achieved once successful genotyping or whole genome sequencing have been completed on all sheep resources (both commercial and indigenous) in South Africa. Then this information can be used to screen both smallholder and commercial sheep flocks for the presence/absence of causal variants related to specific traits of interest to sustainability. Sheep that are positive for the causal variants can then be introgressed into sheep flocks that lack those specific genes necessary to improve both production and robustness through crossbreeding strategies. Genomic selection can also be used to increase genetic gain in smallholder sheep flocks. The limitation, however, is lack of recordkeeping systems and breeding schemes in smallholder sheep farming systems and the costs of genotyping smallholder farming genetic resources. This can potentially be overcome by the collaboration of government, research institutions, higher education and private companies to act as funding bodies for sustainability projects.

2.9 References

Abdoli, R., Zamani, P., Mirhoseini, S.Z., Ghavi Hossein-Zadeh, N. & Nadri, S., 2016. A Review on Prolificacy Genes in Sheep. Reprod. Domest. Anim. 51, 631–637.

Ai, H., Huang, L. & Ren, J., 2013. Genetic diversity, linkage disequilibrium and selection signatures in Chinese and Western pigs revealed by genome-wide SNP markers. PLoS ONE, 8, e56001.

Al-Mamun, H.A., Clark, S., Kwan, P. & Gondro, C., 2015. 'Genome-wide linkage disequilibrium and genetic diversity in five populations of Australian domestic sheep.', Genet. Sel. Evol. 47, 90–104. doi: 10.1186/s12711-015-0169-6.

Almeida, A.M., 2011. The Damara in the context of Southern Africa fat-tailed sheep breeds. Trop. Anim. Health Prod. 43, 1427–1441. doi: 10.1007/s11250-011-9868-3.

Anderies, J.M., Folke, C., Walker, B. & Ostrom, E., 2013. Aligning Key Concepts for Global Change Policy: Robustness, Resilience and Sustainability. Ecol. Soc. 18, 8–24. doi: 10.5751/es-05178-180208.

Atanga, N.L.;Treydte, A.C. & Birner, R., 2013. Assessing the sustainability of different small-scale livestock production systems in the Afar Region, Ethiopia. Land 2,726–755.

Baker, R., Nagda, S., Rodriguez-Zas, S., Southey, B., Audho, J., Aduda, E. & Thorpe, W., 2003. Resistance and resilience to gastro-intestinal nematode parasites and relationships with productivity of Red Maasai, Dorper and Red Maasai ✕ Dorper crossbred lambs in the sub-humid tropics. Anim. Sci. 76,119–136.

Bijlsma, R. & Loeschcke, V., 2012. Genetic erosion impedes adaptive responses to stressful environments. Evol. Appl. 5, 117–129.

Boogaard, B.K., Oosting, S.J., Bock, B.B. & Wiskerke, J.S.C., 2011. The sociocultural sustainability of livestock farming: an inquiry into social perceptions of dairy farming. Animal: an international journal of animal bioscience, 5, 1458–1466.

Brand, A.A., Cloete, S.W.P. & De Villiers, T.T., 1985. Factors that influence mortality amongst lambs in the Elsenburg Dormer and SA Mutton Merino flocks. S. Afr. J. Anim. Sci. 15, 155–161.

Brown, B., Hanson, M., Liverman, D. & Merideth, R., 1987. Global sustainability: Toward definition, Environ. Managem. 11, 713–719.

Bunter, K.L. & Brown, D.J., 2015. Yearling and Adult Expression of Reproduction in Maternal

Sheep Breeds are Genetically Diffferent Traits. Proc. Assoc. Adv. Anim. Breed. Genet. 20, 82–85.

Burger, A., Hoffman, L.C., Cloete, J.J.E., Muller, M. & Cloete, S.W.P., 2013. Carcass composition of Namaqua Afrikaner, Dorper and SA mutton merino ram lambs reared under extensive conditions. S. Afr. J. Anim. Sci. 43, S27-S32

Chagunda, M.G.G., Msiska, A.C.M., Wollny, C.B.A., Tchale, H. & Banda, J.W., 2006. An analysis of smallholder farmers' willingness to adopt dairy performance recording in Malawi. Livest. Res. Rural Develop. 18, p. Article #66. Available at: http://www.lrrd.org/lrrd18/5/chag18066.htm.

Cloete, J.J.E., Cloete; S.W.P., Scholtz, A.J. & Matthee, S., 2013. The effect of breed, ewe age and season on tick counts of indigenous and commercial sheep in South Africa. Proc. Assoc. Advmt Anim. Breed. Genet. 20, 187–190.

Cloete, S.W.P., Cloete, J.J.E., Durand, A. & Hoffman, L. C., 2003. Relative performance and efficiency of five Merino and Merino-type dam lines in a terminal crossbreeding system with Dormer or Suffolk sires. S. Afr. J. Anim. Sci. 33, 223–232.

Cloete, S.W.P., Olivier, J.J., Sandenbergh, L. & Snyman, M.A., 2014. The adaption of the South Africa sheep industry to new trends in animal breeding and genetics: A review. S. Afr. J. Anim. Sci. 44, 307–321.

Cloete, S.W.P., Cloete, J.J.E. & Scholtz, A.J., 2016. Genetic parameters for tick count and udder health in commercial and indigenous ewes in South Africa. Vet. Parasit. 230, 33–42.

Cockett, N.E., Smit, M.A., Bidwell, C.A., Segers, K., Hadfield, T.L., Snowder, G.D., Georges,

M. & Charlier, C., 2005. The Callipyge Mutation and other Genes that Affect Muscle Hypertrophy in Sheep. Genet. Sel. Evol. 37, S65.

Coetzee, L., Montshwe, B.D. & Jooste, A., 2005. The marketing of livestock on communal lands in the Eastern Cape Province: Constraints, Challenges and Implications for the extension services. S. Afr. J. Agric. Ext. 34, 81–103.

Cousins, B., 2010. What is a "Smallholder"? Class analytic perspective on small-scale farming and agrarian reform in South Africa, in Reforming Land and Resource Use in South Africa: Impact on livelihoods.

Daetwyler, H.D., Bolormaa, S., Brown, D.J., Van der Werf, J.H. & Hayes, B.J., 2012. A genomic prediction cross-validation approach combining ewe repeated phenotypes and ram daughter trait deviations. Proc. Assoc. Advmt Anim. Breed. Genet, 360–363.

Demars, J., Fabre, S., Sarry, J., Rossetti, R., Gilbert, H., Persani, L., Tosser-Klopp, G., Mulsant, P., Nowak, Z., Drobik, W., Martyniuk, E. & Bodin, L., 2013. Genome-Wide Association Studies Identify Two Novel BMP15 Mutations Responsible for an Atypical Hyperprolificacy Phenotype in Sheep, PLoS Genetics, 9(4).

Directorate Statistics and economic analysis. 2013. Abstract of Agricultural statistics. Pretoria South Africa.

Duchemin, S.I., Colombani, C., Legarra, A., Baloche, G., Larroque, H., Astruc, J.M., Barillet, F., Robert-Granie, C. & Manfredi, E., 2012. Genomic selection in the French Lacaune dairy sheep breed. J. Dairy Sci. 95, 2723–2733.

Dzivakwi, R., 2010. Determinants of output prices formation in local sheep markets. M.Sc thesis, University of Western Cape.

Erkanbrack, S.K. & Knight, A.D., 1991. Effects of inbreeding on reproduction and wool production of Rambouillet, Targhee, and Columbia ewes. J. Anim. Sci. 4734–4744.

Everett-Hincks, J.M. & Dodds, K.G., 2008. Management of maternal-offspring behavior to improve lamb survival in easy care sheep systems. J. Anim. Sci. 86

Everett-Hincks, J.M. & Cullen, N.G., 2009. Genetic Parameters for Ewe Rearing Performance. J. Anim. Sci. 87, 2753–2758.

Fariello, M.I., Servin, B., Tosser-Klopp, G., Rupp, R., Moreno, C., the International Sheep Genomics Consortium, SanCristobal, M. & Boitard, S., 2014. Selection signatures in worldwide sheep populations. PLos ONE 9, e10381

Fourie, A.J. & Cloete, S.W.P., 1993. Reproductive performance of commercial Merino, Dohne Merino and SA Mutton Merino flocks in the Southern Cape. S. Afr. J. Anim. Sci. 23, 104–110.

Gizaw, S., Komen, J. & Van Arendonk, J.A.M., 2010. Participatory definition of breeding objectives and selection indexes for sheep breeding in traditional systems. Livest. Sci. 128, 67-74.

Goddard, M., 2009. Fitness traits in animal breeding programs. in Adaptation and fitness in farm animal populations. Eds. Van der Werf, J.H.J.; Graser, H-U.;Frankham, R.; Gondro, C. (ed.) Springer Science & Business Media.

Grobler, H., 2010. Evaluation survey at extensive farms in the Central Karoo 2009. Agriprobe, pp. 6–9.

Grova, L., Sae-Lim, P. & Olesen, I., 2014. Genetic parameters of tick-infestation on lambs of the Norwegian White Sheep. 10th World Cong.Genet. Appl. Livest. Prod.

Halimani, T.E., Muchadeyi, F.C., Chimonyo, M. & Dzama, K. 2012. Some insights into the phenotypic and genetic diversity of indigenous pigs in Southern Africa. S. Afr. J. Anim. Sci. 42, 507–510.

Herrero, M., Thornton, P.K., Gerber, P. & Reid, R.S. 2009. Livestock, livelihoods and the environment: understanding the trade-offs. Current Opin. Environ. Sustain. 1, 111–120.

Hlophe, S.R., 2011. Genetic Variation Between and Within Six Selected South African sheep breeds using random amplified polymorphic DNA and protein markers. Masters thesis, University of Zululand.

Hoffmann, I., 2011. Livestock biodiversity and sustainability. Livest. Sci. 139, 69–79.

Holderegger, R., Kamm, U. & Gugerli, F., 2006. Adaptive vs. neutral genetic diversity: Implications for landscape genetics. Landsc. Ecol. 21, 797–807.

Huisman, A.E. & Brown, D.J., 2009. Genetic parameters for bodyweight, wool, and disease resistance and reproduction traits in Merino sheep. 3. Genetic relationships between ultrasound scan traits and other traits. Anim. Prod. Sci. 49, 283–288.

Iniguez, L.C., Quaas, R.L. & Van Vleck, L.D., 1986. Lambing performance of Morlam and Dorset ewes under accelerated lambing systems. J. Anim. Sci. 63,1769–1778.

Irungu, K.R.G., Mbugua, D. & Muia, J., 2015. Information and Communication Technologies (ICTs) Attract Youth into Profitable Agriculture in Kenya. East Afr. Agric. Forest. J. 81, 24–33.

Kijas, J.W., Lenstra, J.A., Hayes, B., Boitard, S., Neto, L.R., Cristobal, M.S., Servin, B., McCulloch, R., Whan, V., Gietzen, K., Paiva, S., Barendse, W., Ciani, E., Raadsma, H., McEwan, J. & Dalrymple, B., 2012. Genome-wide analysis of the world's sheep

breeds reveals high levels of historic mixture and strong recent selection. PLoS Biology 10(2).

Kim, E-S., Elbeltagy, A.R., Aboul-Naga, A.M., Rischkowsky, B., Sayre, B., Mwacharo, J.M. & Rothschild, M.F., 2016. Multiple genomic signatures of selection in goats and sheep indigenous to a hot arid environment. Heredity, 1-10.

Knap, P.W., 2005. Breeding robust pigs. Aus. J. Experim. Agric. 45, 763–773.

Kunene, N., Nesamvuni, E.A. & Fossey, A., 2007. Characterisation of Zulu (Nguni) sheep using linear body measurements and some environmental factors affecting these measurements. S. Afr. J. Anim. Sci. 37, 11–20.

Lebacq, T., Baret, P.V. & Stilmant, D., 2013. Sustainability indicators for livestock farming. A review. Agron. Sustain. Develop. 33, 311–327. doi: 10.1007/s13593-012-0121-x.

Lee, G.J., Sladek, M.A. & Atkins, K.D. 2010. Selection criteria for within flock selection to improve reproduction efficiency. Available at: http://www.livestocklibrary.com.au/bitstream/handle/1234/33711/SheepCRC_2_87.pdf?sequence=1.

Legarra, A., Baloche, G., Barillet, F., Astruc, J. M., Soulas, C., Aguerre, X., Arrese, F., Mintegi, L., Lasarte, M., Maeztu, F., Beltrán de Heredia, I. & Ugarte, E., 2014. Within- and across-breed genomic predictions and genomic relationships for Western Pyrenees dairy sheep breeds Latxa, Manech, and Basco-Béarnaise. J. Dairy Sci. 97, 3200–3212.

Liandris, E., Kominakis, A., Andreadou, M., Kapeoldassi, K., Chadio, S., Tsiligianni, T., Gazouli, M. & Ikonomopoulos, I., 2012. Associations between single nucleotide polymorphisms of GDF9 and BMP15 genes and litter size in two dairy sheep breeds of

Greece. Small Rumin. Res. 107, 16–21.

Ma, Y.,Wei, J., Zhang, Q., Chen, L., Wang, J., Liu, J. & Ding, X., 2015. A genome scan for selection signatures in pigs. PLoS ONE 10, e0116850.

Mahlobo, B., 2016. Multi-criteria livestock assessment for sustainability of smallholder farms in Kwa-Zulu Natal. Masters thesis, Stellenbosch University.

Mapiye, O., 2017. Towards a management database to improve the sustainability of cattle production and its contribution to food security : A case of emerging beef farmers in Limpopo Province , South Africa. Masters thesis, Stellenbosch University.

Marandure, T., Mapiye, C., Makombe, G. & Dzama, K., 2016. Indicator-Based Sustainability Assessment of the Smallholder Beef Cattle Production System in South Africa. Agroecol. Sustain. Food Syst. 41, 3–29.

Matika, O., Van Wyk, J.B., Erasmus, G.J. & Baker, R.L., 2003. Genetic parameter estimates in Sabi sheep. Livest. Prod. Sci. 79, 17–28.

Miar, Y., Salehi, A., Kolbehdari, D. & Aleyasin, S.A., 2014 Application of Myostatin in Sheep Breeding Programs: A review. Mol. Biol. Res. Commun. 3, 33–43.

Mkhabela, T., 2013. Linking farmers with markets in rural South Africa: Rural development and poverty alleviation through supply chain management. National Agricultural Marketmdpoing Council, pp. 1–13. Available at: http://www.namc.co.za/upload/all reports/Linking farmers to markets in Rural SA.pdf.

Morris, C.A., 2009. Review of genetic parameters for disease resistance in sheep in New Zealand and Australia, Matching genetics and environment: a new look at an old topic. Proc. Assoc. Advmt Anim. Breed. Genet. pp. 263–271.

Motiang, D.M. & Webb, E.C., 2016. Herd mortality and cattle off-take rates among small-holder producers in the North West Province of South Africa. Afr. J. Agric. Res. 11, 930–934.

Mtileni, B.J., Muchadeyi, F.C., Maiwashe, A., Groeneveld, E., Groeneveld, L.F., Dzama, K. & Weigend, S., 2011. Genetic diversity and conservation of South African indigenous chicken populations. J. Anim. Breed. Genet. 128, 209–218.

Musemwa, L., Mushunje, A., Chimonyo, M. & Mapiye, C., 2010. Low cattle market offtake rates in communal production systems of South Africa: Causes and migration strategies. J. Sustain. Develop. Afr. 12, 209–226.

Neogen Corporation., 2017. GeneSeek Genomic Sheep (Ovine) and Goat OvineSNP50chip Genotyping Beadchip. Available online: http://genomics.neogen.com/en/sheep-and-goat#ovinesnp50-genotyping-beadchip (accessed on 3 July 2017).

Nielsen, H.M. & Christensen, L.G., 2006. A Method to Define Breeding Goals for Sustainable. J. Dairy Sci. 89, 3615–3625.

Nielsen, H.M., Olesen, I., Navrud, S., Kolstad, K. & Amer, P., 2011. How to Consider the Value of Farm Animals in Breeding Goals . A Review of Current Status and Future Challenges. J. Agric. Environ. Ethics. 24, 309–330.

Nimbkar, C., Ghalsasi, P.M., Maddox, J.F., Pardeshi, V.C., Sainani, M.N., Gupta, V., & Walkden-Brown, S.W., 2003. Expression of the FecB gene in the Garole and crossbred ewes in Maharashtra, India. Proc. Assoc. Advmnt. Anim. Breed. Genet. 15, 111-114

Norberg, E. & Sørensen, A. C., 2007. Inbreeding trend and inbreeding depression in the Danish populations of Texel, Shropshire, and Oxford Down. J. Anim. Sci. 85, 299–304.

Olivier, J.J. & Cloete, S.W.P., 2006. Genetic analysis of the South African Dorper Sheep. World Cong. Genet. Appl. Livest. Prod. Belo Horizonte, MG, Brazil, pp. 26–28.

Omann, I. & Spangenberg, J.H., 2002. Assessing Social Sustainability : The Social Dimension of Sustainability in a Socio-Economic Scenario. in Presented at the 7th Biennial Conference of the International Society for Ecological Economics" in Sousse (Tunisia), 6-9 March 2002 Ab, pp. 1–20.

Organisation for economic co-operation and development [OECD]., 2006. South Africa, Highlights and policy recommendations. OECD Review of Agricultural Policies.

Otte, M.J. & Chilonde, P., 2002. 'Cattle and small ruminant production systems in Sub-Saharan Africa. A systematic review', FAO publishing Rome.

Oudshoorn, F.W., Kristensen, T., Van Der Zijpp, A.J. & De Boer, I.J.M., 2012. Sustainability evaluation of automatic and conventional milking systems on organic dairy farms in Denmark, NJAS - Wagenin. J. Life Sci. Royal Netherlands Society for Agriculture Sciences, 59(1–2), pp. 25–33.

Percival, V. & Homer-Dixon, T., 1995. Environmental scarcity and violent conflict: The case of South Africa.

Peters, F.W., Kotze, A., Van der Bank, F.H., Soma, P. & Grobler, J.P., 2010. Genetic profile of the locally developed Meatmaster sheep breed in South Africa based on microsatellite analysis. Small Rumin. Res. 90, 101–108

Piwczyński, D. & Kowaliszyn, B., 2013. Heritability and breeding value of sheep fertility estimated by means of the GIBBS sampling method using the linear and threshold models. J. Centr. Euro. Agric. 14, 23–32.

Qwabe, S.O., Van Marle-Köster, E. & Visser, C., 2013. Genetic diversity and population structure of the endangered Namaqua Afrikaner sheep. Trop. Anim. Health Prod. 45, 511–516.

Ramey H.R., Decker J.E., McKay S.D., Rolf M.M., Schnabel R.D. & Taylor J.F., 2013. Detection of selective sweeps in cattle using genome-wide SNP data. BMC Genomics. 14, 382-10.

Rege, J.E.O., Marshall, K., Notenbaert, A., Ojango, J.M.K. & Okeyo, A.M., 2011. 'Pro-poor animal improvement and breeding - What can science do?', Livest. Sci. 136, 15–28.

Riggio, V., Matika, O., Pong-Wong, R., Stear, M.J. & Bishop, S.C., 2013. Genome-wide association and regional heritability mapping to identify loci underlying variation in nematode resistance and body weight in Scottish Blackface lambs. Heredity. 110, 420–429.

Ross-Ibarra, J., Morrel, P.L & Gaut, B.S., 2007. Plant domestication, a unique opportunity to identify the genetic basis of adaptation. PNAS 104, 8641-8648.

Roux, C.Z., 1992. Maximum herd efficiency in meat production III . Feeder - breeder dimorphism. S. Afr. J. Anim. Sci. 22, 11–15.

Safari, E., Fogarty, N.M. & Gilmour, A.R., 2005. A review of genetic parameter estimates for wool, growth, meat and reproduction traits in sheep. Livest. Prod. Sci. 92, 271–289.

Safari, E., Fogarty, N.M., Gilmour, A.R., Atkins, K.D., Mortimer, S.I., Swan, A.A., Brien, F.D., Greeff, J.C. & Van Der Werf, J.H.J., 2007. Across Population Genetic Parameters for Wool, Growth, and Reproduction Traits in Australian Merino Sheep. 1. Data Structure and Non-Genetic Effects. Aust. J. Agric. Res. 58, 169–175.

Schoeman, S.J., Cloete, S.W.P. & Olivier, J.J., 2010. Returns on investment in sheep and goat breeding in South Africa. Livest. Sci.130, 70–82.

Scholtz, M.M., Bester, J., Mamabolo, J.M. & Ramsay, K., 2008. Results of the national cattle survey undertaken in South Africa , with emphasis on beef. Appl. Anim. Husb. Rural Develop. 1, 1–9.

Snowder, G.D. & Van Vleck, L.D., 2003. Estimates of genetic parameters and selection strategies to improve the economic efficiency of postweaning growth in lambs. J. Anim. Sci. 81, 2704–2713.

Snowder, G.D. & Fogarty, N.M., 2009. Composite Trait Selection to Improve Reproduction and Ewe Productivity : A Review. Anim. Prod. Sci. 49, 9–16.

Snyman, M.A., Buys, T. & Jonker, M.L., 2005. Production and reproduction performance of Namaqua Afrikaner sheep. in 6th Global Conference on the Conservation of Domestic Animal Genetic Resources. Magalies Park, South Africa.

Snyman, M.A., Van Marle-Koster, E, Qwabe, S.Q. & Visser, C., 2013. Genetic and phenotypic profile of three South African Namaqua Afrikaner sheep flocks. Grootfontein Agric, 13. Available at: http:/gadi.agric.za/Agric/Vol13No1_2013/namaqua.php.

Soma, P., Kotze, A .,Grobler, J.P. & Van Wyk, J.B., 2012. South African sheep breeds: Population genetic structure and conservation implications. Small Rumin. Res.103, 112–119.

Star, L., Ellen, E.D., Uitdehaag, K. & Brom, F.W.A., 2008. A plea to implement robustness into a breeding goal: Poultry as an example. J. Agric. Environ. Ethics, 21, 109–125.

Swanepoel, B.J., Erasmus, B.J. & Schenk, H.W., 2008. South African Human Resources

Management. Theory and Practice. Cape Town, South Africa: Juta & Co. Ltd.

Swanepoel, J.W., Van Wyk, J.B., Cloete, S.W.P. & Delport, G.J., 2007. Inbreeding in the Dohne Merino breed in South Africa. S. Afr. J. Anim. Sci. 37, 176–179.

Tosh, J.J., Wilton, J.W. & Kennedy, D., 2002. Heritability of Fertility in Four Seasons', in 7th World Cong. Genet. Appl. Livest. Prod. Montpellier, France, pp. 23–26.

Van Calker, K.J., Berentsen, P.B.M., Giesen, G.W.J. & Huirne, R.B.M., 2008. Maximising sustainability of Dutch dairy farming systems for different stakeholders: A modelling approach. Ecol. Econ. 65, 407–419.

Vandamme, M., D'Hease, M., Speelman, M., & D'Hease, L., 2010. Livestock against risk and vulnerability: Multifunctionality of livestock keeping in Burundi. In: The role of livestock in developing communities: Enhancing Multifunctionality. Eds. Swanepoel, F., Stroebel, A., Moyo, S. The Netherlands, CTA, pp. 107–122.

Vitousek, P.M., Mooney, H., Lubchenco, J. & Melillo, J.M., 1997. Human Domination of Earth' s Ecosystems. Science 277, 494–499.

Wang, Z., Zhang, H., Yang, H., Wang, S., Rong, E., Pei, W., Li, H. & Wang, N., 2014. Genome-wide association study for wool production traits in a Chinese merino sheep population. PLoS ONE, 9, 3–10.

Van der Werf, J.H.J., 2009. Potential benefit of genomic selection in sheep. Proc. Assoc. Advmt Anim. Breed. Genet. 18, 38–41. Available at: http://www.aaabg.org/livestocklibrary/2009/vanderwerf038.pdf.

Van Wyk, J.B., Fair, M.D. & Cloete, S.W.P., 2009. 'Case study: The effect of inbreeding on the production and reproduction traits in the Elsenburg Dormer sheep stud', Livestock

Science. Elsevier B.V., 120(3), pp. 218–224. doi: 10.1016/j.livsci.2006.10.005.

Williams, J.L., 2005. The use of marker-assisted selection in animal breeding and biotechnology. Revue scientifique et technique (International Office of Epizootics), 24, 379–91.

World Resources Institute [WRI] 2014. Creating a sustainable food future. A menu of solutions to sustainably feed more than 9 billion people by 2050.

Wray, N.R., Yang, J., Hayes, B.J., Price, A.L., Goddard, M.E. & Visscher, P.M., 2013. A commentary on Pitfalls of predicting complex traits from SNPs. Nature 14, 894–894.

Yang, J., Li, W.R., Lv, F.H., He, S.G., Tian, S.L., Peng, W.F., Sun, Y.W., Zhao, Y.X., Tu, X. L., Zhang, M., Xie, X.L., Wang, Y.T., Li, J.Q., Liu, Y.G., Shen, Z.Q., Wang, F., Liu, G.J., Lu, H.F., Kantanen, J., Han, J.L., Li, M.H. & Liu, M.J., 2016. Whole-Genome Sequencing of Native Sheep Provides Insights into Rapid Adaptations to Extreme Environments. Mol. Biol. Evol. 33, 2576–2592.

Zahm, F., Viaux, P., Vilain, L., Girardin, P. & Mouchet, C., 2007. Farm Sustainability Assessment using the IDEA Method : from the concept of farm sustainability to case studies on French farms. Sustainable agriculture: from common principles to common pratices. Proc. Outputs first Symp. Int. Forum Assess Sustain. Agric. (INFASA), March 16, 2006, Bern, CHE, 14(4), pp. 77–110.

Zhang, L., Liu, J., Zhao, F., Ren, H., Xu, L., Lu, J., Zhang, S., Zhang, X., Wei, C., Lu, G., Zheng, Y. & Du, L., 2013. Genome-Wide Association Studies for Growth and Meat Production Traits in Sheep. PLoS ONE, 8(6).

Zhang, L., Ma, X., Xuan, J., Wang, H., Yuan, Z., Wu, M., Liu, R., Zhu, C., Wei, C., Zhao, F.

& Du, L., 2016. 'Identification of MEF2B and TRHDE Gene Polymorphisms Related to Growth Traits in a New Ujumqin Sheep Population', PLoS ONE, 11(7), p. e0159504.

Zishiri, O.T., Cloete, S.W.P., Olivier, J.J. & Dzama, K., 2013. 'Genetic parameter estimates for subjectively assessed and objectively measured traits in South African Dorper sheep', Small Rumin. Res. 109, 84–93.

Chapter 3

Characterisation of sheep farming and breeding practices of smallholder sheep farmers in the Western Cape, South Africa

Abstract

The aim of this study was to characterise the sheep farming systems and breeding practices employed by smallholder sheep farmers in South Africa. Interviews were conducted with 72 farmers, 21 in the West Coast, 26 in Central Karoo and 25 in the Eden district using a structured questionnaire. Information was obtained on the production system, flock structure, the purpose of sheep farming, the sheep breeds and selection objectives of smallholder farmers. Nutrition and disease management practices were also recorded, as well as constraints experienced by smallholder farmers. Phenotypic measurements of body weight, body condition score and reproduction (wet and dry phenotype) were obtained from a sample of ewes from the West Coast district from 2011 until 2014. Range condition scores were estimated for two farms in the Karoo and four farms in West Coast district. SURVEYMEANS and SURVEYFREQ in SAS were used to obtain means and frequencies for qualitative data. The production systems were largely small-scale (43-85%) and communal (10-57%). Sheep were mainly kept for consumption purposes. The Dorper was the prominent breed used in all the farming systems and selection emphasis was different among farming systems. Traits selected for by communal farmers included temperament, control of flies, meat taste, growth rate, fertility and foraging ability; whereas small-scale farmers selected for conformation, mothering ability, disease tolerance, heat tolerance and temperament. Lucerne was the predominant source of supplementation in addition to natural grazing of rangeland. The major constraints mentioned were land availability, drought and water availability. Average range condition scores were low (135-166) for both farming systems implicating overgrazing. Stocking rate was higher than

the recommended carrying capacity in the Eden district (both communal and small-scale farmers) and in West Coast for small-scale farmers. The flock structure showed variation between farming systems with mature ewes (39-86%) and young replacement ewes (0.41-46%), young rams (0.41-15%), rams (0-5%) and lambs (0-2%). The wet-dry phenotype was recorded as a measurement of reproductive success over the three year period. The chi-square test indicated significant differences between reproductive performances over the different years with a repeatability of 0.399. This indicates that it is possible to make genetic improvement if selection is made for wet-dry in smallholder sheep flocks. This study indicates that there were differences in sheep management and breeding practices by communal and small-scale farmers in the Western Cape. Implementation of breeding and management plans should therefore be farm-specific and the impacts of climate change on production should be considered.

3.1. Introduction

Twenty % of the world population are smallholder livestock farmers based in developing countries (McDermott *et al.,* 2010). Livestock fulfil multiple socio-economic roles for small-scale and communal farmers, including the production of meat for home consumption, wool, income, manure, draught power and material for religious and cultural rituals. In South Africa the sheep industry is divided into commercial, emerging and smallholder farmers. There are an estimated 28.8 million sheep in South Africa, of which 21.4 million are owned by commercial farmers (Directorate Statistics and Economic analysis, 2013). The industry is dominated by the commercial sheep sector that supplies meat products locally and wool products for export. Emerging sheep farmers also supply meat and wool products to the informal and formal market, whereas the communal farmers are supplying meat for informal markets. The Dohne Merino,

Merino, South African Mutton Merino and Dorper breeds are the most prominent breeds of sheep in South Africa (Cloete *et al.,* 2014). Other sheep breeds in the industry include Dormer, Ile de France, Meatmaster, Namaqua Afrikaner, Afrino and Merino Landsheep.

The number of sheep owned by smallholder farmers is inadequately documented. Sheep used by most smallholder farmers in South Africa include the Nguni, Damara, Pedi, Namaqua Afrikaner and the Dorper. Some of these breeds are indigenous to South Africa and have characteristics that make them well-adapted to local conditions (Kunene *et al.,* 2007; Almeida, 2011; Snyman *et al.,* 2013; Zishiri *et al.*, 2013). However, the Dorper is the breed of choice for farmers in the semi-arid and arid environments of South Africa. Indigenous breeds used in smallholder systems such as the Damara (Almeida, 2011) and Namaqua Afrikaner (Cloete *et al.,* 2013), however, outperform commercial breeds for fitness traits, survival and disease/pathogen resistance. Fitness traits can be described as a group of traits enabling animals to adapt and includes several reproduction, survival traits including disease tolerance and heat tolerance (Goddard, 2009). It is important to incorporate fitness traits into breeding and selection objectives to ensure resilient breeding programs, especially in the light of climate change. Projections made by the Intergovernmental Panel of Climate Change (IPCC) for the Southern African Development Community (SADC) shows that mean annual temperature will increase by 2 ℃ in the mid-21st century and beyond 6 ℃ in the late 21st century (Niang *et al.,* 2014). Heat tolerance is relevant to select for considering that sheep are raised in the Karoo environments which are known for extreme heat. Heat tolerance can be defined as the ability of an animal to adapt to increases in ambient temperature. It can be measured through various traits, including sweating rate, heart rate, breathing rate, rectal temperature and skin temperature (McManus *et al.,* 2009). Coat colour can also be used to determine the degree of heat tolerance, animal with lighter coats was found to be more heat tolerant than those with darker coats (McManus *et al.,* 2011). An animal that is heat intolerant will experience heat

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stress that can lead to a loss of appetite and thus body weight, less resistance to diseases and reproduction inefficiency (McManus *et al.,* 2009). Temperature humidity index (THI) has been used in dairy cattle and sheep to estimate response for selection to heat stress (Carabaño *et al.,* 2017).

Commercial farmers achieve high production due to selection of exotic breeds for improved growth and reproduction (Schoeman *et al.,* 2010). The use of improved nutritional and grazing management strategies have allowed commercial farmers to excel. Minimal or no selection took place of any of the abovementioned traits in smallholder sheep production systems which could explain the observed low production performance (Grobler, 2010). There has also been reports of overgrazing in smallholder sheep farming systems which could also limit smallholder sheep production (Palmer & Bennett, 2013).

Important traits selected for to enhance production are growth related, like birth weight, weaning weight, body condition score (BCS), and adult weight (Safari *et al.,* 2005). Heritability estimates for growth are moderate to high, with estimates of 0.30-0.41 for adult weight (Huisman & Brown, 2009). Heritability estimates for BCS ranged from 0.16 for BCS during mid-pregnancy and 0.18 for BCS two weeks before lambing (Everett-Hincks & Dodds, 2008). Reproduction is a composite traits and can be measured by component traits such as number of lambs born per ewe's lifetime, or number of lambs weaned per ewe lifetime, litter size, conception rate, lamb survival and mothering ability (Zishiri *et al.*, 2013). The wet-dry phenotype (Fourie & Cloete, 1993) is recorded from an udder examination performed during the marking of recently born lambs or at the weaning of lambs. Wet-dry refers to whether a ewe is lactating or not, and can be used as an indicator of reproductive performance of ewes in low-input farming systems. Heritabilities estimated in Australian Merino flocks ranged from 0.09 to 0.17 for wet-dry at weaning and 0.04 to 0.11 when at lamb marking (Lee *et al.,* 2010). The wet-dry phenotype is a composite trait and includes both conception rate and mothering

ability. Heritability estimates for the component trait conception rate ranges from 0.01 to 0.30 (Iniguez *et al.,* 1986; Tosh *et al.,* 2002; Piwczyński & Kowaliszyn, 2013). Estimates for number of lambs born and number of lambs weaned were 0.05 to 0.10 and 0.05 to 0.07, respectively (Safari *et al.,* 2005; Safari *et al.,* 2007). In smallholder systems, easy to measure traits such as body weight and body condition score can be used as a proxy for growth, and wet-dry can be used as a proxy for reproduction.

There is no formal recordkeeping system in place for smallholder sheep farmers in South Africa. This inhibits genetic improvement of sheep utilised in smallholder sheep systems. It is therefore, important to obtain records of growth and reproduction of sheep kept by smallholders for the development of sustainable breeding plans to improve their production performance.

Therefore the first objective of this study was to characterise sheep management and breeding practices employed in smallholder sheep farming systems in the Western Cape Province. The second objective was to determine rangeland condition score as indicative of overgrazing in smallholder sheep farming systems. The third objective was to determine growth and reproduction (wet-dry) performance of smallholder sheep.

3.2. Materials and methods

3.2.1. Description of the study site

The study incorporated three districts in the Western Cape, namely the West Coast (Ebenheaser) municipality in the West Coast, the Central Karoo and the Eden district (Map 1). These districts were chosen because they are situated in arid environments according to Köppen –Geiger (2006) as sheep are mostly farmed extensively in these areas. The vegetation of the West Coast district is classified under the Succulent Karoo Biome, while the Karoo and Eden are classified as the Nama Karoo Biome (Acocks, 1988). The succulent Karoo mainly consists of succulent plants and is a winter rainfall area. The altitude ranges from sea level to 1500m

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and the mean annual rainfall is between 20 and 350mm. The Nama Karoo consists mainly of grass-shrub vegetation and ranges from 1000 to 1400 m in altitude. It is a summer rainfall area and receives 100 to 520 mm rain per annum. The three sites where farmers were interviewed in Eden district were Zoar, Dysselsdorp and Union dale. In the Central Karoo district farmers who were situated within a 50km radius from Beaufort West were interviewed. In the West Coast district only the farmers in Ebenheaser were interviewed.
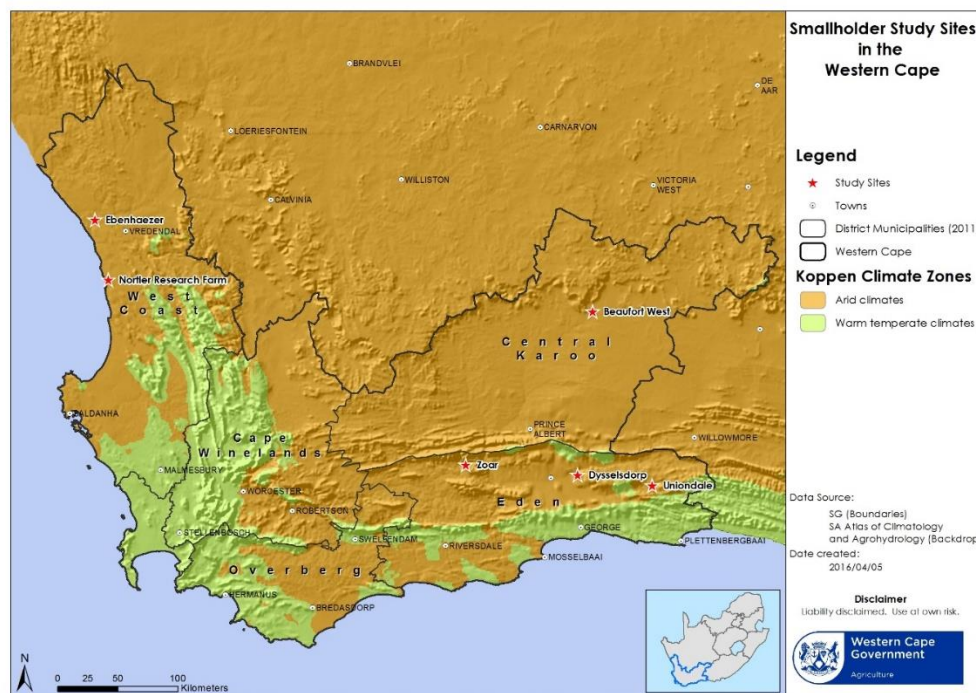
Map 3.1 Map of the Western Cape Province in South Africa with the sites where data were obtained from indicated

3.2.2. Household surveys

The sampling of farmers was based on the number of sheep they kept, which had to be between 5 and 100 breeding ewes as well as involvement with the government projects of CASP, LRAD and PLAS. This information was obtained from the extension officers in each respective district. A list of all the farmers involved in governmental projects or receiving support from government were obtained and farmers were invited for interviews. Farmers who were willing to cooperate in the study were included. Although the focus was mainly on sheep farmers,

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farmers having both sheep and crops as farming activity were also included to increase the sample numbers.

Husbandry practices and flock structure information were collected. Interviews were conducted with 72 smallholder farmers in total, namely 21 in the West Coast, 26 in the Central Karoo and 25 in the Eden district (Map 3.1). The different issues surveyed were the farming system employed, reasons for keeping livestock as well as flock structure and -size. Flock structure is important to consider for a sheep farmer. A commercial flock structure normally consists out of 2% mature rams and 1% young rams, 1% castrated rams, 11% young replacement ewes and 44% mature ewes, 41% lambs (Spies & Cloete, 2013). Flock structure is known to profoundly influence the product output and annual genetic gain of a sheep flock (Turner & Young, 1969).

3.2.3. Rangeland condition scores

Rangeland condition scores were obtained to determine the level of overgrazing or not on veld utilised by smallholder sheep farmers in the Western Cape. Range condition scores were carried out in the wet-season in 2014 on four sites in the Nama Karoo. These four sites were selected from two smallholder farms in the Karoo who participated in the survey. The first farm was located 50km outside of town, whereas the other farm was located 5km outside of town on communal lands. Rangeland condition scores were carried out during the dry season in 2014 on eight sites in the Succulent Karoo biomes (Tainton, 1999). These 8 sites were selected from four smallholder farmers who participated in the survey in Ebenheaser. Two camps were identified of each farmer for rangeland condition scoring. See the sampling sites in Table 1 in the Addendum A.

Recording of vegetation composition was done along transects using a line-point intercept method (Du Toit, 1997). This was done using 1000 points over one transect, spaced at 1m

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intervals to determine canopy cover of species based on canopy hits. The number of hits on a given species was calculated as a percentage of the total number of point observations. The total number of hits is an indication of canopy cover of the site. The percentage values obtained for individual species were multiplied by their grazing-index values (Du Toit *et al.,* 1995). Grazing index values were developed for plants based on 6 agronomic attributes which includes; the ability of a plant to produce forage, the forage value during growing season, forage value during the dormant season, the relative ease with which a species is grazed, perenniality and the ability of species to protect soil against surface erosion (Du Toit *et al.,* 1995). The products were summed and the index of the range-condition was obtained.

3.2.4 Phenotypic measurements

The following phenotypic measurements were done only on interview participants from the West Coast district. These farmers shared farms where sheep grazed, see Table 3.1 below for information on the group of farmers. The number of ewes present in the flocks from 2011, 2012 and 2014. Data were not collected in 2013. Age of ewes was determined based on dentition (Wilson & Durkin, 1984). Body weight and body condition of ewes were recorded during the lambing season. Body condition score (BCS) was determined on a scale from 1 to 5, with 1 being extremely emaciated and 5 obese (Thompson & Meyer, 1994). The 'wet and dry' technique was used to assess reproduction of ewes (Hatcher *et al.,* 2013). The system identifies ewes that were dry, ewes that lambed and lost all progeny and ewes that lambed and suckled at least one lamb at each visit.

Table 3.1 Description of smallholder farmers in Ebenheaser where phenotypic measurements were derived from.

	Farm 1	Farm 2	Farm 3	Farm 4
Number of farmers in group	13	17	13	25
Farm size	2252 ha	2174 ha	2116 ha	1815 ha
Number of camps	4	4	4	4
Total sheep	303	298	350	310
Number of ewes	80	239	255	300
No ewes tagged for recording	60	278	60	60

3.3. Statistical analysis

SURVEYMEANS and SURVEYFREQ in SAS were used to obtain means and frequencies for qualitative variables. Reasons for keeping livestock were recoded using a structured ranking scale of 1 to 4, with 1 being most important and 4 being least important. Indices were calculated for ranking data such as reasons for keeping sheep and selection objectives according to the following formula:

$$\text{Index} = \frac{\Sigma \, (n \, for \, rank \, 1 + (n-1) \, for \, rank \, 2 + (n-2) for \, rank \, 3 \ldots rank \, i) \, for \, variable \, X}{\Sigma \, (n \, for \, rank1 + (n-1) for \, rank \, 2 + (n-2) for \, rank \, 3 \ldots rank \, i) \, for \, all \, variables}$$

Where n is the highest value given to the variable based on the number of ranks (e.g. ranks are 1-4; n = 4) and i = least rank (if least rank is 4, then i = 4) Mbuku *et al.,* (2006). Traits selected for included size, conformation, mothering ability, disease tolerance, heat tolerance, and temperament, control of flies, meat taste, growth rate, fertility and foraging ability. Farmers had to rank the traits from most important (1) to least important (4). A t-test was done to see whether there were differences between grazing camps and district for range condition scores. The number of records available of phenotypic measurements from 2011-2014 were 1120 ewe

records for the different variables. A General Linear Model (GLM) in SAS was used to analyse phenotypic measurements of body weight, body condition score, and wet-dry phenotype. Least square means were obtained for body weight and body condition score and used to plot growth curves in relation to age in Excel (2010). Fixed effects fitted for wet-dry phenotype were the age of the ewe, body condition score, farm and year. Body weight was fitted as a covariate for the wet-dry phenotype. Chi-square was calculated in Excel®, 2010. The repeatability estimate was calculated using the rptR package in R software that used a Generalised Linear Mixed-Effects Model (GLMM) method and logit link to estimate repeatability for binary data (Stoffel *et al.,* 2017).

3.4. Results

3.4.1 Sheep farming systems

Figure 3.1 indicates the different farming types indicated by the survey information in the three districts of the Western Cape. The West Coast district constitutes 57% communal and 43% small-scale sheep farming systems. The Karoo has 84% small-scale, 12% communal and 4% large-scale. Only one farmer indicated his farming system to be large scale. This farmer, however, recently acquired land in 2014 from the PLAS project when the surveys were administered and have not actively farmed for one year. This data point was therefore excluded from further analysis. Eden district constitutes 86% small-scale and 10% communal sheep farming systems and 4% were unclassified as this information was not completed in the questionnaire.
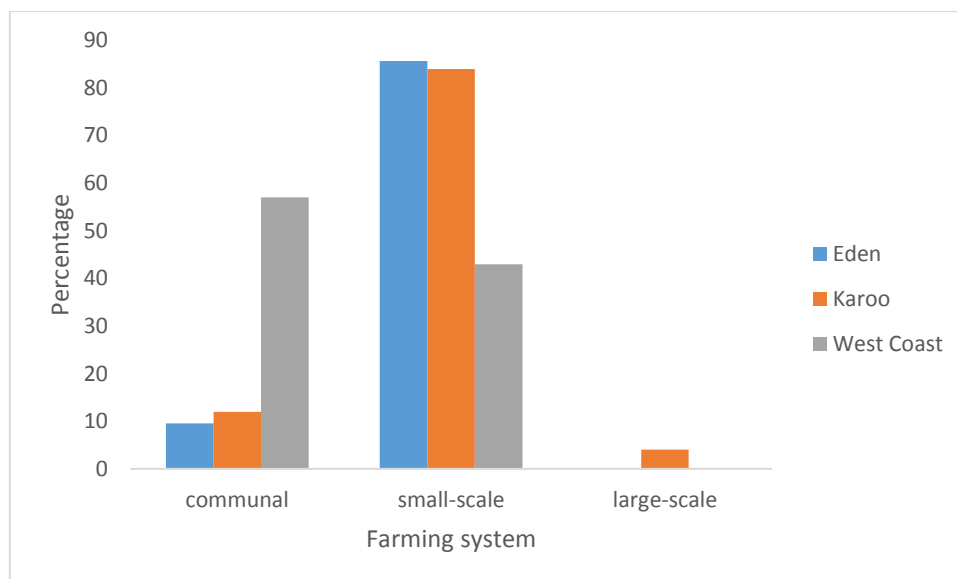
Figure 3.1 Percentages of different farming systems observed in three districts, namely Eden, Karoo and West Coast

Farm size differed significantly ($p < 0.05$) according to farming systems across districts, with the Karoo communal and small-scale farmers having the largest farm size of 2899 ha and 2291 ha respectively as seen in Table 3.1 and the West Coast small-scale farming system having the smallest farm size of 1.7 ha. The average sheep flock sizes also differed ($p < 0.05$) between the farming systems across all three districts as depicted in Table 3.1. West Coast had the lowest average sheep flock size of 3.2 livestock units (LSU) for both farming systems, communal and small-scale. One livestock unit is equal to a cow weighing 450kg. Eden district farmers had an average sheep flock size of 8.5 LSU per household and 8.2 LSU per household for communal and small-scale, respectively, whereas the Karoo farmers had the highest average sheep flock size of 14 LSU and 34 LSU for communal and small-scale farmers, respectively. Land use per LSU was highest for Karoo communal farming system with 120ha/LSU and the lowest for West Coast small-scale farming system with 0.15 ha /LSU. Most farmers belong to a trust, own their own land or are leasing land communally.

Table 3.2 Average livestock numbers per household in the different farming systems across districts (mean ± standard errors)

District	Farming system	Hectarage (Ha)	Livestock species	Mean ± SE	LSU	Ha/LSU
Eden	Communal (N=3)	7.90 ± 0.00	Cattle (n=1)	10.0 ± 0.00	8.00	0.26
			Sheep (n=2)	59.0 ± 24.0	8.50	
			Goats (n=3)	100 ± 0.00	14.4	
	Small-scale (N=18)	825 ± 581	Cattle	18.0 ± 7.10	14.4	18.5
			Sheep (n=6)	57.0 ± 13.1	8.20	
			Goats (n=12)	5.60 ± 3.30	0.80	
			Chickens (n=3)	17.8 ± 8.70	0.09	
			Pigs (n=5)	28.6 ± 25.7	19.1	
			Donkeys (n=3)	1.00 ± 1.00	0.40	
			Horses (n=2)	1.50 ± 0.50	1.60	
Karoo	Communal (N=3)	2899 ± 340.0	Sheep (n=1)	98.0 ± 0.00	14.2	120
			Goats (n=1)	55.0 ± 0.00	7.90	
			Chickens (n=1)	20.0 ± 0.00	0.11	
			Pigs (n=1)	3.00 ± 0.00	2.00	
	Small-scale (N=21)	2291 ± 383.0	Cattle (n=7)	6.60 ± 1.60	5.30	35
			Sheep (n=12)	233.5 ± 57.00	33.7	
			Goats (n=21)	76.8 ± 17.3	11.1	
			Chickens (n=15)	23.6 ± 15.3	0.13	
			Pigs (n=10)	17.0 ± 7.50	11.3	
			Donkeys (n=8)	1.60 ± 0.87	0.64	
			Horses (n=5)	2.80 ± 0.37	3.11	
West Coast		550 ± 0.00	Cattle (n=6)	3.00 ± 0.68	2.40	

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Farming system	Mean ± SE	Species	Mean ± SE		
		Sheep (n=12)	22.0 ± 5.50	3.20	59
		Goats (n=2)	3.50 ± 2.50	0.50	
		Chickens (n=2)	4.00 ± 0.00	0.02	
		Pigs (n=2)	1.00 ± 0.00	0.66	
Communal (N=12)		Donkeys (n=1)	1.00 ± 0.00	0.40	
		Horses (n=4)	2.00 ± 0.48	2.20	
Small-scale (N=9)	1.70 ± 0.00	Cattle (n=3)	2.70 ±1.70	2.20	0.15
		Sheep (n=9)	22.2 ± 3.50	3.20	
		Goats (n=1)	5.00 ± 0.00	0.72	
		Chickens (n=1)	5.00 ± 0.00	0.03	
		Pigs (n=2)	2.50 ± 1.50	1.70	
		Horses (n=2)	3.00 ± 1.00	3.30	

There were no significant differences regarding range condition scores (p>0.05) between the communal and small-scale farming systems. (Table 3.3). There were also no significant differences (p>0.05) between vegetation types in terms of range condition scores.

Table 3.3 Range condition scores for different farming systems communal vs small-scale

Farming system	Mean ± SE	Min	Max
Communal (N=8)	166 ± 18.0	100	251
Small-scale (N=4)	135 ± 31.5	72.0	217

3.4.2. Purposes for keeping sheep

Figure 3.2 shows the different reasons smallholder farmers were keeping sheep. Meat for home consumption was viewed as the most important reason for small-scale farming systems as aligned with a preference of most farmers to keep Dorper sheep primarily for meat production. Cash was the second most important reason for keeping sheep for small-scale farmers. The

third most important reason for small-scale farmers was investment. Keeping sheep for meat for consumption, cash and cultural purposes were ranked highest in communal farming systems, whereas breeding; investment, hobby and wool achieved the lowest ranking.
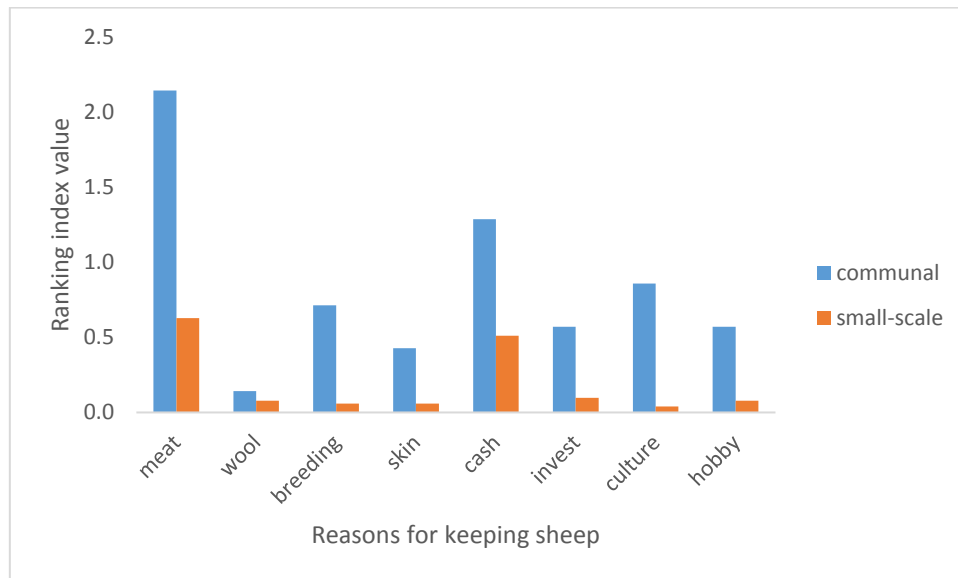
Figure 3.2 Ranking index values for reasons provided by smallholder farmers using different farming systems for keeping livestock

3.4.3. Sheep breeding

The Dorper was the most prominent breed used in all the farming systems, with 71% and 82% of farmers keeping Dorpers for the communal and small-scale farming systems, respectively. Persian (6%) and the White Dorper (6%) were other breeds used in communal farming systems. The rest of the breeds used in small-scale systems were the Merino (12%), Dorper x Damara (2%) crosses, White Dorpers (5%) and Meatmaster (2%).

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Figure 3.3 Breed composition of communal and small-scale farming systems
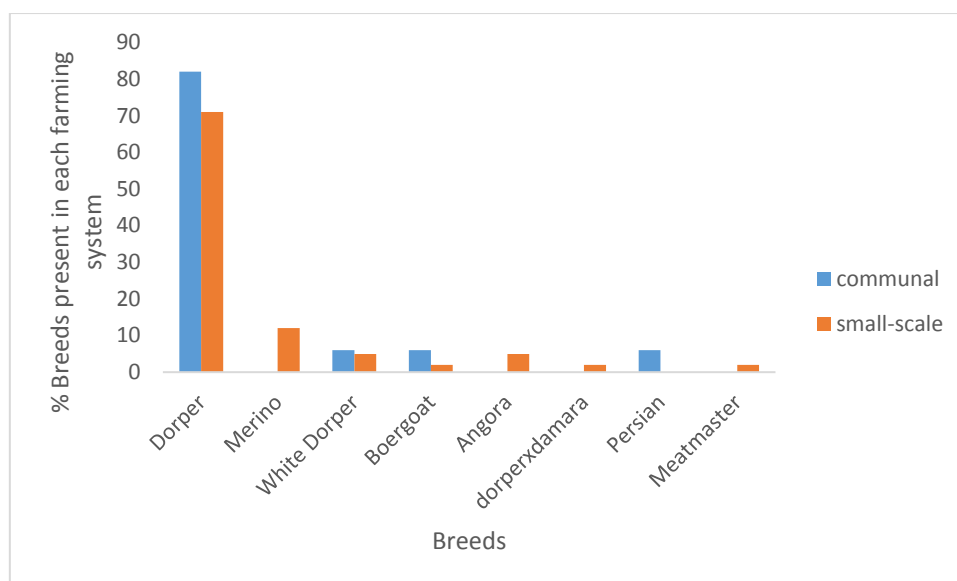
The flock composition for the two different farming systems is given in Table 3.4. The flock structure for the communal farming system in Eden was 46% young replacement ewes, 15% young rams and 39% mature ewes. The flock structure for the small-scale farming systems in Eden amounted to 1% lambs, 6% young replacement ewes, 5% young rams, 86% mature ewes and 2% mature rams.

Table 3.4 Average flock sizes per household given in Livestock Units (LSU) and percentage composition for smallholder sheep production units studied per farming systems across all three districts

District	Farming system	Lambs	Young ewes	Young rams	Ewes	Rams
Eden (N=21)	Communal (n=3)	0.0	1.0 (46%)	0.33 (15%)	0.86 (39%)	0.0
	Small-Scale (n=18)	0.12 (1%)	0.43 (6%)	0.34 (5%)	6.4 (86%)	0.17 (2%)
Karoo (N=24)	Communal (n=3)	0.03 (0.17%)	0.07 (0.41%)	0.07 (0.41%)	16 (95%)	0.7 (4%)
	Small-scale (n=21)	0.67 (2%)	3.6 (13%)	0.48 (2%)	23 (80%)	0.97 (3%)
West Coast (N=21)	Communal (n=12)	0.04 (1%)	0.24 (8%)	0.32 (11%)	2.2 (76%)	0.08 (3%)
	Small-scale (n=9)	0.04 (1.7)	0.33 (14%)	0.01 (0.44%)	1.8 (77%)	0.11 (5%)

Figure 3.4 indicates the selection objectives of smallholder farmers in the Western Cape. The communal farmers ranked temperament, control of flies, meat taste, growth rate, fertility and foraging ability as important attributes. The traits ranked highest for small-scale farmers included; conformation, mothering ability, disease tolerance, heat tolerance and temperament.
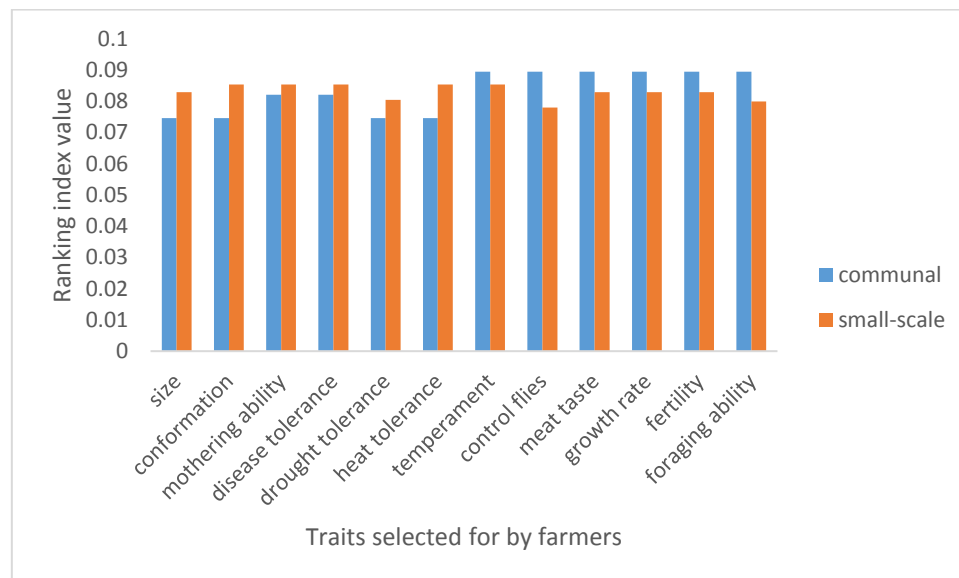
Figure 3.4 Ranking index values for selection objectives by smallholder farmers implementing different farming systems

3.4.4. Feed resources

Figure 3.5 indicates the different supplementation strategies employed by the different farming systems. Lucerne is the predominant source of supplementation in communal farming systems. There are some farmers combining supplementation of lucerne with crushed/whole grain maize and growth diets bought in from the feed supplier. Home-made rations were made by 6% of the farmers in communal farming systems, whereas the large-scale farmers only used pellets to supplement.
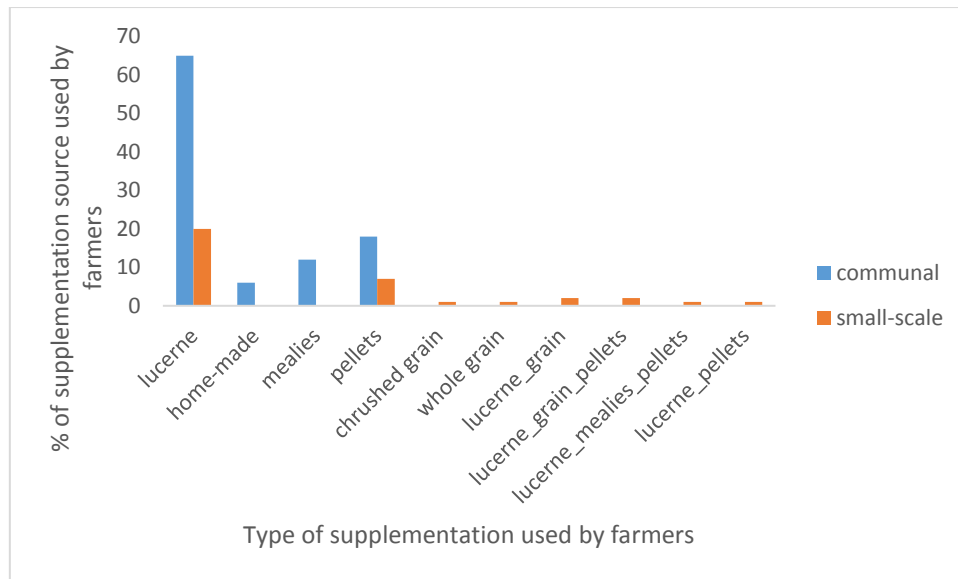
Figure 3.5 Percentages of farmers using different sources of supplementation by smallholder sheep farmers in the three different farming systems

3.4.5. Health

Figure 3.6 indicates the diseases treated for in the different farming systems as obtained from survey results. Internal parasites are the most treated for in both the communal (53%) and small-scale (42%) farming systems. Internal parasites were treated with IVOMEC® or Prodose®. Sheep were dipped to control external parasites. Farmers also vaccinated against bluetongue and pulpy kidney in both communal (6% & 12%) and small-scale (11% & 24%) farming systems.
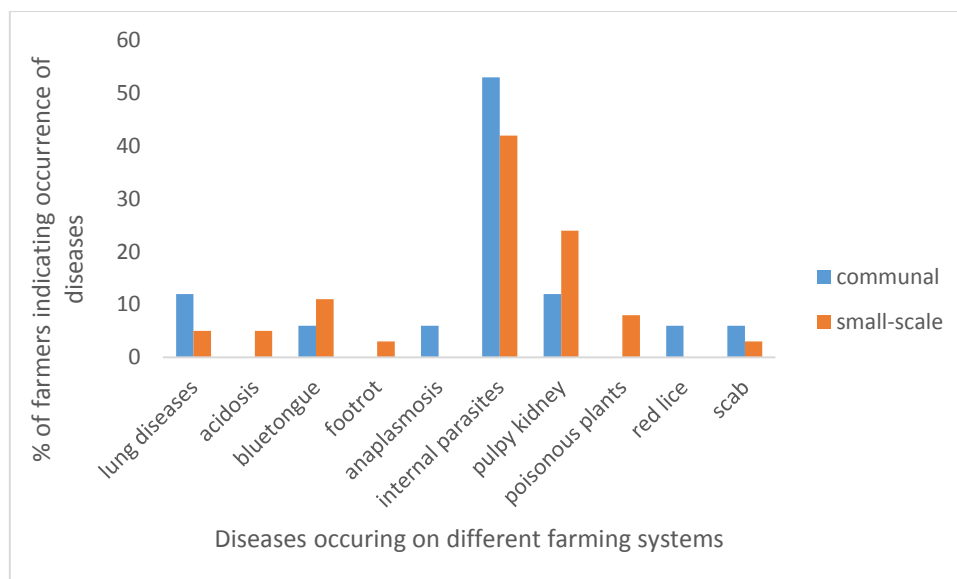
Figure 3.6 Predominant diseases that smallholder sheep farmers treat for within the two different farming systems

3.4.6. Constraints

The main constraint mentioned by communal farmers were the total size of available land (31%) (Table 3.5). The second most important constraint was droughts and a lack of drought assistance supplied by government (19%) and thirdly overgrazing and water availability (12%). Small-scale farmers mentioned lack of infrastructure and fencing as the main constraint (25%). The second constraint indicated by small-scale farmers was water availability (16%) and thirdly predators (11%).

Table 3.5 Constraints mentioned by smallholder farmers in the Western Cape.

Farming system	Constraints	Percentages
Communal	Land too small	31
	Drought	19
	Overgrazing	12
	Water availability	12
	Affordability to buy sheep	6
	Feed availability	6
	Landbank loan	6
	Ability for trust member to work together in a team	6
	Theft	6
	Equipment	6
Small-scale	Infrastructure and fencing	25
	Water availability	16
	Predators	11
	Land available	11
	Droughts	8
	Finances	5
	Strategic partners	5
	Grazing	5
	Live weight of animals	3
	Corruption	2
	Veterinary services	3
	Medicine expenses	3
	Theft	3
	Transport	3
	Electricity	3

3.4.7. Phenotypic measurements

Growth characteristics of sheep of smallholder farmers

Figure 3.6 depicts the growth curve for smallholder sheep follows a similar trend to that of commercial breeds. Body weight of ewes was related to body condition score. Ewes with a BCS of 1 achieved the lowest body weight of 47 ± 7.2, and ewes scored with the high BCS of 4.5 achieved the heaviest body weight of 76 ± 2.6 as shown in Figure 3.8. See Table 2 and 3 in Addendum A for information on the number of records for each datapoint.

$$y = 6.7514\ln(x) + 44.888$$
$$R^2 = 0.909$$
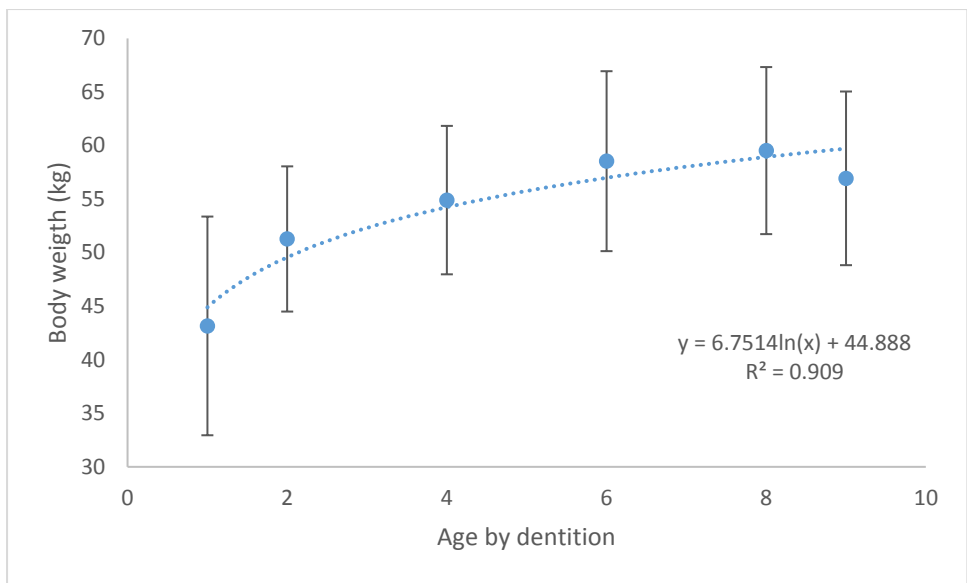
Figure 3.7 Growth curve of smallholder sheep, body weight (kg ± SD) in relation to age in years

$$y = 7.0382x + 38.167$$
$$R^2 = 0.8517$$
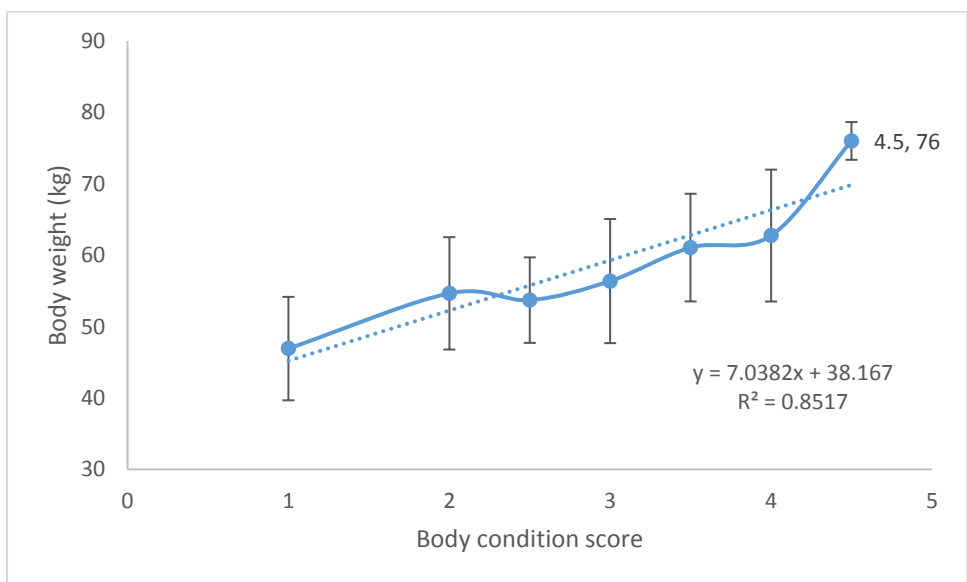
Figure 3.8 Body condition score for smallholder ewes in relation to body weight (kg ± SD)

Wet and dry phenotype

The effects of age of the ewe, body condition score, farm and year significantly influenced the wet-dry phenotype. The overall mean for wet-dry were 0.73 ± 0.37, and the coefficient of variation (CV %) was equal to 52%.

Table 3.6 Fixed effects of age of the ewe, farm, year and body condition score on wet-dry phenotype

| Fixed effect	Mean ± SE
Age of ewe in years	
1	0.71 ± 0.04
2	0.51 ± 0.04
4	0.67 ± 0.04
6	0.75 ± 0.02
8	0.76 ± 0.03
9	0.63 ± 0.06
Farm	
1	0.63 ± 0.05
2	0.67 ± 0.02
3	0.77 ± 0.04
4	0.84 ± 0.03
Year	
2011	0.67 ± 0.03
2012	0.62 ± 0.03
2014	0.82 ± 0.02
Body condition score	
1	0.67 ± 0.21
2	0.89 ± 0.04
2.5	0.87 ± 0.03
3	0.69 ± 0.02
3.5	0.67 ± 0.03
4	0.45 ± 0.05
4.5	0.33 ± 0.33

The wet-dry phenotype was recorded as a measurement of reproductive success over the three year period. The chi-square test indicated significant differences between reproductive performances over the different years as shown in Table 3.7. Repeatability estimate for wet-dry phenotype was 0.399.

Table 3.7 Chi-square results for proportion of wet ewes over three years and the repeatability estimate

Year	Proportion ewes wet (conceived)	Total number of ewes	Repeatability estimate
2011	0.67	264	0.399
2012	0.62	286	
2014	0.94	211	
Chi-square value	72.32349		
DF	2		
Pvalue	0.05		

3.5. Discussion

The farming systems were predominantly small-scale across the Karoo and Eden districts, with communal systems being predominant in the West Coast. Communal farming systems occurred where large areas of state owned rangeland were used by a group of farmers for grazing their livestock.

The number of LSU corresponded to the farm size, thus farmers with larger land owned more livestock. Similar findings were reported by Dagnew *et al.* (2017). The recommended grazing capacity for the West Coast district is 30ha/LSU, 36ha/LSU in the Karoo and 54 ha/LSU in the Eden district (Saayman, 2016). There was variation among farming systems for stocking rate. In the Eden, district both communal (0.26 ha/LSU) and small-scale (18.5 ha/LSU) farmers were overstocking in comparison to all three farming systems represented in the Karoo and West Coast district which were within the limit of the recommended grazing capacity. Rangeland condition scores did not differ between the farming systems or vegetation type. The values for Karoo vegetation type, however, fell within the values derived for farms in Beaufort West (Du Toit, 1995). Range condition scores are influenced by the dominant vegetation type. If the condition score is low (60-199) the range is dominated by climax grasses, and higher range condition scores (200-350) is an indication of where Karoo bushes dominate the vegetation available (Du Toit, 1995). The range condition scores for this study were on average low for the different farming systems. The results for the rangeland condition score between the farming systems could be influenced by the fact that the small-scale farm were assessed during the wet-season. In the wet-season there was an abundance of annual plants species, which have a lower forage value and this could have decreased the rangeland condition score. The communal farms were assessed in the dry season which lacked annual species and therefore attained a higher absolute value. The rangeland condition score is important to assess as it used to estimate grazing capacity of the rangeland. This in turn determines the availability of

adequate nutrition for sheep and agrees with the high carrying capacity (ha/LSU) observed for farmers in Eden and West Coast districts in this study.

The main reason for keeping livestock was for home consumption and secondly for income purposes in both communal and small-scale farming systems. This concur with other studies where livestock was kept mainly for regular cash income and secondly for meat production, both in small stock (Kosgey *et al.,* 2008) and in cattle (Mapiye *et al.,* 2009). The skins obtained from the sheep were of importance for some communal farmers as they stated that it is used as "extra income of the sheep skin for transport cost to the abattoir". Wool as a commodity is expected to be important for farmers keeping Merino-type sheep as this would be a secondary income. It is important to note that the need for livestock for cultural purposes and tradition were ranked lower for small-scale farmers than for communal farmers. This is in contrast to smallholder livestock farmers in the Eastern Cape or Limpopo (Stroebel *et al.,* 2011) who kept livestock primarily for cultural and/or traditional purposes. However, communal smallholder farmers in the Western Cape ranked sheep kept for cultural purposes higher than small-scale farmers even though it was still not the primary reason for keeping sheep.

The Dorper was the most prominent breed used in these farming systems. This is due to the Dorper being known for its favourable growth and carcass traits as well as hardiness. The Dorper is also known as an easy care sheep (Milne, 2000). The limited use of indigenous breeds like the Damara and Persian could be due to the unfavourable carcass characteristics (Tshabalala, 2000; Burger *et al.,* 2013). Indigenous breeds, however, play an important role in terms of adaptability and being more suitable for low-input farming systems. Kosgey *et al.* (2006) confirm the limited use of indigenous breeds in smallholder sheep farming systems in the tropics. However, the introduction of exotic breeds has not always been successful, due to observed genotype x environmental interactions. Introduction of exotic breeds could be accompanied with higher inputs and might not be sustainable to maintain in the long term.

The percentage of breeding ewes ranged from 39%-95% across all three farming systems (Table 3.3). Similar results were obtained in a study by Spies & Cloete (2013) for smallholder sheep farmers in the Free State. The number of mature ewes observed in this study was high in comparison to commercial flock structures that have 44% mature ewes. The percentage of lambs were low ranging from 0.17% to 2% compared to commercial flocks comprising up to 41% lambs (Spies & Cloete, 2013). Flock structure influences the annual genetic gain made in a flock (Turner & Young, 1969). The initial joining age of rams and the number of ram and ewe deaths also impact on annual genetic gain. A high number of rams relative to ewes compromises annual genetic gain (Turner & Young, 1969). It is therefore important for smallholder farmers who want to emerge into the commercial sector to improve their flock structure if they want to enhance genetic gain in their flocks. The age structure of the ewe flock has an effect on the output from the current flock. Achieving good production is difficult when reproduction performance is poor and you need to retain ewes beyond 6.5 years. This will lead to an increase in generation interval and compromise genetic gain.

The highest ranked traits that were selected for in communal farming systems included temperament, control of flies, meat taste, growth rate, fertility and foraging ability. The small-scale farmers selected for traits such as conformation, mothering ability, disease tolerance, heat tolerance and temperament. This is in accordance with other studies in the tropics where smallholder farmers consider fitness traits as most important (Kosgey *et al.,* 2006) in comparison to growth and carcass traits. Heat tolerance is relevant to select for considering that sheep are raised in the Karoo environment, which is known for its extreme heat. Numerous traits can be used to select for heat tolerance in sheep, these include, sweating rate, heart rate, breathing rate, rectal temperature and skin temperature, coat colour and eye temperature (McManus *et al.,* 2009, McManus *et al.,* 2011; McManus *et al.,* 2016). However, in dairy cattle temperature humidity index (THI) has been used to estimate response for selection to heat

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stress (Carabaño *et al.,* 2017). Selection for size is important, as larger sheep will yield more income. Temperament is important to select for ease of handling sheep when tagging and dosing are necessary.

Lucerne was the main source of supplementation used in smallholder systems. This is due to most farmers cropping lucerne on their farms. Lucerne was harvested, bailed, and used as conserved feed during times of food shortages.

Gastrointestinal parasites were one of the prominent conditions treated for by both communal and small-scale farmers in all three districts. This result were consistent with other studies (Adesehinwa *et al.,* 2004; Zvinorova *et al.,* 2016) on communal goats, where internal parasites were mentioned as a major challenge. However, the majority of farmers in this study used IVOMEC® for internal parasites. IVOMEC® is a broad spectrum parasiticide and treats roundworms, lungworms, mange mites and sucking lice. Internal parasites may become resistant to treatment if the same parasiticide is used consecutively. Alternating the active ingredient for drenches is thus recommended to prevent resistance. Considering that internal parasites were one of the prominent ailments both communal and small-scale farmers were treating, selection objective to increase parasite resistance could also be included in breeding objectives. The different types of internal parasites were not studied in detail and further research needs to be conducted. Vaccinations for pulpy kidney and blue tongue were done by a minority of farmers in respective farming systems. Faecal worm egg counts (FEC) as an indicator of gastrointestinal parasite resistance or using the FAMACHA system can be included in selection objective (Cloete *et al.,* 2016). This could lead to reduced input costs to buy anthelmintics. FAMACHA is a subjective score from 1-5 of the conjunctivae of the eye to indicate anaemia due to *Heamonchus contortus* spp (Van Wyk & Bath, 2002). Studies done have indicated that FAMACHA were positively correlated to FEC, indicating that animals with high anaemic scores were more likely to have high FEC counts (Cloete *et al.,* 2016). The

heritability estimates of both FAMACHA and FEC is 0.12 to 0.13 and 0.12-0.14 respectively (Cloete *et al.,* 2016). This latter study indicated that it is possible to achieve genetic progress if selection is made for these traits due to the high additive variation observed for these traits (Cloete *et al.,* 2016).

Land availability was the main constraint mentioned by communal sheep farmers, whereas small-scale indicated infrastructure and fencing as major constraints. This was in contrast to other studies that identified diseases as major constraints of smallstock production (Zvinorova *et al.,* 2016; Dagnew *et al.,* 2017). The reason for the difference could be due to farmers in the Western Cape being able to treat their sheep against diseases and thus does not see intestinal parasites and diseases as major constraints. Communal farmers primarily cited lack of land as a constraint because they were overgrazing their rangelands in relation to the recommended carrying capacity. Droughts and water availability were also prominent constraints mentioned by farmers. This could possibly be linked to predicted changes in climate as reported by the IPCC (Niang *et al.,* 2014).

The recorded body weights for smallholder Dorpers concur with literature figures (Snyman & Herselman, 2005; Cloete *et al.,* 2000). Similar weights were recorded for 10 months lambs that concur with milk tooth ewes observed in our study. The effect of age on body weight is expected as physiologically animals grow in size and weight, as they get older. Body condition score influenced body weight. Body condition score is an indication of the body energy reserves of the sheep. A heavier sheep has more fat reserves than a lighter sheep. The study indicated that ewes with a high BCS achieved a higher body weight. Similar results were obtained in a study comparing the effect of sourveld *vs.* sweetveld on body weight and body condition score (Mvinjelwa *et al.,* 2014).

The wet-dry phenotype is a composite trait and includes both conception rate and mothering ability. The wet-dry phenotype is indicative of the ability of a ewe to conceive, maintain

pregnancy without aborting, successful delivery and survival of lambs. The effects of age, body condition and body weight were expected as reproductive performance have been shown to decrease mating weight is below 45-50 kg and 2 tooth ewes have also been shown to have lower breeding performance than older ewes due to live weight at mating (Coop, 1962). The differences between ewes reproductive performance over the three years was also expected since the ewes grew in age. The repeatability estimate for wet-dry of this study is higher than that of Cloete & Heydenrych (1986). This indicates that it is possible to make genetic improvement if selection is made for wet-dry in smallholder sheep flocks.

3.6. Conclusions

There was variation amongst smallholder sheep production systems in the Western Cape Province of South Africa. The communal and small-scale farmers had similar reasons for keeping sheep, but had different breeding objectives and mentioned different constraints. The unbalanced flock structure could impose a limit on genetic progress and compromise production in the current flock. The limited use of indigenous breeds is of concern and the benefits of incorporation of indigenous sheep breeds should be elucidated to smallholder farmers. The use of wet-dry phenotype to measure reproductive success was identified as a promising tool. It can be used by farmers to select ewes that are more reproductively fit in low-input systems involving limited recordkeeping and to cull ewes that are barren consecutively. This study indicates that there were differences in sheep breeding and management practices by communal and small-scale farmers in the Western Cape. Implementation of breeding and management plans should, therefore, be farm-specific and the impact of climate change on production should be considered.

3.7. References

Acocks, J.P.H., 1988. Veld types of South Africa. Memoirs of the Botanical Survey of South Africa, 57. SANBI, Pretoria.

Adesehinwa, A.O.K., Okunola, J.O. & Adewumi, M.K., 2004. Socio-economic characteristics of ruminant livestock farmers and their production constraints in some parts of South-western Nigeria. Livest. Res. Rur. Develop. 16 (8)

Almeida, A.M., 2011. The Damara in the context of Southern Africa fat-tailed sheep breeds. Trop. Anim. Health Prod. 43, 1427–1441.

Burger, A., Hoffman, L.C., Cloete, J.J.E., Muller, M. & Cloete, S.W.P., 2013. Carcass composition of Namaqua Afrikaner, Dorper and SA mutton merino ram lambs reared under extensive conditions. S. Afr. J. Anim. Sci. 43, S27-S32

Carabaño, M.J., Ramón, M., Díaz, C., Molina, A., Pérez-Guzmán, M.D. & Serradilla, J.M., 2017. Breeding for resilience to heat stress effects: A comparison across dairy ruminant species. J.Anim. Sci. 95, 1813-1826.

Cloete, S.W.P. & Heydenrych, H.J., 1986. The repeatability of reproduction rate in the Tygerhoek Merino flock. S. Afr. J. Anim. Sci. 17, 15-21.

Cloete, J.J.E., Cloete, S.W.P., Scholtz, A.J. & Matthee, S., 2013. The effect of breed, ewe age and season on tick counts of indigenous and commercial sheep in South Africa. Proc. Assoc. Advmt Anim. Breed. Genet. 20, 187–190.

Cloete, S.W.P., Olivier, J.J., Sandenbergh, L. & Snyman, M.A., 2014. The adaption of the South Africa sheep industry to new trends in animal breeding and genetics: A review. S. Afr. J. Anim. Sci. 44, 307–321.

Cloete, S.W.P., Mpetile, Z. & Dzama, K., 2016. Genetic parameters involving subjective FAMACHA scores on two farms in the Mediterranean region of South Africa. Small Rumin. Res. 145, 33-45.

Coop, I.E., 1962. Liveweight productivity relationships in sheep. N. Z. J. Agric. Res. 5, 249-264.

Dagnew, Y., Urge, M., Tadesse, Y. & Gizaw, S., 2017. Sheep production and breeding Systems in North Western lowlands of Amhara Region, Ethiopia: Implication for conservation and improvement of Gumz sheep breed. Open J. Anim. Sci. 7, 179- 197.

Directorate Statistics and economic analysis. 2013. Abstract of Agricultural statistics. Pretoria South Africa.

Du Toit, P.C.V., 1995. The grazing index method of range condition assessment. Afr. J. Range Forag. Sci.12, 61-67.

Everett-Hincks, J.M. & Dodds, K.G., 2008. Management of maternal-offspring behavior to improve lamb survival in easy care sheep systems. J. Anim. Sci. 86

Fourie, A.J. & Cloete, S.W.P., 1993. Reproductive performance of commercial Merino, Dohne Merino and SA Mutton Merino flocks in the Southern Cape. S. Afr. J. Anim. Sci. 23, 104-110.

Goddard, M., 2009. Fitness traits in animal breeding programs. In Adaptation and fitness in farm animal populations. Eds. Van der Werf, J.H.J.; Graser, H-U.;Frankham, R.; Gondro, C. (ed.) Springer Science & Business Media.

Hatcher, S., Curran, G., White, A., Casey, A. & Refshauge, G., 2013. Sheep udder assessment at lamb marking. NSW, Department of Primary Industry.

http://www.dpi.nsw.gov.au/animals-and-livestock/sheep/management/reproduction/sheep-udder-assessment. Accessed on the 13 October 2017.

Huisman, A.E. & Brown, D.J., 2009. Genetic parameters for bodyweight, wool, and disease resistance and reproduction traits in Merino sheep. 3. Genetic relationships between ultrasound scan traits and other traits. Anim. Prod. Sci. 49, 283–288.

Iniguez, L.C., Quaas, R.L. & Van Vleck, L.D., 1986. Lambing performance of Morlam and Dorset ewes under accelerated lambing systems. J. Anim. Sci. 63, 1769–1778.

Kosgey, I.S., Baker, R.L., Udo, H.M.J. & Van Arendonk, J.A.M., 2006. Successes and failures of small ruminant breeding programmes in the tropics: a review. Small Rumin. Res. 61, 12-28.

Kosgey, I.S., Rowlands, G.J., Van Arendonk, J.A.M. & Baker, R.L., 2008. Small ruminant production in smallholder and pastoral/extensive farming systems in Kenya. Small Rumin. Res. 77, 11-24.

Kottek, M., Grieser, J., Beck, C., Rudolf, B. & Rubel, F., 2006. World Map of the Köppen-Geiger climate classification updated. Meteorol. Z., 15, 259-263. DOI: 10.1127/0941-2948/2006/0130.

Kunene, N., Nesamvuni, E. A. & Fossey, A., 2007. Characterisation of Zulu (Nguni) sheep using linear body measurements and some environmental factors affecting these measurements. S. Afr. J. Anim. Sci. 37, 11–20.

Lee, G.J., Sladek, M.A. & Atkins, K.D. 2010. Selection criteria for within flock selection to improve reproduction efficiency. Available at:

http://www.livestocklibrary.com.au/bitstream/handle/1234/33711/SheepCRC_2_87.pdf ?sequence=1.

Mapiye, C., Chimonyo, M., Dzama, K., Raats, J.G. & Mapekula, M., 2009. Opportunities for improving Nguni cattle production in smallholder farming systems of South Africa. Livest. Sci. 124,196-204.

Milne, C., 2000. The History of the Dorper. Small Rumin. Res. 36, 99-102.

McManus, C., Paludo, G.R., Louvandini, H., Gugel, R., Sasaki, L.C.B. & Paiva, S.R. 2009. Heat tolerance in Brazilian sheep: Physiological and blood parameters. Trop. Anim. Health. Prod. 41, 95-101.

McManus, C., Louvandini, H., Gugel R., Sasaki, L.C.B., Biachini, E., Bernal, F.E.M., Paiva, S.R. & Paim, T.P. 2011. Skin and coat traits in sheep in Brazil and their relation with heat tolerance. Trop. Anim. Health. Prod. 43, 121-126.

McManus, C., Dallago, B.S.L., Lehugeur, C., Ribeiro, L.A., Hermuche, P., Guimarães, R.F., de Carvalho Júnior, O.A. & Paiva, S.R., 2016. Patterns of heat tolerance in different sheep breeds in Brazil. Small Rumin. Res. 144, 290-299.

Palmer, A.R. & Bennett, J.E., 2013. Degradation of communal rangelands in South Africa: towards an improved understanding to inform policies. Afr. J. Range Forage Sci. 30, 57-63.

Piwczyński, D. & Kowaliszyn, B., 2013. Heritability and breeding value of sheep fertility estimated by means of the GIBBS sampling method using the linear and threshold models. J. Centr. Euro. Agric. 14, 23–32.

Saayman, N., 2016. Basic guidelines for veld management: Central Karoo. Infopack –
Research and Technology Development Services, Western Cape Department of
Agriculture. Saayman, 2016. (http://elsenburg.com/research-article/basic-guidelines-
veld-management-central-karoo-infopack -accessed 10 April 2017)

Safari, E., Fogarty, N.M. & Gilmour, A.R., 2005. A review of genetic parameter estimates for
wool, growth, meat and reproduction traits in sheep. Livest. Prod. Sci. 92, 271–289.

Safari, E., Fogarty, N.M., Gilmour, A.R., Atkins, K.D., Mortimer, S.I., Swan, A.A., Brien,
F.D., Greeff, J.C. & Van Der Werf, J.H.J., 2007. Across Population Genetic Parameters
for Wool, Growth, and Reproduction Traits in Australian Merino Sheep. 1. Data
Structure and Non-Genetic Effects. Aust. J. Agric. Res. 58, 169–175.

Schoeman, S.J., Cloete, S.W.P. & Olivier, J.J., 2010. Returns on investment in sheep and goat
breeding in South Africa. Livest. Sci.130, 70–82.

Snyman, M.A. & Herselman, M.J., 2005. Comparison of productive and reproductive
performance efficiency of Afrino, Dorper and Merino sheep in the False Upper Karoo.
S. Afr. J. Anim. Sci. 35, 98-108.

Snyman, M.A., Van Marle-Koster, E, Qwabe, S.Q. & Visser, C., 2013. Genetic and phenotypic
profile of three South African Namaqua Afrikaner sheep flocks. Grootfontein Agric,
13. Available at: http:/gadi.agric.za/Agric/Vol13No1_2013/namaqua.php.

Spies, D.C. & Cloete, P.C., 2013. Performance and marketing options for red meat in the
formal and informal value chains in the Free State Province. 19th International Farm
Management Congress, SGGW, Warsaw, Poland.

Stoffel, M.A., Nakagawa, S. & Schielzeth, H., 2017. rprR: Repeatability estimation and variance decomposition by generalized linear mixed-effects models. Method Ecol. Evol. doi: 10.1111/2041-210X.12797

Stroebel, A., Swanepoel, F.J.C. & Pell, A.N., 2011. Sustainable smallholder livestock systems: A case study of Limpopo Province, South Africa. Livest. Sci. 139,186-190.

Thompson, J. & Meyer, H., 1994. Body condition scoring of sheep. Oregon state University Extension services. Available from https://hdl.handle.net/1957/14303 accessed 15 October 2017.

Tosh, J.J., Wilton, J.W. & Kennedy, D., 2002. Heritability of Fertility in Four Seasons', in 7th World Cong. Genet. Appl. Livest. Prod. Montpellier, France, pp. 23–26.

Tshabalala, P., 2000. Meat quality of South African indigenous goat and sheep breeds. MInst Agrar Food Processing. University of Pretoria, South Africa.

Turner, H.N. & Young, S.S.Y., 1969. Chapter 16. The influence of flock structure on productivity. In: Quantitative Genetics in Sheep Breeding. Eds by Cornell University Press, Ithaca, New York.

Wilson, R.T. & Durkin, J.W. 1984. Age at permanent incisor eruption in indigenous sheep and goats in semi-arid Africa. Livest. Prod. Sci. 11, 451-455.

Zishiri, O.T., Cloete, S.W.P., Olivier, J.J. & Dzama, K., 2013. 'Genetic parameter estimates for subjectively assessed and objectively measured traits in South African Dorper sheep', Small Rumin. Res. 109, 84–93.

Zvinorova, P.I., Halimani, T.E., Muchadeyi, F.C., Katsande, S., Gusha, J. & Dzama, K., 2016. Management and control of gastrointestinal nematodes in communal goat farms in

Zimbabwe. Trop. Anim. Health Prod. 49, 361-367.

Chapter 4

Factors influencing offtake in smallholder sheep farming systems in the Western Cape, South Africa

Abstract

The purpose of this study was to determine factors that influence sustainable offtake in smallholder sheep farming systems in the Western Cape province of South Africa. Interviews were conducted with 72 smallholder farmers in three districts of the Western Cape, namely the West Coast, Karoo and Eden. General information on the socio-economic status of the farmers was obtained through semi-structured questionnaires. Numbers of lambs sold and offtake rates were assessed as economic indicators. A logistic regression was fitted to determine which socio-economic factors influenced sources of income and sale outlet. The effects of district, farming type, sources of income, participation in government programs and flock size on number of lambs sold and offtakes rates were analysed by fitting a general linear model. Livestock production was the major activity for 76 % of the smallholder farmers while cropping represented 24%. Fifty one percent of the respondents fell within the age range of 40 to 60 years of age, whereas 20% were younger than 40 and 29% were older than 60 years of age. Sixty seven percent of the farmers ranked themselves as having a medium wealth status, while 32% ranked themselves as poor. The households interviewed were male dominated with 90% of the respondents being male and only 10% female. Land ownership was categorised as 36% self-owned, 29% leased and 29% communal land. District significantly influenced sale-outlet. The West Coast obtained a chance of 15% to sell their product to the abattoir. Whereas the Karoo and Eden were not different in terms of sale outlet.

Land ownership significantly influenced the farmers' source of income. The probability of males obtaining income from their salary vs. obtaining income from grants was 13 times more than females. The probability of those farmers who lease land vs. communal land ownership patterns to obtain their main income from salary was 4 times more than obtaining income from grants/pension. The main sources of income for the Karoo farmers was livestock (46%) and for Eden crops (32%). Contrary to other districts, farmers in the West Coast area mostly relied on salaries (43%), thus off-farm income. The results of the general linear model indicated that only district significantly ($P<0.05$) influenced average number of lambs sold and offtake rate. The Karoo district sold a higher average number of lambs per year (41 ± 8.8), with West Coast and Eden selling the same average number of lambs per year at 7 ± 2.2 and 7 ± 2.6 respectively. Offtake rates did not differ among districts and were $17 \pm 17\%$ for Eden, $48\% \pm 20\%$ for the Karoo and $46 \pm 20\%$ for West Coast. Based on the social status of the farmers (age of farmer, gender and wealth status), the farming systems in the three districts were moderately sustainable. Based on the economic status (average number of lambs sold and offtake rate) the farming systems in the three districts were poorly sustainable.

4.1. Introduction

Small stock is mainly kept for socio-economic benefits by poor Southern Africa communities. Such benefits include household food security, capital and direct income (Moyo & Swanepoel, 2010). Most of the surface area in South Africa is semi-arid which makes it unsuitable for anything but extensive ruminant livestock farming (Cloete & Olivier, 2010). The ability of sheep to adapt to diverse and often adverse climatic conditions (Rust & Rust, 2013) ensures that the species plays an important role in resource-poor systems. It is crucial to understand the adaptation of sheep to such systems to ensure the sustainable utilisation of vast areas of low-potential shrubland in the rural parts of South Africa. Smallholder farming systems in tropical areas are seen as unsustainable, as measured against social, economic and environmental

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dimensions (Manyong & Degand, 1996). Few studies in South Africa have described smallholder sheep farming systems in the Western Cape (Grobler, 2010). Some studies were also done in the Eastern Cape and Limpopo and focussed on communal farming systems in rural villages (Marais, 2007; Stroebel, 2011) including market access and the economics of smallholder systems. These studies highlighted the difficulty of smallholder farmers to attain market access and improve their livelihoods, thereby implying economic unsustainability.

There are different socio-political issues at hand. The implementation of black economic empowerment (BEE) in South Africa after the 1994 election profoundly affected smallholder farmer production. Farming dynamics are different in each province of South Africa and need to be understood before implementing any strategy to improve production (Schwalbach *et al.*, 2001). Programmes like the Land Redistribution for Agricultural Development (LRAD) and the Comprehensive Agricultural Support Programme (CASP) have been initiated by the Department of Agriculture to assist in the agricultural development and land restitution of underprivileged communities benefitting from BEE. These initiatives aimed to increase overall agricultural production in rural areas. Increased agricultural production is expected to improve national and household food security, which is under pressure in Southern Africa (Aliber, 2009). These programmes had some shortcomings and more recent programmes have been introduced as compensation. The Proactive Land Acquisition Strategy (PLAS) is a program that acquires land for smallholder candidates that have commercial farmers assigned as mentors for the first five years of farming.

Smallholder farmers in South Africa are vulnerable to food insecurity and mostly under the poor in the social ranks (Altman *et al.,* 2009, Thamaga-Chitja & Morojele, 2014). The average monthly income per household is $390.29 (Statistics South Africa, 2014) with an average household size of 7 members (Mapiye *et al.*, 2009). The role that sheep play to provide food and income is of paramount importance for sustaining the rural livelihood. The offtake of sheep

production depends on the ewes as the main productive units producing lambs that are sold for generating income. The prices for lamb in South Africa is currently $5.15 p/kg for lambs with a medium fat cover on the carcass (Webb, 2015) in the formal market. A carcass weighing 16-20 kg can thus earn up to $82.4 – $103 for a resource-poor farmer. Smallholder farmers, however, prefer to sell lambs/adult sheep on the hoof for any price ranging between $60-$91 on the informal market (personal communication with smallholder farmers). Commercially the important factor determining the success of a sheep farmer would be lamb output (numbers or weight marketed) expressed relative to the number of ewes maintained. Acceptable performance in an extensive commercial system ranges between 110-156% for lambing percentages (Snyman & Herselman, 2005) and between 94-132% (Snyman & Herselman, 2005) for weaning percentage (both expressed over ewes joined). Smallholder farmers in contrast do not achieve high lambing and weaning percentages due to a number of constraints. These constraints include obsolete management practices, poor environmental conditions resulting from the overexploitation of resources, unstable feed availability, limitations to grazing rights and the adaptability of the breed(s) used, as well as the number of sheep owned by the individual relative to the resources allocated (Mapiye *et al.,* 2009, Rust *et al.,* 2015). Grobler (2010) indicated that, of the 17 farms benefitting from the LRAD and CASP programmes, only 4 showed acceptable lamb marketing percentages. Low lamb marketing percentages (defined as lambs sold per ewe mated) resulted from severe drought conditions and lamb losses due to predators. Measuring accurate lambing percentages for smallholder sheep farmers is challenging as these farmers mostly farm extensively and do not keep records. Offtake can therefore be used as a proxy to determine farm productivity. Offtake rate can be defined as the proportion of animals sold or consumed within a year relative to the breeding flock maintained (Otte & Chilonda, 2002).

In Chapter 3 the sheep farming characteristics including breeding practices were investigated. However, a holistic approach is needed to address limitations to production in smallholder sheep farming systems (Kosgey *et al.,* 2006). Determining the socio-economic factors that contributes to offtake is therefore important. Against this background, the present study elucidates factors that influence the different sale outlets and sources of income as well as the average number of lambs sold and offtake rate.

4.2. Material and methods

4.2.1. Description of the study site

The sampling site was described in Chapter 3.

4.2.2. Household surveys

As described in section 3.2.2. in Chapter 3 (Map 3.1). Information on the number of lambs sold per year as indication of production performance of the flock and the number of animal entries and exists per annum were also recorded.

4.2.3. Statistical analysis

Descriptive data pertaining to farming systems were analysed using the Statistical Analysis Systems (SAS, 2014) procedures SURVEYMEANS and the SURVEYFREQ. An ordinal logistic regression analysis was used to predict the odds of different sources of income, and different sale outlets given the socio-economic profile and district, farm size and farming system of the farmers (see Chapter 3). Sources of income were classified into 5 levels: 1) crops, 2) livestock, 3) home industries, 4) salary and 5) grants. Sale outlets were classified into 4 levels: 1) auction, 2) butchery, 3) privately and 4) abattoir.

A general linear model (GLM) was conducted using SAS (2014) to determine differences between the three districts regarding the average number of lambs sold per year and offtake

rate. Socio-economic effects fitted as fixed effects were age of the farmer, farm type, sources of income, wealth status, tribe, gender of the household head, whether farmer participated in LRAD, CASP and/or PLAS program and flock size. The Bonferroni posthoc test was applied to test for differences between districts for the average number of lambs sold and offtake rate.

4.3. Results

4.3.1. Farmers socio-economic profile

Livestock production was the major activity for 76 % of the smallholder farmers that contributed to this survey, while cropping represented 24%. Fifty one percent of the respondents fell within the age range of 40 to 60 years of age, whereas 20% were younger than 40 and 29% were older than 60 years of age (Table 4.2). Sixty seven percent of the farmers ranked themselves as having a medium wealth status, while 32% ranked themselves as poor. The households interviewed were male dominated with 90% of the respondents being male and only 10% female. Land ownership was categorised as 36% self-owned, 29% leased and 29% communal land. The remaining 6% of the farmers preferred not to disclose information on their land ownership.

Table 4.1 Socio-economic description of farmers in the Western Cape.

Socio-economic profiles	Proportions
Age	
<40 years	20%
40-60 years	51%
>60 years	29%
Gender	
Male	90%
Female	10%
Wealth status	
Poor	32%
Medium	67%
Rich	
Land Ownership	
Self-owned	36%
Leased	29%
Communal	29%
Undisclosed	6%

Farm size, did not significantly influence the sale outlet of farmers. District significantly influenced sale outlet with the West Coast obtaining a chance of 15% to sell their product to the abattoir. There was no significant difference between the Karoo and Eden district in terms of sale outlet.

Table 4.2 Odds ratio estimates for sale outlets private vs. abattoir for smallholder sheep farmers.

Effect	Odds ratio	95% Wald confidence limit
Farm size	1.000	0.999-1.000
District Eden vs. West Coast	1.076	0.155-7.493
District Karoo vs. West Coast	0.145	0.018-1.174

Table 4.3 Analysis of Maximum likelihood estimates for sale outlets.

Parameter		DF	Estimate	Standard Error	Wald Chi-Square	Pvalue
Intercept	01:01	1	-1.074	0.5226	4.2232	0.0399
Intercept	02:02	1	-0.4512	0.4926	0.839	0.3597
Intercept	03:03	1	1.4245	0.5562	6.5607	0.0104
Farmsize		1	-0.0001	0.000219	0.1963	0.6577
District	E	1	0.6931	0.5013	1.9121	0.1667
District	K	1	-1.3127	0.5519	5.6579	0.0174

Table 4.5 shows the sale outlets of smallholder farmers per district. Outlets for the Eden district included home consumption and private sales during holiday seasons like Easter or Christmas. The activity of farmers in Eden was focused on crop production, which was also their main source of income. Farmers in the Karoo district were actively involved in a LRAD project. It was evident that these farmers choose to supply meat to the formal market. Farmers in the West Coast district sold sheep to the informal market and the money so obtained was used for subsistence and emergency cash. Based on the sale outlet the different districts can be classified as either being market-orientated or subsistence orientated. Thus Eden and West Coast were more subsistence orientated and the Karoo district more market orientated.

Table 4.4 Description of the farming systems and sale outlets per district in the Western Cape, South Africa

Farming system	District	Different sources of income	Sale outlet for livestock
Both communal and small-scale (subsistence orientated)	Eden	Crops (32%) Grants (20%) Livestock (16%) Salaries (16%) Other (12%) No indication (4%)	Home consumption and private sales
Communal, Small-scale and Large-scale (market orientated)	Karoo	Livestock (46%) Salaries (23%) Home industries (15%) Crops (12%) Grants (4%)	Abattoir
Communal and small-scale (subsistence orientated)	West Coast	Salary (43%) Grants (29%) Crops (14%) Not indicated (14%)	Private sales

District, farm size, farm type, flock size and wealth status did not significantly influence the source of income for farmers. Land ownership (leased vs. communal, OR = 4), however, significantly influenced the farmers' source of income as shown in Table 4.6. The probability of those farmers who leased land vs. communal land ownership to obtain their main income from salary was 4 times more than obtaining income from grants/pension. The main sources of income for the Karoo farmers was livestock (46%) and for Eden crops (32%). Contrary to other districts, farmers in the West Coast area mostly relied on salaries (43%), thus off-farm income (Table 4.5).

Table 4.5 Odds estimate ratio for sources of income for smallholder sheep farmers

Effect	Point Estimate	95% Wald confidence limits	
Farmsize	1	0.999	1
District Eden vs West Coast	0.755	0.078	7.26
District Karoo vs West Coast	1.887	0.196	18.161
wealth 2 vs 3	0.463	0.128	1.673
Land ownership self-owned vs communal	0.761	0.132	4.378
Land ownership leased vs communal	4.094	0.508	33.004

Table 4.6 Analysis of maximum likelihood estimates for sources of income

Parameter		DF	Estimate	Standard Error	Wald Chi-Square	P value
Intercept	01:01	1	-1.243	0.5588	4.949	0.0261
Intercept	02:02	1	0.6746	0.5303	1.6184	0.2033
Intercept	03:03	1	1.0544	0.5434	3.7654	0.0523
Intercept	04:04	1	2.8037	0.7019	15.9565	<.0001
farmsize		1	-0.00024	0.000245	0.9963	0.3182
District	E	1	-0.3993	0.591	0.4566	0.4992
District	K	1	0.5172	0.5911	0.7658	0.3815
wealth	2	1	-0.385	0.3277	1.3802	0.2401
Land ownership	Self-owned	1	-0.6516	0.4163	2.4494	0.1176
Land ownership	Leased	1	1.0306	0.5346	3.7161	0.0539

4.3.2. Average number of lambs sold

Significant differences were obtained between districts for average number of lambs sold. Income source, whether the farmer participated in government support programs and farm type did not significantly influence the average number of lambs sold. The results in Table 4.8 suggest that smallholder farmers from the Karoo district sold a higher absolute number of lambs per year (41 ± 8.8), with West Coast and Eden selling the same average number of lambs per year at 7 ± 2.2 and 7 ± 2.6 respectively. Lambs born per ewe (as recorded from the surveys based on interviews with individual respondents) were used to calculate average lambing

percentages (±SE) per district. Lambing percentages averaged 139 ± 38% for the Eden district, 83 ± 15% for the Karoo district and 61± 12% for the West Coast district, as derived from the survey data.

Table 4.7 Means (±SE) depicting the measures of lamb output per household in the Eden, Karoo and West Coast districts.

District	Average number of lambs sold per breeding season/year (±SE)	Total flock size (± SE)	Ewes (±SE)	Rams (±SE)	Lambs born per breeding season (±SE)	Lambing percentage (±SE)
Eden	7 ± 2.6[b]	45 ± 11[b]	32 ± 9.3[b]	1.2 ± 0.26[a]	26 ±6.1[b]	139 ± 38[b]%
Karoo	41±8.8[a]	256 ± 61[c]	184 ± 45[c]	6.5 ± 1.2[b]	105 ± 20[c]	83 ± 15[a]%
West Coast	7±2.2[b]	23 ± 2.5[a]	16 ± 2.5[a]	1.3 ± 0.16[a]	12 ± 2.1[a]	61 ± 12[a]%

[a-b] $P<0.05$, means in rows differ significantly from each other

4.3.3. Offtake rate

District significantly influenced offtake rate as scaled relative to flock size. Other factors, namely the age of the farmer, farm type, wealth status, tribe and gender of household head, whether or not farmer participated in any type of the LRAD, CASP and PLAS programmes and flock size, did not influence offtake rate and were excluded from the analysis. The overall average offtake rate (±SD) for smallholder farmers in the Western Cape was 33 ± 39% with a coefficient of variation of 119%. Offtake rate for the respective districts were 17 ± 17% for Eden, 48 ± 20% for Karoo and 46 ± 20% for West Coast.

4.4. Discussion

This study provides insights on the socio-economic profile of smallholder sheep farmers in South Africa and its influence on sources of income, sale outlets, average number of lamb sold and offtake rate. Most of the smallholder farmers fell within the age range of 40 to 60 years. This concurs with literature that the smallholder farmers in South Africa are mostly above the age of 40 (Marandure *et al.,* 2016, Motiang & Webb, 2016). It could be due to the effects of

migration of young rural residents to urban areas in search of better working and living conditions (Dossa *et al.,* 2008). In addition, the rural youth are generally not interested in agriculture as a career. According to the sustainability classification in Table 4.1, the age of the respondent as an indicator is moderately sustainable. Sheep farming was dominated by males in this study, a result corresponding to other studies where males are more likely to farm with sheep and females with goats (Dossa *et al.,* 2008).

Sale outlets were influenced by district. The farmers in the West Coast were more likely to sell their product to the informal market. These farmers have indicated that the price received per lamb was better when sold privately compared to marketing lambs at the local abattoir (personal communication). This could be due to the market costs levied in the formal market if you do not sell a high number of lambs at any given time as well as transport costs. The Karoo farmers were also described as being more market orientated and selling their products to the abattoir. Sources of income were influenced by land ownership. The observed differences in land ownership could be explained by the enhanced financial stability of farmers receiving their income from salaries, enabling them to lease land in comparison to those farmers receiving income from grants/pension.

Sources of income also varied with district, with West Coast receiving most income from salaries and grants and Eden from crops and grants. This outcome can partly be explained by the reasons for keeping sheep, as some farmers indicated that they kept sheep for a hobby or cultural reasons, thus not necessarily to obtain income (see Chapter 3). This concurs with the study of Motiang & Webb (2016) who indicated that 55% of households relied on income from livestock and 47% from social grants. Farmers in the Mopeane-Rustenburg area also derived most of their income from off-farm sources of income (Schwalbach *et al.,* 2001). These farmers were only farming as a part-time activity, a scenario which also observed in West Coast where communal farming has been practiced for many generations.

The results above indicated that the variation in sources of income and sale outlets are due to differences in socio-economic aspects such as land ownership. The assumption that the West Coast district was mainly subsistence orientated (see Chapter 3) and the Karoo being more market-orientated were confirmed by the results of this study. The Eden district did not show any differences to the Karoo in terms of sale outlets. The different districts can be associated with different farming systems when considering the different sale outlets and sources of income.

Although the Karoo farmers were more market orientated in their sale-outlets and achieved the highest absolute number of lambs sold, they achieved lower lambing percentages than Eden and higher lambing percentage than West Coast. This could be due to their recent inclusion in the PLAS program and the need to grow their ewe flocks. Even though Eden district achieved the highest lambing percentage, their offtake rate was the lowest of the three districts. This could be due to losing lambs between birth and weaning. Unfortunately, no information was available on mortality rate in the flock, as this could have contributed to the low offtake rate observed in Eden district. The previous contention that livestock did not contribute to the income of smallholder farmers in the West Coast district does not seem to be borne out by these results. This contradiction could be related to the 14% of respondents who did not identify their main source of income.

Converting the average number of lambs sold to monetary terms, assuming that the price per kg/lamb is $5.2 /kg with an average carcass weight of 20kg, then the income per farming unit in each district will be $1033.2 for the Karoo and 728$ for both the West Coast and Eden districts per annum. Considering the costs involved in any farming operation these values are low and would not be able to sustain the livelihood of the farmers involved on their own. These income values amount up to $61 − $86 per month which is below the $280 minimum wage requirement, and under Table 4.1 is classified as poorly sustainable. Another study showed that

the annual income for smallholder farmers in Mopeane-Rustenburg amounted to $75-$149 per month for 42% of the respondents interviewed (Schwalbach *et al.,* 2001). These values were below the monthly income from livestock for smallholder farmers in the Karoo and higher than the income of smallholder farmers in both West Coast and Eden. The majority of South Africans indicated that their monthly expenditure was between $187 − $374 (Statistics South Africa, 2014). The income of smallholder farmers derived from livestock is therefore below the amount needed for monthly sustenance. This situation is economically unsustainable, as the farmer's livelihood cannot be solely secured from income of livestock.

The overall offtake reported for this study is higher than the offtake reported for communal sheep farmers in the Free State province (Spies & Cloete 2013) and lower than offtake rate for commercial farmers ranging between 77-91% (Snyman & Herselman, 2005) where offtake was calculated as the lambs weaned per 100 lambs born. Offtake as an indicator falls within category 3 as sustainable (Table 4.1). Offtake was independent of flock size because even though Karoo farmers had higher flock numbers their offtake did not differ significantly from the offtake of the West Coast farmers. The reason for this is that flock size has already been accounted for in the calculation of offtake rate. A study by Fourie & Cloete (1993) however, suggested that a larger flock at mating could result in lower output of lambs. This could be due to various reasons; including ram serving capacity that could be decreased in larger groups. Other factors that could also influence offtake rate are the breed used, whether or not the sheep received adequate nutrition, the age of the ewe and ram, as well as body condition of the ewe and ram. These factors were not accounted for in this study and a follow-up study is needed to determine the effects of these factors on smallholder offtake rates. Enkono *et al.* (2013) estimated an offtake rate of 6.1% for communal livestock farmers in Namibia. The offtake rate in the present study is higher than that observed by the latter author. This could be due to differences in farming practices, as well as in differences in how offtake rate was calculated.

4.5. Conclusions

The mean age of smallholder sheep farmers is a cause for concern as most farmers are above the age where farming is recommended as an occupation. This leaves the question of how sheep farming will be sustained in the long term and how to re-engage the interest of the youth in sheep farming. The percentage of farmers indicating their wealth status as poor is also of concern for the livelihood of these farmers and the long-term sustainability of smallholder sheep production in the Western Cape. The average offtake rate for smallholder farmers in the Western Cape was lower than commercial figures, and the income derived from livestock (calculated by the average number of lambs sold) is low and not economically sustainable. There is potential for income derived from livestock to increase if the average number of lambs sold can be increased, as seen in Karoo farmers. However, for income to be at a sustainable level, husbandry aspects (such as nutrition, breeding plan etc.) should be addressed, as well as other socio-economic and political issues. Addressing issues like age, gender imbalances and land ownership could have a positive influence on the overall sustainability of sheep farming systems in the Western Cape. The latter issues can be addressed by increasing awareness to the youth and women about career opportunities in animal husbandry. The creation of more platforms for training and education of youth and females in the field of agriculture is also necessary. This is a complex issue and will need innovation and collaboration in terms of how to make animal husbandry a promising and sustainable option for the future.

4.6. References

Aliber, M., 2009. Exploring Statistics South Africa's national household surveys as sources of information about household-level food security. Agrekon, Vol 48, pp 384-409.

Altman, M., Hart, T. & Jacobs, P., 2009. Household food security status in South Africa. Agrekon 48, 345-361.

Cloete, S.W.P. & Olivier, J.J., 2010. South African Sheep and Wool Industries. In: The International Sheep and Wool Handbook. Eds. D.J. Cottle, 95-112, Nottingham University Press.

Dossa, L.H., Rischkowsky, B., Birner, R. & Wollny, C., 2008. Socio-economic determinants of keeping goats and sheep by rural people in Southern Benin. Agric. Hum. Values. 25, 581-592.

Enkono, S.G., Kalundu, S.K. &Thomas, B., 2013. Analysis of factors influencing cattle off-take rate and marketing in Ndiyona constituency of Kavango region, Namibia. Journal of Agricultural Extension and Rural Development. 5, 201-206.

Grobler, H.J.F., 2010. Evaluation survey at extensive farms in the Central Karoo 2009. Agriprobe, June, 6-9.

Jahnke, H.E., Tacher, G., Keil, P. & Rojat, D., 1988. Livestock Production in Tsetse-Affected Areas of Africa. ILCA/ILRAD, Nairobi, Kenya 3–21.

Kosgey, I.S., Rowlands, G.J., Van Arendonk, J.A.M. & Baker, R.L., 2008. Small ruminant production in smallholder and pastoral/extensive farming systems in Kenya. Small Rumin. Res. 77, 11-24.

Manyong, A.M. & Degand, J., 1996. Sustainability of African smallholder farming systems: Case study of highland areas of central Africa. J. Sustain. Agric. 6, 17-42.

Mapiye, C., Chimonyo, M., Dzama, K., Raats, J.G. & Mapekula, M., 2009. Opportunities for improving Niguni cattle production in smallholder farming systems of South Africa. Livest. Sci. 124,196-204.

Marais, P.G., 2007. Evaluation of the genetic potential for growth and wool production of typical Transkei ewes and rams. Research report of the Grootfontein Agricultural

Development Institute, 2007. Private Bag x529, Middelburg 5900, South Africa. pp 33-34.

Meissner, H.H., Scholtz, M.M. & Engelbrecht, F.A., 2013. Sustainability of the South African Livestock Sector towards 2050 Part 2: Challenges, changes and required implementations. S. Afr. J. Anim. Sci. 43, 298-319.

Motiang, D.M. & Webb, E.C., 2016. The influence of household characteristics on cattle off-take rates in the North West Province of South Africa. Livest. Res. Rural Devel. 28, 6.

Otte, M.J. & Chilonda, P., 2002. Cattle and small ruminant production systems in Sub-Saharan Africa. A systematic review. FAO publishing, Rome.

Rust, T., Goosen, W.J. & Mbatsha, Z., 2015. Characterization of production outputs and ewe flock structure of communal wool sheep in Ngqolowa, Eastern Cape. Appl. Anim. Husb. Rur. Develop. 8, 6-18.

Rust, J.M. & Rust, T., 2013. Climate change and livestock production: A review with emphasis on Africa. S. Afr. J. Anim. Sci. 43, 255-267.

SAS, 2014. SAS Institute Inc. Cary, NC.

Schwalbach, L.M., Groenewald, I.B. & Marfo, C.B., 2001. A survey of smallholder cattle farming systems in the North West Province of South Africa. S. Afr. J. Anim. Sci. 31, 200-204.

Snyman, M.A. & Herselman, M.J., 2005. Comparison of productive and reproductive performance efficiency of Afrino, Dorper and Merino sheep in the False Upper Karoo. S. Afr. J. Anim. Sci. 35, 98-108.

Smith, B., 2006. Small Stock Production. In: The Farming Handbook. Eds. S. Hines, 196-236 University of Kwa-Zulu Natal Press.

Spies, D.C. & Cloete, P.C., 2013. Performance and marketing options for red meat in the formal and informal value chains in the Free State Province. 19th International Farm Management Congress, SGGW, Warsaw, Poland.

Statistics, South Africa. 2014. General household survey, 2013. Published by Statistics South Africa, Private Bag X44, Pretoria 0001. www.statssa.gov.za/publications/P0318/P03182013.pdf (accessed 12/04/2016)

Stroebel, A., Swanepoel, F.J.C. & Pell, A.N., 2011. Sustainable smallholder livestock systems: A case study of Limpopo Province, South Africa. Livest. Sci. 139,186-190.

Thamaga-Chitja, J.M. & Morojele, P., 2014. The context of smallholder farming in South Africa: Towards a livelihood asset building framework. J. Human Ecol. 45, 147-155.

Turner, H.N. & Young, S.S.Y., 1969. Chapter 16. The influence of flock structure on productivity. In: Quantitative Genetics in Sheep Breeding. Eds by Cornell University Press, Ithaca, New York.

Webb, E.C., 2015. Description of carcass classification goals and the current situation in South Africa. S. Afr. J. Anim. Sci. 35, 98-108.

Chapter 5

Genetic diversity and population structure of South African smallholder farmer sheep breeds determined using the OvineSNP50 beadchip

Abstract

A population structure study was performed on South African ovine populations using the OvineSNP50 beadchip. Blood samples were obtained from 295 sheep of which 172 had been identified as smallholder Dorpers, 4 as smallholder White Dorpers, 46 as purebred Dorpers, 26 as purebred South African Mutton Merinos and 47 as purebred Namaqua Afrikaners. Blood from the latter three breeds were obtained from a resource flock maintained on the Nortier research farm. Genetic diversity was estimated using allelic richness (A_r), observed heterozygosity (H_o), expected heterozygosity (H_e) and inbreeding coefficient (F). Population structure analysis was performed using fastSTRUCTURE to determine the breed composition of each genotyped individual. The Namaqua Afrikaner had the lowest H_e of 0.280 ± 0.18 while the H_e of smallholder Dorper, Dorper and South African Mutton Merino did not differ and were respectively 0.364 ± 0.13, 0.332 ± 0.16 and 0.329 ± 0.17. The average inbreeding coefficient was highest for the pure breeds, Namaqua Afrikaner, Dorper and South African Mutton Merino compared to the average inbreeding coefficient for the smallholder Dorper population. The smallholder Dorper population was introgressed with Namaqua Afrikaner, South African Mutton Merino and White Dorper germplasm. Similarly, the smallholder Dorper population was more genetically diverse compared to purebred Dorper, South African Mutton Merino and Namaqua Afrikaner sheep from the research farm. The higher genetic diversity among the smallholder sheep may be advantageous for their fitness and can be used to facilitate selective breeding.

5.1. Introduction

Some of the major sheep breeds kept by smallholder farmers include Dorper, Merino, Namaqua Afrikaner and Damara sheep. The Dorper is a composite breed derived from an initial cross between Black headed Persian and Dorset Horn sheep in the early 1900's and is widely farmed in the arid and semi-arid environments of South Africa. This is because of the ability of Dorpers to grow and reproduce well in harsh environments (Milne, 2000). The Namaqua Afrikaner is one of the oldest indigenous breeds in South Africa (Ramsay *et al.,* 2001). The breed was associated with the nomadic Nama people between 200 to 400 AD in the harsh dry areas of the North-Western Cape and Southern Namibia. The Namaqua Afrikaner is adapted to harsh environments (Snyman *et al.,* 2005) and is currently listed as an endangered breed (Qwabe *et al.,* 2013). The South African Mutton Merino was derived from the German Merino and was selected for both wool and meat production (Schoeman *et al.,* 2010).

Smallholder sheep farmers in South Africa possess flocks with a low reproductive performance (Grobler 2010; Marais 2007). This may be due to many factors, including nutrition, management, ambient temperature as well as genetics. Genetics however play an important role in establishing permanent change that can be sustainable in the long term by improving traits related to robustness. Robustness traits are important for the low-input farming systems employed by smallholder farmers and are likely to become more important as the effects of climate change in Southern Africa become more evident (Nardone *et al.,* 2010). Smallholder sheep farmers, however, do not have formal breeding programs to genetically improve their breeds. The genetic population structure of smallholder flocks is generally unknown as uncontrolled crossbreeding of different breeds is frequently practiced (Gizaw *et al.,* 2014).

Methods that are frequently used to analyse population structure include principal component analysis (PCA) based methods and model-based methods such as STRUCTURE (Pritchard *et al.,* 2000), ADMIXTURE (Alexander *et al.,* 2009) and fastSTRUCTURE (Raj *et al.,* 2014).

Principal component analysis constructs low-dimensional projections of data and decomposes the variance-covariance structure among sample genotypes into independent contrasts. The disadvantage of PCA is that it may be difficult to interpret estimates of the global ancestry of the sampled individuals based upon their projection coordinates (Novembre & Stephens 2008). Model-based methods use a Bayesian framework and compute global ancestry estimates as the posterior distributions of population membership. Limitations to STRUCTURE include a lengthy convergence time for large genotype datasets and fastSTRUCTURE was developed to increase the speed of inference and achieve accuracies comparable to those produced by STRUCTURE and ADMIXTURE (Raj *et al.,* 2014).

It is important to know the genetic structure of a breeding population to provide sound breeding advice. Due to the existing unstructured breeding strategies it is possible that smallholder sheep flocks could either have high levels of inbreeding; or, if populations are sufficiently large and diverse, they could be completely outbred by random mating within a multi-breed context. Inbreeding or the level of genetic homozygosity in a population is inversely proportional to fitness and robustness in sheep (Ercanbrack & Knight 1991; Wiener et al. 1992; Van Wyk *et al.,* 2009; Leroy, 2014). Ensuring genetic diversity is important for increased robustness, as a reduction in genetic diversity can lead to a decrease in population means for fitness traits (Goddard, 2009). Sustainable levels of inbreeding would be below 20-25% as higher levels can putatively lead to inbreeding depression (Ercanbrack & Knight, 1991). Genetic diversity of sheep resources in South Africa have been studied using microsatellites (Buduram, 2004; Qwabe *et al.,* 2013), random amplified polymorphic DNA (RAPD) (Hlophe, 2011) and single nucleotide polymorphisms (SNPs) (Sandenbergh *et al.,* 2015). Population structure of these populations was assessed using STRUCTURE (Qwabe *et al.,* 2013) and PCA (Sandenbergh *et al.,* 2015). Low estimates of genetic diversity were obtained for the Namaqua Afrikaner breed using SNPs (Kijas *et al.,* 2009, Sandenbergh *et al.,* 2015) and microsatellites (Qwabe *et al.,*

2013). Literature has also reported the Dorper and SAMM to have relatively high levels of genetic diversity using SNPs (Sandenbergh *et al.,* 2015) as well as in the Merino breed which had the highest level of genetic diversity in a worldwide breed comparison (Kijas *et al.,* 2009). In contrast, studies using RAPD markers have shown the Merino (12%) and Dorper (24%) breeds to have lower levels of genetic diversity than indigenous Nguni sheep breeds (29%) (Hlophe, 2011). The contradictory results could be due the marker type used, as RAPD markers are less likely affected by ascertainment bias compared to SNP markers (Vignal *et al.,* 2002). No studies have yet been conducted to investigate the genetic composition of sheep obtained from smallholder farmers in the Western Cape, South Africa. Population structure analysis is also important for use in downstream genetic analyses such as genome wide association studies (Price *et al.,* 2006).

The objective of this study were to determine genetic diversity and population structure within the Dorper breed sampled from smallholder farmers in the Western Cape, South Africa relative to the Namaqua Afrikaner, Dorper and SAMM sheep obtained from the Nortier research farm situated in the same Province.

5.2. Materials and Methods

The sites of sample collection were Nortier research farm and the Ebenheaser smallholder community in the West Coast district. Nortier is located at 32º 5' 32.0833" S, 18º 18' 18.3000" E and Ebenheaser are located at 31º 35' 8.5856" S, 18º 14' 39.2442" E. Animals on both sites were maintained on natural shrub pastures typical of the region.

Blood samples from the smallholder sheep were collected from the jugular vein into EDTA vacutainer tubes from all animals and on blood cards for animals from the resource sheep flock. Ethical clearance was obtained from the Departmental Ethics Committee for Research on Animals (DECRA) approval numbers of R12/53 for smallholder flocks and R14/100 for the

resource flock from the Western Cape Department of Agriculture. DNA was extracted using a Purelink® Genomic DNA Mini kit (Thermo Fisher Scientific, Johannesburg, South Africa). The blood samples from the research farm were stored at -80 ℃ before being applied to blood cards and were then submitted for genotyping at GeneSeek (Lincoln, NE, USA). SNP genotyping was performed using the Illumina® OvineSNP50 Beadchip.

In this study, we focused on characterizing the genetic variation present within the Dorper, and Namaqua Afrikaner (Namafr) breeds. The Namaqua Afrikaner is a fat-tailed breed and is used in this study to represent fat-tailed indigenous sheep breeds. The South African Mutton Merino (SAMM) will be used to represent the Merino type breeds. The total number of sampled sheep was 295 and of the 176 smallholder sheep, 172 were identified by the owners as Dorpers (Dorpersm) and 4 as White Dorpers. Sheep selected from the smallholder flock were breeding ewes, with ages ranging from 1 year to 6+ years. Sheep sampled from the Nortier research flock were identified as 46 purebred Dorpers, 26 purebred SAMM and 47 purebred Namafr. Unrelated ewes were selected from the research farm flock, ranging in age from 2 years to 6+ years.

Genotypic data were analysed using PLINK (Purcell *et al.,* 2007). The number of polymorphic SNPs and average MAF were derived for each of the sampled breed groups using PLINK. Quality control was performed on the data for all of the genetic groups simultaneously with filtering thresholds set to 5% for minor allele frequency, Hardy Weinberg Equilibrium at $P < 0.001$, and 95% genotype call rate per animal. After filtering 43,500 SNPs were retained and used in the analyses. Genetic diversity was estimated using observed heterozygosity (H_o), expected heterozygosity (H_e) and allelic richness (A_r). Inbreeding coefficients, F, were estimated using PLINK based on the observed versus expected proportions of homozygous genotypes. An ANOVA was fitted to examine differences between the inbreeding coefficients of animals from the research and smallholder farms, as well as to determine differences

between the breeds for inbreeding levels. Allelic richness (A_r) was estimated using ADZE (Szpiech *et al.,* 2008). A principal component analysis was performed using the SNPRelate package in R (Zheng *et al.,* 2012) to visualise the clustering of animals by breed types. Population structure analyses were performed using fastSTRUCTURE (Raj *et al.,* 2014) to determine the breed composition of members of the resource and smallholder flocks. The choice for the number of *K* was made by using two criteria: 1) model complexity that maximizes the marginal likelihood, and 2) model components used to explain structure in the data. For this study, $K = 4$ produced the highest average marginal likelihood and was used to represent the number of ancestral populations.

5.3. Results

The percentages of polymorphic SNPs were 76%, 77%, 66% and 81% for the Dorper, SAMM, Namafr and Dorpersm respectively. Average minor allele frequencies (MAF) were 0.258, 0.249, 0.218 and 0.279 for the Dorper, SAMM, Namafr and Dorpersm, respectively. The Namaqua Afrikaner ranked the lowest for genetic diversity with a $H_e = 0.280$ and the Dorpersm ranked the highest with $H_e = 0.364$ (Table 5.1). The Dorpersm had the highest allelic richness ($A_r = 1.976$) and the Namafr the lowest ($A_r = 1.799$). The average inbreeding coefficients differed between the smallholder and resource flock animals with the research farm animals attaining a higher average inbreeding coefficient of 0.13 ± 0.008 relative to animals on the smallholder farms with an average inbreeding coefficient of 0.04 ± 0.003. Average inbreeding was also estimated for the different genetic groups and the Dorpersm (0.034 ± 0.042) populations had the lowest inbreeding coefficients compared to the Dorper (0.074 ± 0.047), SAMM (-0.050 ± 0.046) and Namafr (0.237 ± 0.054) (Table 5.1).

Table 5.1 Genetic diversity statistics (±s.d.) for the sheep in the smallholder flock(s) (Dorpersm) relative to pure breeds from the Nortier resource flock (Dorper, SAMM and Namafr).

	Dorper	Dorpersm	SAMM	NamAfr
Sample size	46	172	25	47
Polymorphic SNP	40,954	43,777	42016	35,678
Polymorphic %	76%	81%	77%	66%
Mean MAF	0.258	0.279	0.249	0.218
H_e	0.332 ± 0.160	0.364 ± 0.131	0.270 ± 0.206	0.280 ± 0.183
H_o	0.348 ± 0.190	0.368 ± 0.142	0.351 ± 0.328	0.295 ± 0.222
F_{is}	0.074 ± 0.047	0.034 ± 0.042	-0.050 ± 0.046	0.237 ± 0.054
A_r	1.897 ± 0.001	1.976 ± 0.001	1.789 ± 0.001	1.799 ± 0.001

He – Expected heterozygosity, Ho – Observed heterozygosity, Fis –Inbreeding coefficient, Ar –Allelic richness

The first and second principal components accounted for 8.86% and 5.99% of the variation within the samples, whereas the third principal component accounted for 1.84% of the variation. The first and second principal components (Figure 4.1A) indicated that the majority of the Dorpers from the smallholder farmers (Dorpersm – red colour) clustered in the same group as the Dorpers (black colour) from the research farm. The White Dorper (turquoise colour) also clustered within the Dorper cluster. The Namafr and SAMM clustered into distinct groups. The first and third principal component analysis (Figure 4.1B) reveals the dispersion within the Dorper, Dorpersm and White Dorper populations.
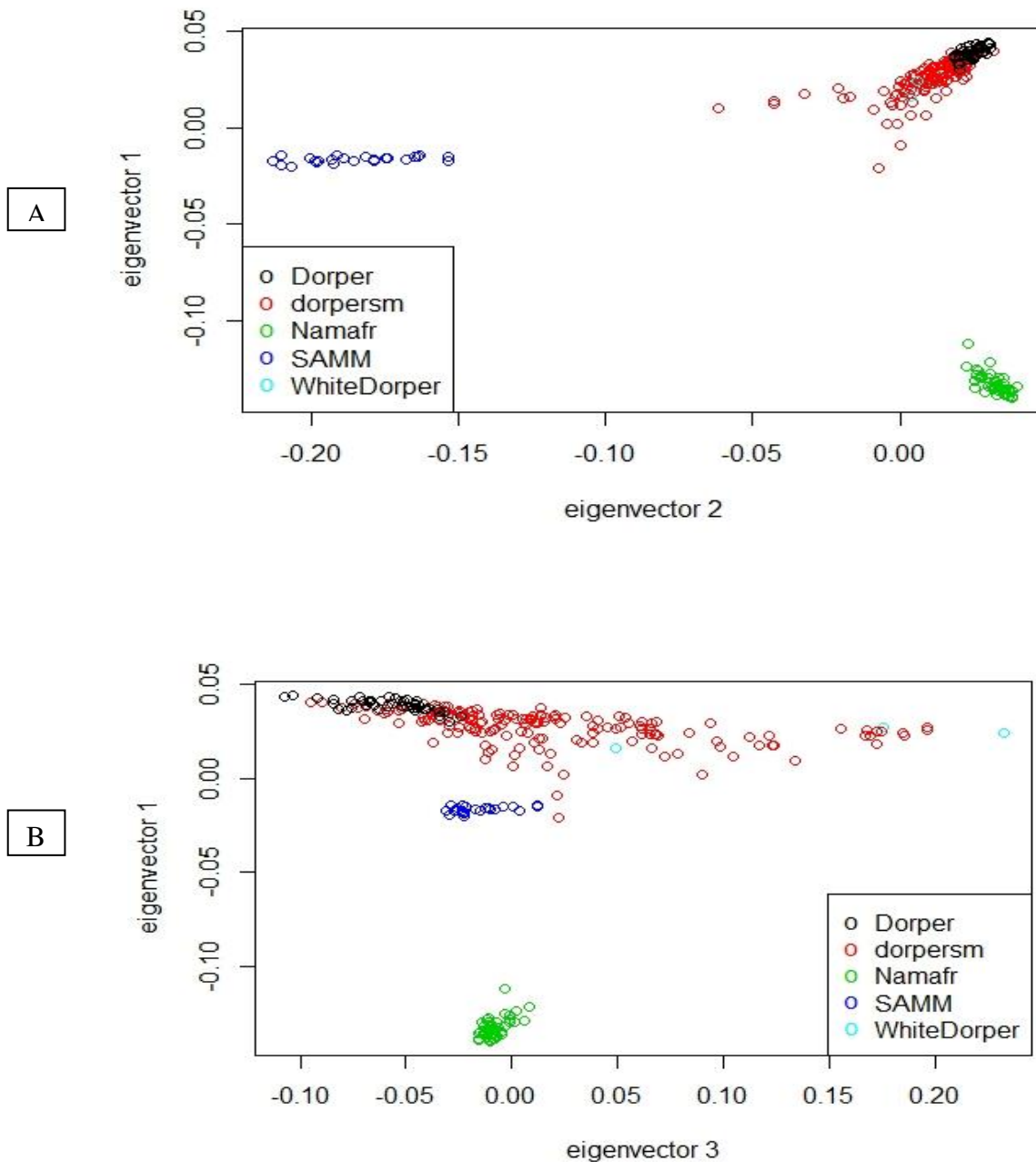
Figure 5.1. Scatter-plots depicting A) Principal component 1 vs. Principal component 2 and B) Principal component 1 vs. Principal component 2 for the Dorper (resource flock), South African Mutton Merino (SAMM - resource flock), Namaqua Afrikaner (Namafr – resource flock), Dorpersm (smallholder flock), White Dorper (WhiteDorper-smallholder flock).

Figure 5.2 shows the ancestry of sheep from smallholder farmers, and admixture is apparent within these flocks. At $K = 4$ the first population (light blue) represents the Dorpers from Nortier farm, the second population the Dorpers from smallholder farms, the third the Namaqua

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Afrikaner (green), the fourth population the South African Mutton Merino (dark blue) and the fifth population the four White Dorper (red) sheep from smallholder farms. The results infer that the Dorper, SAMM and Namafr from Nortier are purebred. The Dorpers from the smallholders has 24% White Dorper, 2% Namaqua Afrikaner and 2% SAMM ancestry (Table 4.2).
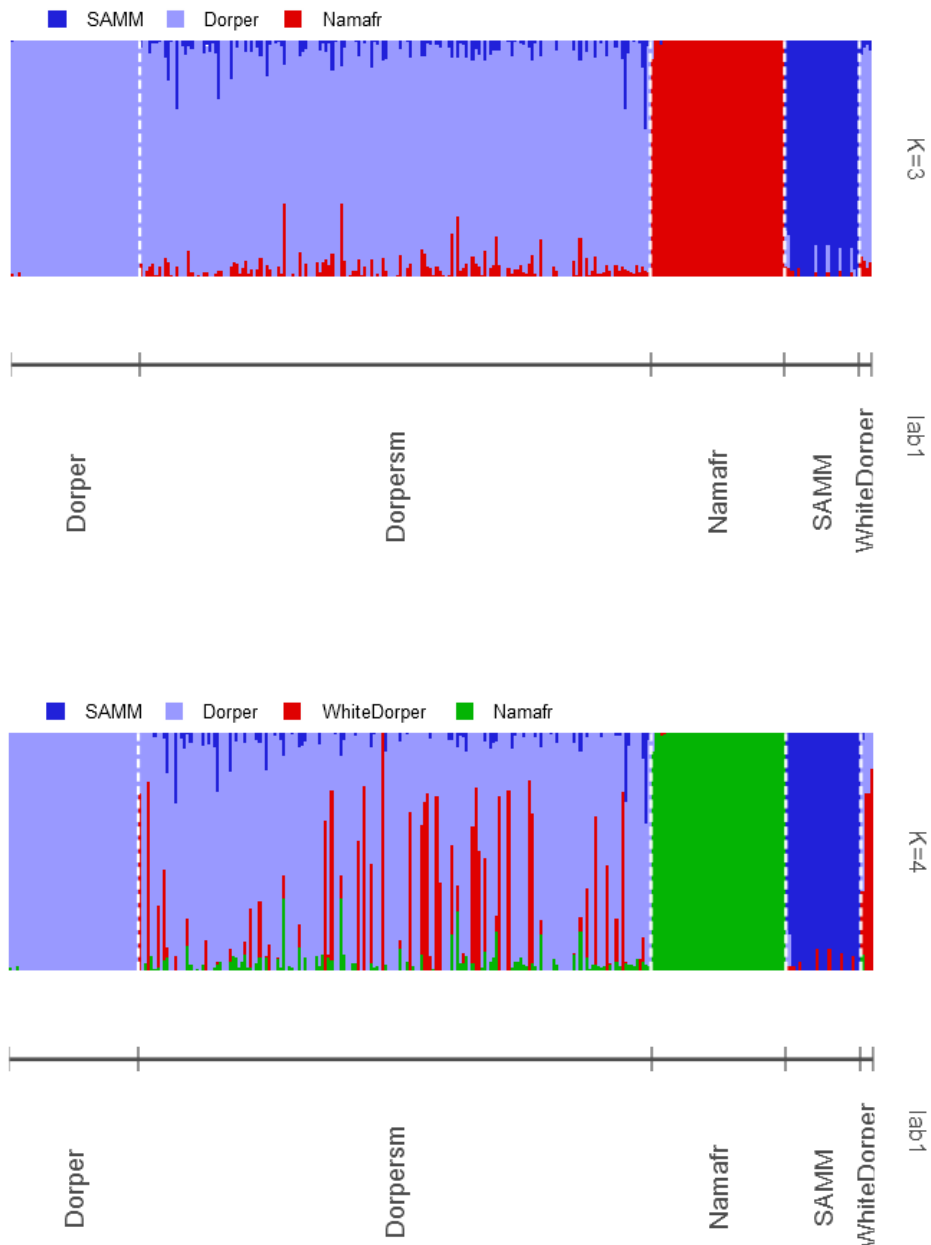
Figure 5.2. FastStructure plots depicting the proportion of ancestry for ovine populations from *K*=3 until *K*=4 ancestral genepools inferred with the FastStructure program

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Table 5.2. FastSTRUCTURE results for average breed composition per sampled group

Sampled Group	Predicted Breed Composition			
	Namafr	SAMM	WDorper	Dorper
Dorpersm	0.022	0.022	0.241	0.715
Dorper	0.001	0.000	0.000	0.999
White Dorper	0.016	0.007	0.652	0.325
Namaqua Afrikaner	0.998	0.000	0.000	0.001
SAMM	0.000	0.972	0.017	0.011

5.4. Discussion

This the first study to report on the genetic diversity of smallholder sheep in South Africa utilising SNP genotyping information. Genetic diversity studies conducted for sheep in South Africa have previously relied primarily on the use of microsatellites and RAPD markers (Hlope, 2011; Soma *et al.,* 2012, Qwabe *et al.,* 2013). The use of SNP genotype data to investigate genetic diversity and population structure in South African sheep flocks has previously focused on commercial/resource flocks (Sandenbergh *et al.,* 2015), and other studies have included goats (Visser *et al.,* 2016) and beef cattle (Zwane *et al.,* 2016).

The number of polymorphic SNPs within a population is important for future genome-wide association studies, as this will determine the suitability of the specific SNP panel for genome-wide association studies within a specific population. The Dorpersm had the highest number of polymorphic SNP suggesting that this array could be utilised for smallholder Dorpers for association studies, provided phenotypic data are available for traits of interest. The percentage of polymorphic SNPs for this study was 76% for SAMM and 66% for Namafr, which concurs with literature indicating a higher rate of SNP polymorphisms for Merino-type breeds compared to the Namafr (Kijas *et al.,* 2009).

The average MAF was lower for the Namafr suggesting either a lower genetic diversity for this breed, or a greater genetic distance from the discovery breeds used to identify common SNPs for inclusion on the assay. The Namaqua Afrikaner had lower levels of genetic diversity with the lowest H_e and highest inbreeding levels of all of the breeds, suggesting that inbreeding in conjunction with a small population size has resulted in a loss of variation within the breed. This low diversity was previously also reported in other studies using microsatellites (Buduram, 2004, Qwabe *et al.,* 2013) and SNP panels (Kijas *et al.,* 2009; Sandenbergh *et al.,* 2015). The breed was originally sourced from the conservation flock at Carnarvon Experimental Station as described by Qwabe *et al.* (2013). There is an estimated number of 2000 Namaqua Afrikaner sheep in South Africa with two conservation flocks consisting of 100 ewes each (Snyman, 2014), thus the effective population size for the Namaqua Afrikaner sheep used in this study is small. The results could also be influenced by SNP ascertainment bias in the development of the Ovine SNP50 beadchip, since the Namafr and other African fat-tailed breeds were underrepresented among the breeds used for the development of the chip (Kijas *et al.,* 2012; Sandenbergh, 2015). Estimates of H_e for the Dorper and SAMM agree with literature estimates that indicate high levels of genetic diversity for these breeds (Kijas *et al.,* 2009). Allelic richness for the Dorper was similar to literature estimates of 1.828 but, for the Namafr, allelic richness in this study exceeded the value of 1.576 reported by Kijas *et al.* (2009). This could be due to the use of a larger SNP panel in this study as well as to the origin of the Namaqua Afrikaner samples used in the latter study.

The Dorpersm had the highest genetic diversity of all the breeds as assessed by all the diversity parameters. The higher genetic diversity observed in the smallholder Dorper sheep can be attributed to admixture of these animals with other breed types. The population structure analysis suggested introgression of the Dorpersm with indigenous fat-tailed breeds such as the Namafr as well as wool types, here represented by the SAMM. These results confirm the

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assumption that smallholder sheep populations are genetically more diverse than purebred sheep populations and this stems from ancestral crossbreeding. The analyses could not verify whether these results reflect recent or historical admixture among the breeds. The Dorpersm and the White Dorper clustered into the same group as purebred Dorpers in the PCA. The Dorpersm population consisted out of purebred Dorpers as depicted from the fastSTRUCTURE results. There are, however, other Dorper-derived animals that contain germplasm from fat-tailed and/or wool breeds. Namafr and SAMM ewes from the research farm clustered into distinct groups, which was expected as these were purebred populations. Comparing the differences between farms, the smallholder farms had lowest inbreeding levels, which was also expected since the breeding program at the research farm was expected to accumulate inbreeding. The level of inbreeding in smallholder sheep populations and purebred Dorper and SAMM ewes is below 20% which is a sustainable level of inbreeding to have in a sheep flock. The inbreeding in the Namafr (24%) reaches the level of being unsustainable.

5.5. Conclusions

The high genetic diversity is favourable for the smallholder sheep as it can facilitate rapid genetic change if a coherent selection strategy is formulated based on heritable traits of economic relevance. The Namaqua Afrikaner as an indigenous breed to South Africa has an important role to play in smallholder farming systems, as it is able to survive and reproduce in low input systems. Introgression of Dorpers with Namaqua Afrikaner (fat-tailed breeds) and South African Mutton Merino have been confirmed in this study. The Namaqua Afrikaner (and other fat-tailed sheep breeds) are commonly used in smallholder sheep systems and thus the low genetic diversity observed in the Namaqua Afrikaner is of some concern for the future of this breed as a genetic resource. Strategies to mitigate this may include a structured rotation plan between the conservation flocks that are currently being maintained in South Africa as described by Qwabe *et al.* (2013). These conservation flocks were found to be distinct

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populations from one another (Qwabe *et al.,* 2013) and thus could be used to source unrelated animals from the breed to assist in reducing inbreeding and increasing diversity. Alternatively, crossing the Namaqua Afrikaner with other adapted breeds could retain those adaptive traits characteristic of the breed in crossbred progeny, while also assimilating advantages such as an improved growth rate and improved carcass composition derived from the other parent. To take advantage of such a system on the commercial and smallholder level, purebred populations of the Namaqua Afrikaner need to be maintained.

5.6. References

Alexander, D.H., Novembre, J. & Lange, K., 2009. Fast model-based estimation of ancestry in unrelated individuals. Genome Res.19, 1655-1664.

Buduram, P., 2004. Genetic characterization of South African sheep breeds using DNA markers. M.Sc. thesis. University of Free State. South Africa.

Ercanbrack, S.K. & Knight, A.D., 1991. Effects of inbreeding on reproduction and wool production of Rambouillet, Targhee, and Columbian ewes. J. Anim. Sci. 69, 4734-4744.

Gizaw, S., Van Arendonk, J.A.M., Valle-Zarate, A., Haile, A., Rischkowsky, B., Dessie, T. & Mwai, A.O., 2014. Breeding programmes for smallholder sheep farming systems: II. Optimization of cooperative village breeding schemes. J. Anim. Breed. Genet. 131, 350-357.

Goddard, M., 2009. Fitness traits in animal breeding programs, in: Adaptation and fitness in farm animal populations: Evolutionary and breeding perspectives on genetic resource management. Eds. Van der Werf, J., H.-U. Graser, R., Frankham, & C., Gondro, 41-52 Springer Science & Business Media.

Grobler, H.J.F., 2010. Evaluation survey at extensive farms in the Central Karoo 2009. Agriprobe, June, 6-9.

Hlophe, S.R., 2011. Genetic variation between and within six selected south African sheep breeds using random amplified polymorphic DNA and protein markers, Master's thesis, University of Zululand, South Africa.

Kijas, J.W., Townley, D., Dalrymple, B.P., Heaton, M.P., Maddox, J.F., McGrath, A., Wilson, P., Ingersoll, R.G., McCulloch, R., McWilliam, S.,Tang, D., McEwan, J., Cockett, N., Oddy, V.H., Nicholas, F.W. & Raadsma, H., for the International Sheep Genomics Consortium. 2009. A genome wide survey of SNP variation reveals the genetic structure of sheep breeds. PLoS One 4, e4668.

Kijas, J.W., Lenstra, J.A., Hayes, B., Boitard, S., Porto Neto, L.R, San Cristobal, M., Servin, B., McCulloch, R., Whan, V., Gietzen, K., Paiva, S., Barendse, W., Ciani, E., Raadsma, H., McEwan, J., Dalrymple, B. & the International Sheep Genomics Consortium Members. 2012. Genome-wide analysis of the world's sheep breeds reveals high levels of historic mixture and strong recent selection. PLoS Biol 10, e1001258.

Leroy, G., 2014. Inbreeding depression in livestock species: review and meta-analysis. Anim. Genet. 45, 618-628.

Marais P.G., 2007. Evaluation of the genetic potential for growth and wool production of typical Transkei ewes and rams. Research report of the Grootfontein Agricultural Development Institute, 2007. Private Bag x529, Middelburg 5900, South Africa. p. 33-34.

Milne, C., 2000. The History of the Dorper. Small Rumin. Res. 36, 99-102.

Nardone, A., Ronchi, B., Lacetera, N., Ranieri, M. S. & Berrabucci, U., 2010. Effects of climate change on animal production and sustainability of livestock systems. Livest. Sci.130, 57-69.

Novembre, J. & Stephens, M., 2008. Interpreting principal components analyses of spatial population genetic variation. Nature Genet. 40, 646-649.

Price, A.L., Patterson, N.J., Plenge, R.M., Weinblatt, M.E., Shadick, N.A & Reich, D., 2006. Principal components analysis corrects for stratification in genome-wide association studies. Nature Genet. 38, 904-909.

Pritchard, J.K., Stephens, M. & Donnelly, P., 2000. Inference of population structure using multilocus genotype data. Genet. 155, 945-949.

Purcell, S., Neale, B., Todd-Brown, K., Thomas, L., Ferreira, M.A.R., Bender, D., Maller, J., Sklar, P., De Bakker, P.I.W., Daly, M.J. & Sham, P.C., 2007. PLINK: a toolset for whole-genome association and population-based linkage analysis. Amer. J. Hum. Genet. 81, 559-575.

Qwabe, S.O., Van Marle-Köster, E. & Visser, C., 2013. Genetic diversity and population structure of the endangered Namaqua Afrikaner sheep. Trop. Anim. Health Prod. 45, 511-516.

Raj, A., Stephens, M. & Pritchard, J.K., 2014. fastSTRUCTURE: Variational inference of population structure in large SNP data sets. Genet. 197, 573-589.

Ramsay, K. H., Harris, L. & Kotze, A., 2001. Landrace breeds: South Africa's indigenous and locally developed farm animals. Publication Farm Animal Conservation Trust, ISBN: 0-620-25493-9.

Sandenbergh, L., 2015. Identification of SNPs associated with robustness and greater reproductive success in South African Merino using SNP chip technology. PhD thesis. University of Stellenbosch, South Africa

Sandenbergh, L. Cloete, S.W.P. Roodt-Wilding, R., Snyman, M.A. & Van der Merwe, A.E., 2015. Genetic diversity and population structure of four South African sheep breeds. Proc. Assoc. Advmt Breed. Genet. 21, 294-297.

Schoeman, S.J., Cloete, S.W.P. & Oliver, J.J., 2010. Returns on investment in sheep and goat breeding in South Africa. Livest. Sci. 130, 70-82.

Snyman, M. A., Buys, T. & Jonker, M. L., 2005. Production and reproduction performance of Namaqua Afrikaner sheep. 6th Global Conference on the Conservation of Domestic Animal Genetic Resource, Magalies Park, South Africa, 9-13 October

Snyman, M.A., 2014. South African sheep breeds: Namaqua Afrikaner. Info-pack ref. 2014/023. Grootfontein Agricultural Development Institute.

Soma, P., Kotze, A., Grobler, J.P. & Van Wyk, J.B., 2012. South African sheep breeds: Population genetic structure and conservation implications. Small Rumin. Res.103, 112–119.

Szpiech, Z.A., Jakobsson, M. & Rosenberg, N.A., 2008. ADZE: a rarefaction approach for counting alleles private to combinations of populations. Bioinformat. 24, 2498-2504.

Van Wyk, J.B., Fair, M.D. & Cloete, S.W.P., 2009. Case study: The effect of inbreeding on the production and reproduction traits in the Elsenburg Dormer sheep stud. Livest. Sci. 120, 218-224.

Vignal, A., Milan, D., Sancristobal, M. & Eggen, A., 2002. A review on SNP and other types of molecular markers and their use in animal genetics. Genet. Sel. Evol. 34, 275-305.

Visser, C., Lashmar, S.F., Van Marle-Köster, E., Poli, M.A. & Allain, D. 2016. Genetic diversity and population structure in South African, French and Argentinian Angora Goats from Genome-Wide SNP data. PLOS One 11, 0154353.

Wiener, G., Lee, G.J. & Wooliams, J.A., 1992. Effects of rapid inbreeding and crossing of inbred lines on the body weight growth of sheep. Anim. Prod. 55, 89-99.

Zheng, X., Levine, D., Shen, J., Gogarten, S.M., Laurie, C. & Weir, B.S., 2012. A high-performance computing toolset for relatedness and principal component analysis of SNP data. Bioinformat. 28, 3326-3328.

Zwane, A.A., Maiwashe, A., Makgahlela, M.L., Choudbury, A., Taylor, J.F. & Van Marle-Köster, E., 2016. Genome-wide identification of breed-informative single-nucleotide

polymorphisms in three South African indigenous cattle breeds. S. Afr. J. Anim. Sci. 46, 302-311.

Chapter 6

Genome-wide association study for wet-dry phenotype in smallholder ovine populations in South Africa

Abstract

The aim of this study was to identify single nucleotide polymorphisms (SNPs) associated with genomic region underlying variation in the binomial reproductive trait 'wet-dry' in sheep. The wet-dry phenotype was used to represent the reproductive status of the ewes, divided into two categories, dry (ewes that did not lamb or that lost a lamb) and wet (ewes that had lambed and had at least one suckling lamb). Wet-dry records were obtained from smallholder farmers (n = 176) and Nortier Research Farm (n = 131) for the 2014 breeding season. Ages of the ewes ranged from 1 year to 6+ years. Data from 307 individuals were analysed, of which 172 Dorpers and 4 White Dorpers were from smallholder sheep flocks and 48 Dorpers, 46 Namaqua Afrikaners, 26 South African Mutton Merinos, 4 South African Mutton Merino x Dorper and 7 Dorper x South African Mutton Merino crossbreds were from the research farm. A logistic regression model was fitted to adjust the data for the fixed effects of farm, breed, and age of the ewe and weight at mating as a covariate. Linkage disequilibrium (LD) and inbreeding coefficient were estimated using PLINK. Association analysis was performed using the genome-wide efficient mixed-model association package (GEMMA) to determine whether any significant SNPs were associated with the wet-dry reproductive trait. The wet-dry phenotype differed significantly between the smallholder (0.63 ± 0.04) and research farm flocks (0.79 ± 0.04). Genome-wide LD across all populations was $r^2 = 0.36$. Dorpers from the smallholder flock exhibited rapid LD decay versus the resource ovine populations. Inbreeding levels were also lower for the smallholder flock ($4 \pm 0.003\%$) versus the research flock ($13 \pm 0.008\%$). No

significant SNPs were identified after correction for false discovery rate. The heritability estimate for wet-dry using SNP information was 0.24. This estimate concurs with the literature and indicates the possibility of using genomic selection to improve reproduction in smallholder sheep flocks

6.1. Introduction

Smallholder sheep farmers in South Africa have been reported to have flocks with low reproductive performance (Marais, 2007; Grobler, 2010). This may be owing to many factors, including nutrition, management and genetics. Genetic selection plays an important role in establishing permanent change that is sustainable for the long term in improving traits related to fitness. Fitness traits are linked to the reproduction of animals and can be measured with various indicator traits. Reproduction can be measured by composite traits such as number of lambs born per ewe lifetime or the number of lambs weaned per ewe lifetime, or by components traits such as litter size, fertility, conception rate and mothering ability (Zishiri *et al*., 2013). Quantifying and measuring fitness traits in smallholder production systems can be challenging owing to a lack of recordkeeping. It is therefore necessary to use easy-to-measure indicator traits that involve minimal recordkeeping and input costs.

In Chapter 2, under section 2.5 we discussed the genetic traits important for sustainability under which the wet-dry phenotype were mentioned. The wet-dry phenotype (Fourie & Cloete, 1993) is recorded from an udder examination performed during the marking of recently born lambs or at the weaning of lambs. Wet-dry refers to whether a ewe is lactating or not, and can be used as an indicator of reproductive performance of ewes in low-input farming systems. The wet-dry phenotype is a composite trait and includes conception rate and mothering ability. Heritabilities have yet to be estimated for this trait in South Africa. Heritabilities have previously been estimated for Australian Merino flocks and range from 0.09 to 0.17 for wet-

dry recorded at weaning and 0.04 to 0.11 when recorded at lamb marking (Lee *et al*., 2010). Heritability estimates for the component conception rate/fertility traits range from 0.01 to 0.30 (Iniguez *et al*., 1986; Tosh *et al*., 2002; Vatankhah *et al*., 2006; Piwczynski & Kowaliszyn, 2013). Wet-dry is therefore an easy to measure trait that can be recorded in smallholder sheep farming systems as a proxy for reproduction. The underlying genetic regulation of reproduction has not been fully elucidated. However, some genes that influence fecundity and oestrous cycle in sheep have been identified. Genes affecting litter size in sheep include the *BMPR1B/FecB* mutation on chromosome 6, *GDF9* on chromosome 5 and *BMP15* on the X chromosome (Montgomery *et al*., 2001; Souza *et al*., 2001; Davis, 2004; Juengel *et al*., 2004; McNatty *et al*., 2005; Polley *et al*., 2010). Genes influencing the oestrous cycle include *PGFS* (*AKR1B5*/*AKR1C3*), *PGES*, *PGFR,* and *PTGS2* (Kumar *et al*., 2013). Genotyping using SNPs makes it possible to investigate population structure and establish pedigree relationships among animals. Linkage disequilibrium (LD) in a population is important to consider for genome-wide association studies (GWAS). This is because LD is the ability of an allele from one marker to predict the allelic status of another marker (Meadows *et al*., 2008). A preliminary genome-wide association study was conducted to investigate whether the wet-dry phenotype was influenced by variation in any of these genes. If indications of associations were found, then these genes could be further investigated to identify variants that could be used in marker-assisted selected programmes to improve reproduction in smallholder farming operations.

The aim of this study therefore was to identify SNPs associated with quantitative trait loci (QTL) underlying variation in the binomial wet-dry reproductive trait.

6.2. Materials and methods

The sites of sample collection were Nortier Research Farm and the Ebenheaser smallholder community in Western Cape, South Africa. Ethical clearance was obtained from the

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Departmental Ethics Committee for Research on Animals (DECRA), namely approval numbers R12/53 for smallholder flocks and R14/100 for the resource flock from the Western Cape Department of Agriculture. Nortier is located at 32º 5' 32.0833" S, 18º 18' 18.3000" E. Ebenheaser is located at 31º 35' 8.5856" S, 18º 14' 39.2442" E. These farms are located in the West Coast district and are classified under the Succulent Karoo Biome, described by Acocks (1988). The succulent Karoo consists mainly of succulent plants and is a winter rainfall area. The altitude ranges from sea level to 1500 m and the mean annual rainfall is between 20 and 350 mm. A winter lambing season was implemented, and wet-dry data were collected after the lambing season in July–August 2014. The wet-dry phenotype was used to represent the reproductive status of the ewes. The ewes were divided into two categories: dry (ewes that did not lamb, or that lost all their lamb(s) and were thus not lactating) and wet (ewes that had lambed and were suckling one or more lambs). Wet-dry records were obtained from smallholders (n = 176) and the resource flock at Nortier Research Farm (n = 131) for the 2014 breeding season. The ages of the ewes ranged from 1 year to 6+ years. A logistic regression model was fitted in SAS (2012) to adjust the phenotypic data for the fixed effects of farm, breed, age of the ewe and mating weight as a covariate. The sheep sampled from the smallholder farms were identified in a fastSTRUCTURE analysis (Raj *et al*., 2014) as being 172 Dorpers (Dorpersm) and 4 White Dorpers. The sheep sampled from the research farm were identified as 48 Dorpers, 46 Namaqua Afrikaners (Namafr), 26 South African Mutton Merinos (SAMM), 4 South African Mutton Merino x Dorper (SAMMDX) and 7 Dorper x South African Mutton Merino (DSAMMX) crossbreds.

The DNA samples were genotyped using the Ovine 50K SNP bead chip. Genotypic data were analysed using PLINK (Purcell *et al*., 2007). Data for 307 individuals were analysed. Quality control was conducted by setting thresholds for minor allele frequency at 5%, Hardy Weinberg Equilibrium at P <0.001, and genotype call rate per animal at 95%. The data were pruned

according to these criteria and 43 500 SNPs were retained and used in the analyses. Linkage disequilibrium and inbreeding coefficient were calculated with PLINK. Association analysis was performed using the genome-wide efficient mixed-model association package (GEMMA) (Zhou & Stephens, 2012), to determine whether any significant large-effect SNPs were associated with the wet-dry reproductive trait.

Breed proportions were fit as covariates, and the farm of origin (smallholder or research farms) was fit as a covariate in the model for the genotypic data. The genetic similarity matrix was estimated using GEMMA. A univariate linear mixed model was fit in GEMMA for testing marker associations with wet-dry accounting for population stratification and pedigree structure. Chip heritability was estimated as the proportion of the phenotypic variance explained by genotypes.

The model used was:

$$y = W\alpha + x\,\beta + \mu + \varepsilon \qquad \mu \sim MVN_n\,(0,\,\lambda_T^{-1}K)\ \text{and}\ \varepsilon \sim MVN_n\,(0,\,_T^{-1}I_n)$$

Where: y is an n-vector of binary trait values (1 for wet, 0 for dry) for the n individuals

$W = (w_1, \ldots, w_c)$ is an n x n matrix of covariate values corresponding to the fixed effects and including a column of 1s

α = is an c-vector of the corresponding fixed effect parameters including the intercept

x = n-vector of marker genotypes

β = effect size of the marker

μ = n-vector of random residual additive genetic effects

ε = is an n-vector of errors

$_T^{-1}$ = is the variance of the residual errors

λ = ratio of additive genetic to residual variance components

K is a known n x n relatedness matrix

I_n = is an n x n identity matrix

MVN_n = the n-dimensional multivariate normal distribution

R was used to plot the $-\log_{10}(P\text{-value})$ for each SNP genome-wide. Two methods were used to identify significant SNPs: i) using the P-value from the likelihood ratio test calculated using GEMMA; and ii) after adjusting the P-value to q-values using the q-value package in R (Storey & Tibshirani, 2003) to account for multiple testing. Identification of genes associated with significant SNPs was done using NCBI map viewer for *Ovis Aries* annotation release 102.

6.3. Results

The genome-wide LD across all populations was $r^2 = 0.36$. Average inbreeding was also estimated for the various breeds, namely 0.6% for the White Dorper, -7% for the DSAMMX, 1.2% for the SAMMDX, 3% for Dorpersm, 7% for the Dorper, 9% for the SAMM and 24% for the Namafr. Average inbreeding coefficient was $4 \pm 0.003\%$ for the smallholder flock and $13 \pm 0.008\%$ for the resource flock.
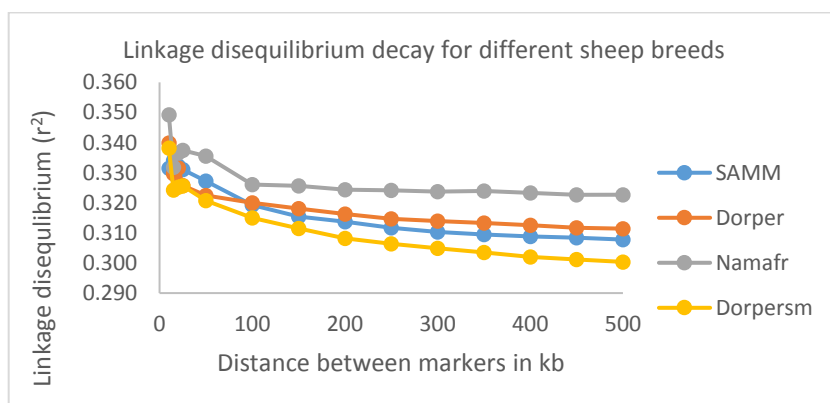
Figure 6.1 Linkage disequilibrium (r^2) decay with LD pruning within each breed

Farm significantly influenced the wet-dry phenotype. The proportion of wet ewes was significantly lower in the smallholder flocks (0.63 ± 0.04) relative to the research farm flocks (0.79 ± 0.04). Heritability estimated with the SNP information was $h^2 = 0.24 \pm 0.14$ with the genetic variance component explained by the model as 0.14 and the environmental variance as 0.098.

The genome-wide association study (Figure 6.2) suggests that SNP rs428728584 at 14,286,396 bp on chromosome 20 might be associated with wet-dry ($P < 0.0005$), uncorrected for false discovery rate (FDR). However, after adjusting for multiple testing using a q-value at an false discovery rate (FDR) level of 5%, no SNPs were found to be significantly associated with wet-dry phenotype.
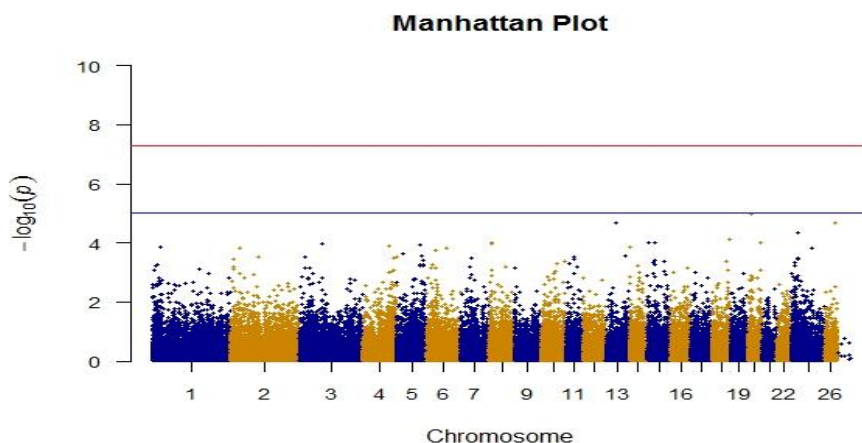
Figure 6.2 Manhattan plot indicating $-\log_{10}(P)$ values for single nucleotide polymorphisms associated with wet-dry phenotype

6.4. Discussion

The Dorpersm exhibited the most rapid LD decay with the Namafr breed achieving slower rates of decay as depicted in Figure 6.1. Similar inbreeding coefficients and LD levels for LD pruned within each breed have been estimated for the Nortier resource flock, with the Namafr exhibiting the highest level of inbreeding and slow LD decay because of its low effective population size (Sandenbergh *et al.*, 2015). The high negative inbreeding coefficient observed

for the DSAMMX might be because these crossbreds were F_1s and possessed higher levels of heterozygosity. The Dorpers and White Dorper obtained from smallholder flocks exhibited low levels of inbreeding in comparison to the purebred Dorper, SAMM and Namafr obtained from the resource flocks. This could be due to the willingness of smallholder farmers to crossbreed. The inbreeding levels for the purebred Dorper and SAMM are in line with literature estimates (Sandenbergh *et al*., 2015) and are as expected for close nucleus breeding schemes.

These results for wet-dry phenotype are consistent with those in the literature, ranging from 0.72 in Merino ewes to 0.80 for SA Mutton Merino ewes in the Bredasdorp region (Fourie & Cloete, 1993). Lee *et al*. (2010) report heritability estimates of 0.09 to 0.17 for wet-dry at weaning and 0.04 to 0.11 for wet-dry at marking. The SNP heritibility estimate of the current study falls in the range of heritability estimates for conception rate (0.01 to 0.30) reported in the literature (Iniguez *et al*., 1986; Lee *et al*., 2009, Piwczynski & Kowaliszyn, 2013). The variation observed in heritability estimates is probably because of different methods used for estimation, and different variance components between breeds and production environments.

The high level of genome-wide LD, however, implies the possibility of identifying SNPs that form haplotype blocks that influence reproduction in sheep. Sandenbergh (2015) accordingly suggested that many loci of small to medium effect might influence the expression of reproduction traits in sheep. The different patterns of LD observed between the breeds implicate the number of markers that can be used for identification of QTL. The smallholder sheep had the shortest LD stretches and thus dense SNP marker panels should be used to identify significant SNPs. The genome-wide association analysis did not yield significant SNPs for wet-dry when a false discovery rate correction was applied to the SNP association *P*-values, which is because of the limited number of records available for this study.

6.5. Conclusions

The smallholder sheep flock exhibited low levels of inbreeding, which is promising for future genetic improvement in these populations. It is thus possible to use this approach to estimate additive genetic merit of animals in smallholder populations, allowing an opportunity for selection to improve genetic gain. Identifying causal variants related to the wet-dry phenotype, which is affordable and easy to measure in smallholder farming systems, could aid in improving the intensity of selection for this trait. This is the first study implicating the possible use of SNP data to investigate genetic structure in smallholder sheep populations in South Africa and to estimate a heritability estimate for wet-dry phenotype relevant to smallholder sheep farmers. The next step would be to improve the collection of phenotypic data and increase sample size for further genomic studies. The use of the Ovine SNP 600 K BeadChip or whole genome sequencing could also be of value for future studies.

6.5. References

Acocks, J.P.H., 1988. Veld types of South Africa. Memoirs of the Botanical Survey of South Africa, 57. SANBI, Pretoria.

Davis, G.H., 2004. Fecundity genes in sheep. Anim. Reprod. Sci. 82-83, 247-253.

Fourie, A.J. & Cloete, S.W.P., 1993. Reproductive performance of commercial Merino, Dohne Merino and SA Mutton Merino flocks in the Southern Cape. S. Afr. J. Anim. Sci. 23, 104-110.

Grobler, H.J.F., 2010. Evaluation survey at extensive farms in the Central Karoo 2009. Agriprobe, June, 6-9.

Iniguez, L.C., Quass, R.L. & Van Vleck, L.D., 1986. J. Anim. Sci. 63, 1769-1778.

Juengel, J.L., Bodensteiner, K.J., Heath, D.A., Hudson, N.L., Moeller, C.L., Smith, P., Galloway, S.M., Davis, G.H., Sawyer, H.R. & McNatty, K.P., 2004. Physiology of GDF9 and BMP15 signalling molecules. Anim. Reprod. Sci. 82-83, 447-460.

Kumar, R., Ramteke, P.W., Nath, A., Pramod, R.K., Singh, S.P., Sharma, S.K. & Kumar, S., 2013. Role of candidate genes regulating uterine prostaglandins biosynthesis for maternal recognition of pregnancy in domestic animals. ISRN Physiol., Hindawi Publishing, Volume 2013, article ID 854572, http://dx.doi.org/10.1155/2013/854572. pp.8

Lee, G.J., Atkins, K.D. & Sladek, M.A., 2009. Genetic parameters for lifetime reproductive performance of merino ewes. Proc. Assoc. Advmt. Anim. Breed. Genet. 18, 382-385.

Lee, G.J., Sladek, M.A. & Atkins, K.D., 2010. Selection criteria for within flock selection to improve reproduction efficiency. http://www.livestocklibrary.com.au/bitstream/handle/1234/33711/SheepCRC_2_87.pdf?sequence=1 (accessed 21/01/2016)

Marais, P.G., 2007. Evaluation of the genetic potential for growth and wool production of typical Transkei ewes and rams. Research report of the Grootfontein Agricultural Development Institute, 2007. Private Bag x529, Middelburg 5900, South Africa. pp. 33-34.

McNatty, K.P., Smith, P., Moore, L.G, Reader, K., Lun, S., Hanrahan, J.P., Groome, N.P., Laitinen, M., Ritvos, O. & Juengel, J.L., 2005. Oocyte-expressed genes affecting ovulation rate. Mol. Cell. Endocrinol. 234, 57-66.

Meadows, J.R.S., Chan, E.K.F. & Kijas, J.W. 2008. Linkage disequilibrium compared between five populations of domestic sheep. BMC Genet. 9, 61-71.

Montgomery, G.W., Galloway, S.M., Davis, G.H. & McNatty, K.P., 2001. Genes controlling ovulation rate in sheep. Reprod. 121, 843-852.

Piwczynski, D. & Kowaliszyn, B., 2013. Heritability and breeding value of sheep fertility estimated by means of GIBBS sampling method using linear and threshold models. J. Cent. Eur. Agric. 14, 23-32.

Polley, S., De, S., Brahma, B., Mukherjee, A., Vinesh, P.V., Batabyal, S., Arora, J.S., Pan, S., Samanta, A.K., Datta, T.K. & Goswami, S.L., 2010. Polymorphism of BMPR1B, BMP15 and GDF9 fecundity genes in prolific Garole sheep. Trop. Anim. Health Prod. 42, 985-993.

Purcell, S., Neale, B., Todd-Brown, K., Thomas, L., Ferreira, M.A.R., Bender, D., Maller, J., Sklar, P., De Bakker, P.I.W., Daly, M.J. & Sham, P.C., 2007. PLINK: a toolset for whole-genome association and population-based linkage analysis. Am. J. Hum. Genet. 81, 559-575.

Raj, A., Stephens, M. & Pritchard, J.K. 2014.fastSTRUCTURE: Variational inference of population structure in large SNP data sets. Genet. 197, 573-589.

Sandenbergh, L., 2015. Identification of SNPs associated with robustness and greater reproductive success in South African Merino using SNP chip technology. PhD thesis. University of Stellenbosch.

Sandenbergh, L., Cloete, S.W.P., Roodt-Wilding, R., Snyman, M.A. & Van der Merwe, A.E., 2015. Genetic diversity and population structure of four South African sheep breeds. Proc. Assoc. Advmt. Anim. Breed. Genet. 21, 294-297.

SAS, 2012. SAS Institute Inc. Cary, NC.

Souza, C.J.H., MacDougall, C., Campbell, B.K. & McNeilly, A.S., 2001. The Booroola (FecB) phenotype is associated with a mutation in the bone morphogenetic receptor type 1 B (BMPR1B) gene. J. Endocrinol. 169, R1-R6.

Storey, J.D. & Tibshirani, R., 2003. Statistical significance for genome-wide experiments. Proc. Natl. Acad. Sci. USA. 100, 9440-9445.

Tosh, J.J., Wilton, J.W. & Kennedy, D., 2002. Heritability of fertility in four seasons for ewes under accelerated lambing. Seventh WCGALP – August 19-23, Montpellier, France

Vatankhah, W., Poortahmasb, A. & Merzaei, H.R., 2006. Estimation of performance and genetic parameters of reproductive traits in Lori-Bakhtiari sheep using linear and threshold models. EAAP, 57th Annual Meeting, Antyla, 64.

Zhou, X. & Stephens, M., 2012. Genome-wide efficient mixed-model analysis for association studies. Nat. Genet. 44, 821-824.

Zishiri, O.T., Cloete, S.W.P., Olivier, J.J. & Dzama, K., 2013. Genetic parameters for growth, reproduction and fitness traits in the South African Dorper sheep breed. Small Rumin. Res. 112, 39-48

Chapter 7

Identification of selection signatures related to traits of robustness in South African sheep populations using the Bayesian Fst and HAPFLK approaches

Abstract

A study was conducted using HAPFLK and Bayescan to identify selection signatures in purebred Dorper, Namaqua Afrikaner and South African Mutton Merino sheep breeds. Selection signatures obtained using HAPFLK identified 26 significant SNP markers with selective sweeps on chromosome 1 and chromosome 2. Heat shock protein 28 (DNAJC28) were under selection on chromosome 1 and genes on chromosome 2 were gonadotropin releasing hormone (*GNRH1*), melanoregulin (*MREG*), spermatogenesis associated protein 31C2 –like and testis-expressed sequence 10 protein –like. The Bayescan method suggested 92 loci that were under selection. A signature was found on chromosome 10 in relaxin/insulin-like family peptide receptor 2 (*RXFP2*) that plays a role in the absence of horns (polledness) in sheep. This study suggested that some important genes for reproduction and adaptation to heat stress as suggested by HAPFLK, whereas the Bayescan confirmed traits like polledness and keratin that indicates ancient selection.

7.1. Introduction

Currently, there are 21.2 million sheep in South Africa (Abstract of Agriculture, 2015), which consists of more than 20 different breeds of which the Dorper and Merino are most prominent breeds (Cloete & Olivier, 2010). Other sheep breeds include the Merino, Dohne Merino, Dorper, South African Mutton Merino, Dormer, Ile de France, Merino Landsheep, Afrino, Van Rooy, Meatmaster, Damara, Nguni, Pedi and the Namaqua Afrikaner amongst others. Sheep

are mainly commercially farmed for meat and wool in South Africa. The Dorper, Merino and South African Mutton Merino are some of the prominent commercial breeds used in South Africa.

The Dorper is a composite breed derived from an initial cross between Black headed Persian and Dorset Horn sheep in the early 1900's and is widely farmed in the arid and semi-arid environments of South Africa. This is because of the ability of Dorpers to grow and reproduce well in harsh environments (Milne, 2000). The Namaqua Afrikaner is one of the oldest indigenous breeds in South Africa (Ramsay *et al.,* 2001). The breed was associated with the nomadic Nama people between 200 to 400 AD in the harsh dry areas of the North-Western Cape and Southern Namibia. The Namaqua Afrikaner is adapted to harsh environments (Snyman *et al.,* 2005) and is currently listed as an endangered breed (Qwabe *et al.,* 2013). The South African Mutton Merino was derived from the German Merino and was selected for both wool and meat production (Schoeman *et al.,* 2010).

Selection signatures are used to determine selection patterns in populations. It is a backward approach inferring selected mutations with their associated phenotypes (Ross-Ibarra *et al.,* 2007). Different methods are used to detect selection signatures, including the Fst and more recently FLK approach (Fariello *et al.,* 2013). Fst outlier approach is commonly used in selection signatures studies; however there are some limitations to only using Fst measures. Fst does not account for sampling errors, whereas FLK accounts for population size, heterogeneity and for the hierarchal structures between populations (Fariello *et al.,* 2013). Kijas *et al.,* 2012 used the Fst approach to determine selection signatures in sheep populations and found 31 genomic regions under selection. A study using HAPFLK using the same HAPMAP dataset observed 41 selection signatures with only 10 regions overlapping with the study of Kijas *et al.* (2012) (Fariello *et al.,* 2014). Strong selection signatures were detected for polledness in studies using both Fst and HapFLK methods (Kijas *et al.,* 2012; Fariello *et al.,* 2014) indicating

that this trait has been selected for many years. Selection signature studies are important to determine selection for traits of economic importance in livestock. They have also been widely used in several studies to determine regions under selection in different livestock species including cattle, goats and pigs (Ramey *et al.,* 2013; Ai *et al.,* 2013; Ma *et al.,* 2015; Kim *et al.,* 2016). Limited research has been done on selection signatures in South African sheep populations. A study done on South African Merinos using Fst statistics identified 31 signatures of selection within this population (Sandenbergh, 2015).

Knowledge on how sheep populations differentiated is of value to improve further sheep breeding schemes. The objective of this study was to compare HAPFLK and Bayesian Fst to detect selection signatures related to physiological pathways putatively linked to robustness traits in three South African purebreds namely the Dorper, South African Mutton Merino and Namaqua Afrikaner.

7.2. Materials and Methods

Refer to section 6.2 in Chapter 6 for the description of materials and methods.

7.3. Statistical analysis

7.3.1. Quality control

The DNA samples were genotyped using the OvineSNP50 Bead Chip. Genotypic data were analysed using PLINK (Purcell *et al*., 2007). Data for 307 individuals were analysed. Quality control was conducted by setting thresholds for minor allele frequency <0.01, genotype call rate per animal at 95% across all breeds. The data were pruned according to these criteria and 48078 SNPs for 193 sheep were retained and used in the analyses.

The population structure was investigated using fastSTRUCTURE (Raj *et al.,* 2014) to identify outlier animals that are admixed. These animals were excluded from the HAPFLK analysis.

HAPFLK analysis was run for four breeds, the Dorper (46), Namaqua Afrikaner (48), South African Mutton Merino (26) and Australian Merino (51), using the Valais Blacknose Sheep as an outgroup (24). The Australian Merino and Valais Blacknose sheep data were obtained from the HAPMAP sheep data (Kijas *et al.,* 2009, Kijas *et al.,* 2012). Bayescan 2.1 was used to do an Fst test on the same dataset. A q-value threshold of 0.01 were applied to reduce the number of false positives for both analysis. BayeScan is based on a multinomial Dirichlet model and uses Reversible Jump Markov Chain Monte Carlo (RJ-MCMC) algorithms to obtain posterior distributions (Foll & Gaggiotti, 2008). The Bayesian approach corrects for the uncertainty of allele frequencies due to small samples sizes. Ensuring a reduction in the observation of false positives among outlier markers (the prior odds) for the neutral model is set and posterior odds (PO) is used to make decisions. Therefore, in the analysis of this data, the PO was set at 4000 to identify loci under selection within the populations. The SNPs under selection were investigated further to determine genes putatively in linkage disequilibrium with the SNP loci. Identification of genes associated with significant SNPs was done using NCBI map viewer for *Ovis Aries* annotation release 102, 1Mb upstream or downstream of the markers under selection.

7.4. Results

From the HAPFLK analysis, 26 SNPs were predicted to have been under strong selection as shown in Table 7.1. Heat shock protein (*DNAJC28*) were under selection on chromosome 1 which plays an important role in the adaptation of sheep in extreme heat situations (Edwards & Hansen, 1996) and gonadotropin releasing hormone (*GNRH1*), melanoregulin (*MREG*), spermatogenesis associated protein 31C2 –like and testis-expressed sequence 10 protein –like on chromosome 2. A population tree were rooted using the ValaisBlacknose as an outgroup to infer selection for specific regions in different populations as seen in Figure 7.1. Selection for the DNAJC28 is evident in the Australian Merino and Namaqua Afrikaner. A significant

selection sweep for GNRH1 was observed in the Australian Merino and South African Mutton Merino sheep, whereas MREG were only significant in the Namaqua Afrikaner population.

Table 7.1. Significant SNPs under selection using the HAPFLK method

Chromosome	BP	FLK value	P value	Candidate genes
1	60,681,744	12.8	0.005	THRAP3 (Thyroid hormone receptor associated protein 3)
1	120,096,443	13.3	0.004	DNAJC28 (Heat shock protein
2	40,730,561	14.6	0.002	GNRH1 (Gonadotropin releasing hormone 1)
2	47,886,520	13.6	0.004	TEX10 (Testis expressed 10)
2	216,812,059	14.5	0.002	MREG (Melanoregulin)
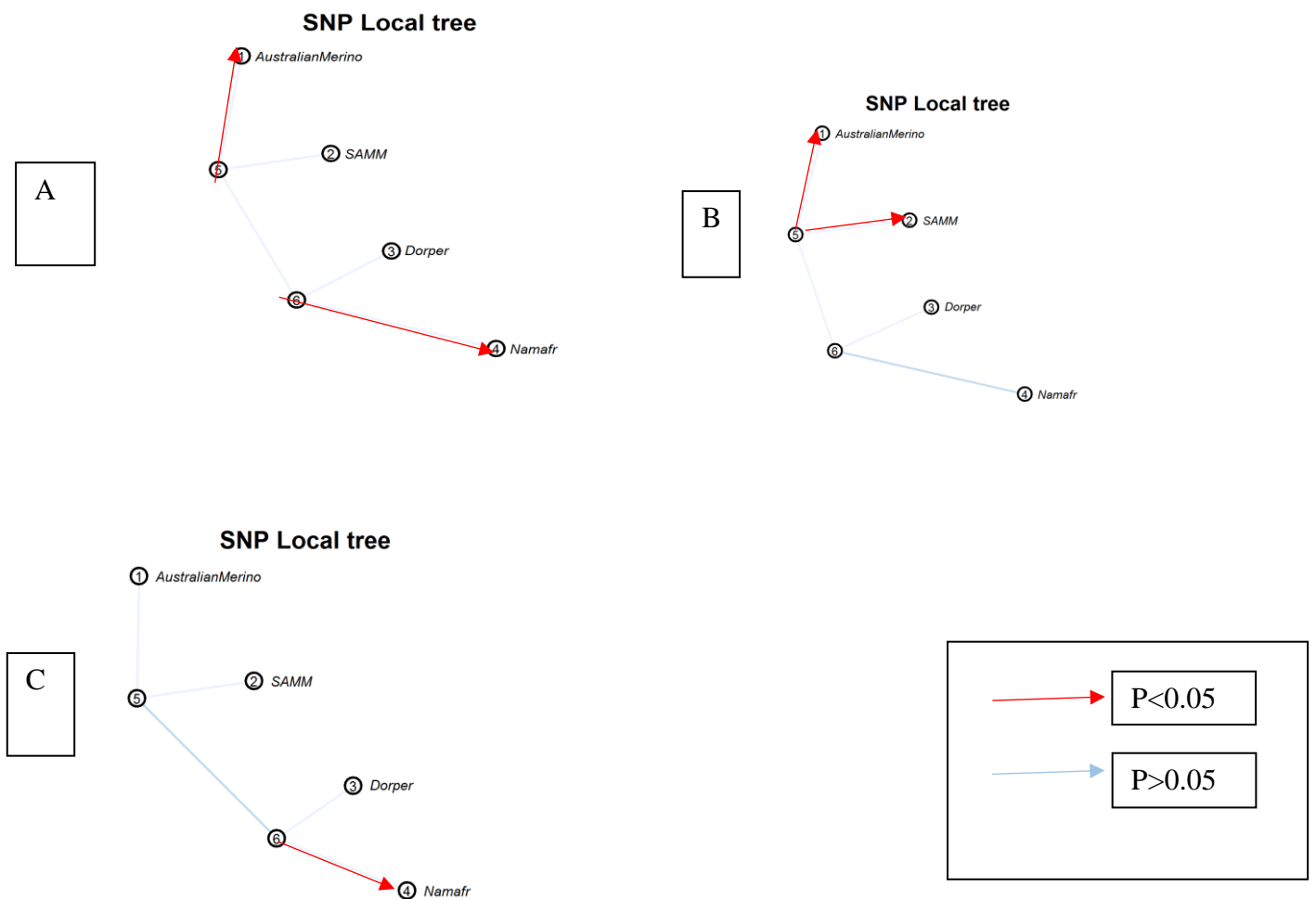
Figure 7.1 A) DNAJC28- OAR1, 120.1-121Mb B) GNRH1- OAR2, 40.0-41.3Mb C) MREG - OAR 2, 216.9 – 217.0 Mb

Results from the Bayesian Fst test indicated that 92 loci were under selection as indicated in Figure 7.2. The locus with the highest Fst value (0.574) was OAR3_130491628.1 located on chromosome 3. Genes in close proximity to this locus included plexin C1 (*PLXNC1*), centrosomal protein 83 (*CEP83*) and transmembrane and coiled-coil domain family 3 (*TMCC3*). A selection signature for relaxin/insulin-like family peptide receptor 2 (*RXFP2*) that

plays a role in the absence of horns (polledness) in sheep was identified on chromosome 10 at 29,546,872 bp. This was also found by Kijas *et al.* (2012) and Fariello *et al.* (2014). This result was expected, as South African Mutton Merino are polled animals. A signature of selection was also indicated for the *KITLG* gene located on chromosome 3 at 124, 569,037 bp. This gene plays two very diverse roles in cattle: the roan coat colour phenotype (Seitz *et al.,* 1999) and in ovarian follicular development (Parrot & Skinner, 1998).
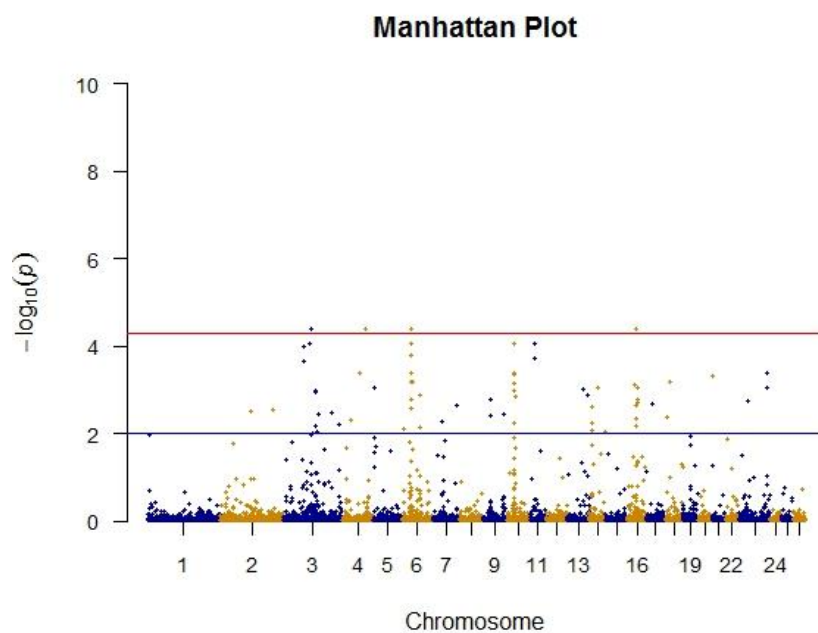
Manhattan Plot

Figure 7.2 Manhattan plot of Bayescan selection signatures, -log10(p) against the chromosome

Table 7.2 Significant loci under selection using the BayeScan method

SNP	CHR	BP	Fst	Genes			
OAR3_124569037.1	3	124,569,037	0.562	KITLG	KIT ligand	124632457	124762970
OAR3_130491628.1	3	130,491,628	0.574	CEP83	Centrosomal protein 83	130427042	130569058
OAR3_133356568.1	3	133,356,568	0.530	EIF4B	Eukaryotic translation initiation factor 4B	133259209	133283017
OAR10_29469450.1	10	29,469,450	0.545	LOC101110773	Elongation factor 1-alpha 1-like	29456030	29458184
OAR10_29511510.1	10	29,511,510	0.558	RXFP2	Relaxin/insulin like family peptide receptor 2	29457857	29518295
OAR10_29546872.1	10	29,546,872	0.544		No genes annotated		
OAR10_29654158.1	10	29,654,158	0.523		No genes annotated		
OAR10_29907137.1	10	29,907,137	0.524	B3GLCT	Beta 3-glucosyltransferase	29891958	30002883
s52637.1	11	42,641,540	0.534	BRCA1	BRCA1, DNA repair associated	42539960	42608927
s12884.1	13	67,997,490	0.532	TRNAE-UUC	Transfer RNA glutamic acid (anticodon UUC)	67566716	67566787

7.5. Discussion

The reason why only a few of the genomic regions predicted as being under selection in this study overlap with those previously reported in the literature using the same method may be due to the fact that the dataset used by Fariello *et al.* (2014) included 32 breeds which excluded South African breeds. The South African breeds used in the current study are likely to have been selected for traits that differ to the other populations worldwide. SNP ascertainment bias could also contribute to this finding, as South African breeds were not included in the development of the OvineSNP50 BeadChip.

Most of the regions predicted to be under selection differed between the two approaches. The reasons for the differences in regions identified by the two methods may be linked to the fact that Fst analysis can produce false positive results in subpopulations that share a high correlation in allele frequencies (Bierne *et al.,* 2013). Negative selection against deleterious mutations can also increase Fst values (Bierne *et al.,* 2013). HapFLK also detect recent events of selection, whereas Fst detect ancient selective sweeps. An issue with both approaches is that it is difficult to identify the specific target of selection, since there are numerous genes and regulatory regions located near the SNPs identified as being under strong selection. Further, the functions of many sheep genes are not fully understood and more investigation is necessary to elucidate their functions in this species.

Unique candidate genes obtained from this study using the HAPFLK method included genes that play a role in reproduction (GNRH), pigmentation (MREG) and heat shock protein (DNAJC28). The selective sweep observed for the heat shock protein in the Namaqua Afrikaner is expected. The heat shock protein has been associated with heat tolerance (Carabaño *et al.,* 2017). This is of relevance for this study, as the Namaqua Afrikaner were kept in semi-arid environments and there could possibly be natural selection for heat tolerance.

The selective sweep observed for GNRH1 in the South African Mutton Merino and Australian Merino is expected, as both these breeds have been selected for prolificacy

The reason why only a few of the regions in this study overlap with those in literature using the same method could be due to the fact that the dataset used by Fariello *et al.* (2014) included 32 breeds of which South African breeds were not represented. South African breeds were mainly used in our analysis except for the Australian Merino and the Valais Blacknose sheep populations that were used as an outgroup population for the HAPFLK and selection emphasis for South African breeds could be different in comparison to other populations worldwide. SNP ascertainment bias could also add to this observation, as South African breeds were not included in the development of the Ovine50K SNP beadchip.

Using the BayeScan method selection signature for Relaxin/insulin-like family peptide receptor 2 (RXFP2) that plays a role in the absence of horns (polledness) in sheep were identified on chromosome 10, 29,546,872. This concurs with the finding of Kijas *et al.* (2012) and Fariello *et al.* (2014). These results are not unexpected as the South African Mutton Merino are polled animals. Signals of selection were also indicated for the KITLG gene located on chromosome 3. This gene has been known to play two very diverse roles as in the roan phenotype in cattle (Seitz *et al.,* 1999) as well as ovarian follicular development in cattle (Parrot & Skinner, 1998). Keratin genes were observed on chromosome 3 and may be linked to wool fiber in sheep (McLaren *et al.,* 1997). These signatures of selection can be expected as SAMM and Australian Merino sheep were strongly selected for improved wool traits. The location of the keratin genes on chromosome 3 concurs with the study of McLaren *et al.,* 1997. Keratin genes have also be found to be under selection in Nguni breeds (Makina *et al.,* 2015). Most of the regions under selection differed between the two approaches. In this study, most of the regions identified to be under selection were different depending on the method used.

The reasons for the differences in regions identified by the two different methods could be linked to the fact that Fst values can produce false outliers in subpopulations that share high correlation in gene frequencies (Bierne *et al.,* 2013). Soma *et al.,* 2012 indicated that the Dorper and SAMM was genetically close compared to the Namaqua Afrikaner that is further distanced from the Dorper and Merino-type breeds. Negative selection against deleterious mutations can also increase Fst values (Bierne *et al.,* 2013). Artificial selection for various traits such as conformation, size, fat distribution, colour pattern, hair/wool type has been made in the South African Dorper (Milne, 2000). The SAMM has been selected for improved wool traits, conformation and growth traits (Neser *et al.,* 2000). The HAPFLK focus on haplotype differentiation which identifies selection sweeps of haplotypes inherited together. A setback with both methods is that it is difficult to identify with certainty the specific target under selection, since there are numerous genes within the regions of selection. The functions of some of the genes in sheep species are not clearly described in the literature and more investigation is necessary to elucidate their functions in sheep species.

7.6. Conclusions

Selective sweep have been identified on regions of chromosome 1 and 2 that has been selected for adaptation to heat and reproduction respectively. Candidate genes under strong selection in South African sheep populations identified include pigmentation (*KITLG*); selection appears to have been applied to variation in relaxin/insulin-like family peptide receptor 2 (*RXFP2*) and keratin genes. These selected regions concur with the observation that artificial selection has been placed on traits such as colour/pigmentation and growth in the development of the Dorper and on wool and growth traits in the South African Mutton Merino and Australian Merino. Natural selection has also occurred for traits related to adaptability.

7.7. References

Ai, H., Huang, L. & Ren, J., 2013. Genetic diversity, linkage disequilibrium and selection signatures in Chinese and Western pigs revealed by genome-wide SNP markers. PLoS ONE, 8, e56001.

Bierne, N., Roze, D. & Welch J.J., 2013. Pervasive selection or is it ...? Why are Fst outliers sometimes so frequent? Mol. Ecol. 22, 2061-2064.

Carabaño, M.J., Ramón, M., Díaz, C., Molina, A., Pérez-Guzmán, M.D. & Serradilla, J.M., 2017. Breeding for resilience to heat stress effects: A comparison across dairy ruminant species. J.Anim. Sci. 95, 1813-1826.

Cloete, S.W.P. & Olivier, J.J., 2010. South African Sheep and Wool industry. In: International Sheep and Wool handbook. Ed. D.J. Cottle. Nottingham University Press, Manor Farm, Thrumpton, Nottingham NG11 0AX, united Kingdom. Pp 95-112.

Deng, W.D., Shu, W., Yang, S. L., Shi, X.W. & Mao, H.M., 2009. Pigmentation in black-boned sheep (Ovis aries): association with polymorphism of the MC1R gene. Mol. Biol. Reports 36, 431-436.

Edwards, J.L. & Hansen, P.J. 1996. Elevated temperature increases heat shock protein 70 synthesis in bovine two-cell embryos and compromises function of maturing oocytes. Biol. Reprod. 55, 340-346.

Fariello, M.I., Boitard, S., Naya, H., SanCristobal, M. & Servin, B., 2013. Detecting signatures of selection through haplotype differentiation among hierarchically structured populations. Genet. 193, 929-941.

Fariello, M.I., Servin, B., Tosser-Klopp, G., Rupp, R., Moreno, C., International Sheep Genomics Consortium, SanCristobal, M. & Boitard, S., 2014. Selection signatures in worldwide sheep populations. PLoS ONE 9, e103813

Foll, M. & Gaggiotti, O., 2008. A genome-scan method to identify selected loci appropriate for both dominant and codominant markers: A Bayesian perspective. Genet. 180, 977-993.

Garcia-Garcia, M.J. Eggenscwiler, J.T., Caspary, T., Alcorn H.L., Wyler, M.R., Huangfu, D., Rakeman, A.S., Lee, J.D. Feinberg, E.H., Timmer J.R. & Anderson K.V., 2005. Analysis of mouse embryonic patterning and morphogenesis by forward genetics. Proc Natl Acad Sci USA 102, 5913-5919.

Kijas, J.W., Townley, D., Dalrymple, B.P., Heaton, M.P., Maddox, J.F., McGrath, A., Wilson, P., Ingersoll, R.G., McCulloch, R., McWilliam, S., Tang, D., McEwan, J., Cockett, N., Oddy, V.H., Nicholas, F.W. & Raadsma, H., 2009. A Genome wide survey of SNP variation reveals the genetic structure of sheep breeds. PLoS ONE 4, e4668, doi: 10.1371/journal.pone.0004668

Kijas, J.W., Lenstra, J.A., Hayes, B., Boitard, S., Porto Neto, L.R, San Cristobal, M., Servin, B., McCulloch, R., Whan, V., Gietzen, K., Paiva, S., Barendse, W., Ciani, E., Raadsma, H., McEwan, J., Dalrymple, B. & the International Sheep Genomics Consortium Members., 2012. Genome-wide analysis of the world's sheep breeds reveals high levels of historic mixture and strong recent selection. PLoS Biol 10, e1001258.

Kim, E-S., Elbeltagy, A.R., Aboul-Naga, A.M., Rischkowsky, B., Sayre, B., Mwacharo, J.M. & Rothschild, M.F., 2016. Multiple genomic signatures of selection in goats and sheep indigenous to a hot arid environment. Heredity, 1-10.

Ma, Y.,Wei, J., Zhang, Q., Chen, L., Wang, J., Liu, J. & Ding, X., 2015. A genome scan for selection signatures in pigs. PLoS ONE 10, e0116850.

Makina, S.O., Muchadeyi, F.C., Van Marle-Köster, E., Taylor, J.F., Makgahlela, M.L. & Maiwashe A. 2015. Genome-wide scan for selection signatures in six cattle breeds in South Africa. Genet. Sel. Evol. 47, 92-106.

McLaren, R., Rogers, G.R., Davies, K.P., Maddox, J.F. & Montgomery G.W., 1997. Linkage mapping of wool keratin and keratin-associated protein genes in sheep. Mamm. Genome 8, 938-940.

Milne, C., 2000. The History of the Dorper. Small Rumin. Res. 36, 99-102.

Moyo, S. & Swanepoel, F.J.C., 2010. Multifunctionality of livestock in developing communities. In: The role of livestock in developing communities: enhancing multifunctionality. Eds. Swanepoel, F.J.C., Stroebel, A., Moyo, S. publ. UFS & CTA. pp. 1-12.

Neser, F.W.C., Erasmus, G.J. & Van Wyk, J.B. 2000. Genetic studies on the South African Mutton Merino: growth traits. S. Afr. J. Anim. Sci. 30, 172-177.

Parrott, J.A. & Skinner, M.K. 1998.Thecal cell-granulosa cell interactions involve a positive feedback loop among keratinocyte growth factor, hepatocyte growth factor, and Kit ligand during ovarian follicular development. Endocrinology [Pubmed]

Purcell, S., Neale, B., Todd-Brown, K., Thomas, L., Ferreira, M.A.R., Bender, D., Maller, J., Sklar, P., De Bakker, P.I.W., Daly, M.J. & Sham, P.C., 2007. PLINK: a toolset for whole-genome association and population-based linkage analysis. Am. J. Hum. Genet. 81, 559-575.

Raj, A., Stephens, M. & Pritchard, J.K., 2014. fastSTRUCTURE: Variational inference of population structure in large SNP data sets. Genetics. 197, 573-589.

Ramey H.R., Decker J.E., McKay S.D., Rolf M.M., Schnabel R.D. & Taylor J.F., 2013 Detection of selective sweeps in cattle using genome-wide SNP data. BMC Genomics. 14, 382-10.1186/1471-2164-14-382.

Rezaie, H., Marc, D., Choiset Y., Takahashi, M., Hoa, G.H.B., Haertle T., Grosclaude J. & Debey, P., 2000. High yield purification and physio-chemical properties of full-length recombinant allelic variants of sheep prion protein linked to scrapie susceptibility. Eur. J. Biochem 267, 2833-2839.

Ross-Ibarra, J., Morrel, P.L. & Gaut, B.S., 2007. Plant domestication, a unique opportunity to identify the genetic basis of adaptation. PNAS 104, 8641-8648

Sandenbergh, L., 2015. Identification of SNPs associated with robustness and greater reproductive success in South African Merino using SNP chip technology. PhD thesis. University of Stellenbosch.

Seitz, J.J., Schmutz, S.M., Thue, T.D., Buchanan, F.C. & Mamm. 1999. A missense mutation in the bovine MGF gene is associated with the roan phenotype in Belgian Blue and Shorthorn cattle. Genome

Soma, P., Kotze, A., Grobler, J.P. & Van Wyk, J.B., 2012. South African sheep breeds: Population genetic structure and conservation implications. Small Rumin. Res.103, 112–119.

Chapter 8

Conclusions and recommendations

8.1 Conclusions

The aim of the study was to investigate the productivity of smallholder sheep farming in the Western Cape, South Africa, using an interdisciplinary approach. This included integrating genomics and socio-economic aspects. Knowledge on socio-economic factors influencing average number of lambs and offtake rate was obtained from the survey. The part of the study based on genomic analyses yielded knowledge on genetic diversity and the population structure of smallholder animal genetic resources, as well as selection signatures related to physiological pathways putatively linked to robustness traits.

The need for this study stems from integral role that sheep plays in the livelihood of smallholder farmers in South Africa. A number of constraints are impeding sustainable sheep production, including socio-economic factors (wealth status, gender, age, education) and environmental factors (land availability, water resources, nutrition, and livestock biodiversity). A farming system needs to be resilient in terms of its ability to adapt to environmental changes to ensure long term sustainability.

Sheep breeding practices of smallholder farmers were elucidated. The overwhelming popularity of Dorper sheep over Merino, Damara and Meatmaster breeds was confirmed. Smallholder farmers also indicated that they select for traits such as heat tolerance, size and temperament.

Socio-economic factors such as age of the farmer, farm type, wealth status, tribe and gender or LRAD/CASP participation did not significantly influence offtake. The offtake of smallholder sheep farmers was lower compared to offtake figures for commercial sheep farmers as reported

in the literature. Sale outlets and sources of income which is descriptive of the type of farming system were influenced by the district. Factors that influenced sale outlets were the age of the farmer and whether or not the farmers own land. Therefore farming systems are not different according district. The districts are therefore representative of different farming systems.. Those in the West Coast and Eden area were more subsistence farming, whereas the farmers in the Karoo were more commercially orientated and achieved a higher average numbers of lambs sold. Overall the smallholder sheep farmers were found not to be economically viable due to low income derived from average number of lambs sold, even though their offtake levels were similar with commercial farmers. The reasons for their income being low could be because of the number of lambs sold per annum being lower than commercial farmers in general. The large variation in offtake rate observed within the farming systems could be explained by certain farmers that recently joined a land reform project and that were accumulating breeding ewes to build their breeding flock and thus obtaining low offtake rates and farmers that are selling lambs during December holiday for cash income. There is, however, scope to increase economic viability of farming systems if the average number of lambs sold is increased. This can be achieved by ensuring that suitable breeding and management plans with breeding objectives suitable for the farming system are implemented. However, other socio-economic issues should also be addressed such as age, gender and land ownership, as these factors are known to influence decision-making to farm with small ruminants.

The study also focused on the animal genetic resources of smallholder sheep farmers to determine whether their gene pool was diverse and adapted/robust to their environment. The survey indicated that smallholder sheep farmers in the Western Cape mostly farm with Dorpers. These Dorpers are admixed and not purebred. This was confirmed by the FastStructure analysis in Chapter 5 that indicated admixture of the Dorper breeds used in smallholder sheep farming

systems. The Dorpers used by smallholder farmers were admixed with Merino type breeds and indigenous fat-tailed like the Namaqua Afrikaner. Some of the sheep indicated as White Dorpers by smallholder sheep farmers were confirmed through the FastStructure analysis. The Dorper sheep from smallholder sheep farmers also had a lower inbreeding coefficient than the Dorpers sourced from the research farm as well as the two other pure breeds (Namaqua Afrikaner and South African Mutton Merino) used in this study as a base population. Thus from these results, smallholder sheep genetic resources can be classified as being environmentally viable, as there is sufficient genetic diversity within their ovine resources. This high genetic diversity, however, needs to be maintained and managed to the benefit of the farmers to increase smallstock production performance. The genetic diversity may be explained by migration, as smallholder farmers constantly bring new genes into their population to improve their flocks.

The study also investigated whether there has been selected for traits related to robustness and reproduction in smallholder sheep populations. This was important to determine in terms of evaluating the ability of animals to adapt to changing environments. This was done using GWAS (GEMMA) and selection signatures (HAPFLK and BayeScan) to identify causal variants associated with adaptability. The GWAS did not yield significant results. It needs to be conceded that small sample size in the study was small. The nature of the trait that was defined (wet-dry) was also unlikely to support uncomplicated inheritance depending on a relatively small number of quantitative trait loci (QTL) despite a moderate heritability based on SNP-data. The infinitesimal model is much more likely, where many QTL (each of small effect) contribute to the phenotypic expression of the wet-dry phenotype (Hill, 2010). From the HAPFLK and Bayescan in chapter 7, signals of selection were detected for genes related to reproduction, pigmentation, polledness and heat tolerance. The low inbreeding and the fact that the sheep from smallholders have putatively been selected for robustness traits makes it

possible for future genetic gain in this population. Genetic gain can lead to improved offtake and will influence the economic sustainability of the farmers. Selection signatures linked to fitness and robustness are also of value to add to current literature important for future studies involving adaptation of sheep to changes in ambient temperature.

The survey results provided information on the breeds farmed and selection objectives of farmers. This was integrated with the genomic studies because the genetic diversity and population study confirmed the assumed breeds utilised by smallholder farmers and high diversity; whereas the selection signature study confirmed the selection objectives of smallholder sheep farmers such as selection for heat tolerance of sheep. The wet-dry phenotype measurement and GWAS can be integrated with the average number of lambs sold and offtake rate obtained from the survey. Rangeland condition scores for both communal and small-scale farmers were low and could explain low offtake rate in both farming systems. Improvement in rangeland condition could lead to improvement of sheep productivity.

8.2 Recommendations

The different constraints as mentioned by communal and small-scale farmers should first be addressed to ensure that farmers have access to land, grazing, water and infrastructure. These are the basics of a farming operation even before the issue of genetic resources can be addressed. Genomics, however, provide many options and opportunities in terms of information on genetic structure, relationships between individual animals and genomic selection. The stage at which genomics should be included into a breeding plan will differ between farmers. Farmers that have already progressed in overcoming major constraints can utilise genomics for further improvement in terms of decreasing generation interval, identifying pedigree and for instance enhancing traits of importance for their farming system. Literature

has indicated many genetic improvement programs which have failed due to a lack of attention to the social aspects.

There are many more aspects to consider in terms of social/political, economic and environmental indicators but this will need the collaboration of more stakeholders. For future studies it would also important to take a more participatory approach and involve more stakeholders to determine the necessary indicators to address before attempting introducing any new technology.

The study showcases the use of genomics to evaluate breed diversity as an indicator of environmental sustainability. Only 307 sheep were genotyped in this study using a 50K SNP chip. Due to the levels of LD a denser chip would be recommended for future studies like the 600K SNP bead chip or even the use of whole genome sequencing using more sheep. Attempts should be made to obtain reliable phenotypes of traits related to robustness and not only one trait. Farmers should include traits in their breeding objectives applicable to their sheep farming system to enable genetic improvement. Use of selection indices in smallholder sheep production has been demonstrated elsewhere.

Recording of phenotypes to include in selection indices and genomic selection is of importance for genetic improvement. This is one of the major challenges for smallholder and even commercial sheep farmers in South Africa due to the extensive nature of sheep farming systems. The availability of the national small stock improvement scheme (NSIS) makes it possible for registered stud farmers and commercial sheep farmers to participate in genetic improvement program. Recordkeeping can be done using applications developed for smartphones. Similar recordkeeping systems have been developed using ICT technologies in Kenya (Irungu *et al.,* 2015). Blood samples can also be collected from each individual sheep with phenotypic information recorded in the database and this can aid in the development of a suitable reference population for smallholder farmers for genomic selection of the traits

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important for their specific farming system. The feasibility of such programs is likely to increase as genotyping costs per individual decline.

Depending on resources available to smallholder farmers the following easy to measure phenotypes can be recorded:

1. Body condition score on a scale from 1 to 5, where 1 is extremely emaciated and 5 is obese. This can be recorded before the mating season to ensure that ewes have a body condition score of 3. This will increase the chances of successful conception and hence influence the number of lambs born per ewe joined.

2. Wet and dry phenotype can be recorded during the lambing season; ewes can be classified as dry or lactating. Ewes that are dry in two years consecutively should be culled from the breeding flock. Selection can be made on offspring of ewes who are proven to produce lambs every year.

3. The number of lambs born per ewe can be measured by the end of lambing season when ewes are kraaled together to be counted by farmers.

4. FAMACHA can also be recorded as an indication of *Haemonchus contortus* spp. in summer rainfall areas. This trait is important as it allows for the selection of sheep that are resistant to gastro-intestinal parasites. Faecal worm egg counts can also be recorded to select for resistance to gastro-intestinal parasites. This can be done with the help of state veterinarians.

In situations where smallholder farmers have scales or weigh bands available farmers can also record live weights, such as weaning weight and body weight of ewes before mating. Linear measurements that are correlated with body weight can also be used.

The successful recording of phenotypes can be achieved by the collaboration of farmers, government, research institutions, higher education and private companies to act as funding bodies for sustainability projects.

Carrying capacity also varied between farming systems with communal farmers from Eden and West Coast overgrazing their land. Increasing the number of LSU could lead to an increase in offtake rate and improved economic sustainability. Farmers should, however, take care to prevent overgrazing of their land to ensure sustainable usage. Land is a limited resource and options should be considered for the optimal use of land already available to farmers. Options should thus be provided to smallholder farmers on how to increase their LSU to the recommended carrying capacity from the Western Cape Department of Agriculture. Good grazing and rangeland management techniques to ensure sustainable use of land resources should also be adhered to.

8.3. Research Outputs

8.3.1. Peer-reviewed publications

Molotsi, A.H., Taylor, J.F., Cloete, S.W.P., Decker, J.E., Muchadeyi, F., Sandenbergh, L. & Dzama, K. 2017. Preliminary genome-wide association study for wet-dry phenotype in smallholder ovine populations in South Africa. S. Afr. J. Anim. Sci. 47, 327-331.

Molotsi, A.H., Dube, B., Oosting, S., Marandure, T., Mapiye, C., Cloete, S.W.P. & Dzama, K. Genetic traits of relevance to sustainability of smallholder sheep farming systems in South Africa. Sustainability, 9, 1225. DOI:10.3390/su9081225

Molotsi, A.H., Taylor, J.F., Cloete, S.W.P., Muchadeyi, F., Decker, J.E., Whitacre, L.K., Sandenbergh, L., & Dzama, K. Genetic diversity and population structure of South African

smallholder farmer sheep breeds determined using the OvineSNP50 beadchip. Trop. Anim. Health Prod. 49, 1771-1777. DOI: 10.1007/s11250-017-1392-7.

8.3.2. Conference outputs

Davids, A.H. & Dzama, K. 2013. Linking small-scale livestock farming to food security in South Africa from an animal breeding perspective. Poster at 1st Food security conference 2013

Molotsi, A.H., Taylor, J.F., Cloete, S.W.P., Whitacre, L., Dzama, K. & Zvinorova, I. 2016. Genetic structure of smallholder sheep in the Western Cape, South Africa. Presented at the 49th Congress for South African Society of Animal Sciences, 3-6 July 2016, Stellenbosch, South Africa

Molotsi, A.H., Oosting, S.J., Cloete, S.W.P. & Dzama, K. 2017. Offtake and genetic diversity as indicators of sustainability for smallholder sheep farming systems in the Western Cape, South Africa. Presented at the 6th Forum on Sustainability, 28-29 January 2017, Cape Town, South Africa.

8.4 References

Hill, G., 2010. Understanding and using quantitative genetic variation. Phil. Trans. R. Soc. 365, 73-85.

Irungu, K. R. G., Mbugua, D. & Muia, J., 2015. Information and Communication Technologies (ICTs) Attract Youth into Profitable Agriculture in Kenya. East Afr. Agric. Forest. J. 81, 24–33.

Addendum A

UNIVERSITEIT
STELLENBOSCH
UNIVERSITY

MANAGEMENT OF FARM ANIMAL GENETIC RESOURCES

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Department of Animal Sciences
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SOUTH AFRICAN FARM ANIMAL GENETIC RESOURCES SURVEY

QUESTIONNAIRE - SHEEP

Enumerator   Name _____   Code no.   Date of interview   /   /

Supervisor   Name _____   Code no.

1. Province   Name _____   Code no.

2. District   Name _____   Code no.

3. Station / camp   Name _____   Code no.

4. Village (VIDCO)   Name _____   Code no.

5. Farm type   Communal   Small-scale commercial   Large-scale commercial

6. GPS reading _____ *(to be filled in later)*   **7. Household**   No

8. Wealth category | rich | medium | poor | not classified | *(tick one)*

The overall objective of the survey, is to obtain reliable estimates of population size and distribution of farm animal breed resources as well as to determine management/ production and socio-cultural practices employed by farmers in raising these animals. The surveys will enable simple, regular updating of breed information and facilitate updating of the databank on the FAO DAD-IS system. With this information, countries will be able to:

- develop comprehensive plans for the management of FAnGR,
- develop and harmonize support policies for FAnGR Management,
- facilitate development of appropriate animal recording systems and sustainable breeding programs,
- facilitate development and implementation of relevant conservation activities.

HOUSEHOLD   General Information   Page 1

1. Interviewee _____

Position in household
1. Household head [ ]
2. Spouse of head [ ]
3. Brother [ ]
4. Sister [ ]
5. Son [ ]
6. Daughter [ ]

Other (specify)

7. _____ [ ]

2. Household head

Sex of head   Male [ ]
               Female [ ]

Age (yrs)   ≤ 30 [ ]
               31-40 [ ]
               41-50 [ ]
               51-60 [ ]
               61-70 [ ]
               > 70 [ ]
               Not known [ ]

3. Tribe

Name _____

Code [ ]

4. Number of people residing in household

Males [ ]
Females
Children < 15 yrs

5. Land holding / farm size
(enter X in box in first column if not known)

	Area	Units *(tick)*
Crops	[ ]	Acres [ ]
Grazing *	[ ]	Hectares [ ]
Forest	[ ]	
Total size	[ ]	

* Other than communal

7. Livestock activity

Is livestock the major activity on your farm?
Yes [ ]   No [ ]

8. Sources of income

(Tick first column as appropriate, rank level of source of income in second column – 1 highest.)

1. Crops [ ] [ ]
2. Livestock and products * [ ] [ ]
3. Home industries [ ] [ ]
4. Salary / wages [ ] [ ]

Other (specify)

5. _____ [ ] [ ]

* Include the value of non-cash outputs or products e.g. manure, traction etc.

6. Land ownership
(Tick one or more)

Own [ ]
Lease [ ]
Other [ ]   (specify) _____

9. Livestock kept
(enter numbers in first column)

Most important species *(rank up to 3: (1, 2, 3)*

	Numbers	
1. Cattle	[ ]	[ ]
2. Sheep	[ ]	[ ]
3. Goats	[ ]	[ ]
4. Chickens †	[ ]	[ ]
5. Pigs	[ ]	[ ]
6. Donkeys	[ ]	[ ]

Other (specify)

7. _____ [ ] [ ]

† Adult birds only

10. Flock composition

	Numbers
1. Lambs	[ ]
2. young ewes	[ ]
3. young rams	[ ]
4. Rams	[ ]
5. Ewes	[ ]

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SHEEP   **Production system**   **Page 2/3**

1. System of production

(Tick one or more)

1. Industrial/intensive .. ☐
2. Semi-intensive ……. ☐
3. Extensive/pastoral … ☐
4. Free range / backyard ☐

Other (specify)

5. _____ ☐

2. Purpose of keeping sheep

Ask an open question and tick any purpose considered in first half of box-one or more boxes to be ticked. Then rank top three by writing in second half of a box 1 for primary purpose, 2 for second, 3 for third.

1. Meat ……………... ☐☐
2. Skins
3. Wool
4. Stud breeding …… ☐☐
5. Cash from sales …
6. Investment ……….
7. Dowry ……………
8. Ceremonies ………
9. Cultural ………..… ☐☐

Other (specify)

11. _____ ☐☐

3. Members of household who own sheep *(Tick one or more)*

Head …………………... ☐

Spouse …………………. ☐

Daughters ……………... ☐

* Describe _____

4. Members of household responsible for sheep activities
   (Tick as appropriate; more than one column in a row may be ticked)

	Adults Males	Females	Boys (<15y)	Girls (<15y)	Hired labour
1. Purchasing sheep …………	☐	☐	☐	☐	☐
2. Selling / slaughtering sheep	☐	☐	☐	☐	☐
3. Breeding decisions …………..	☐	☐	☐	☐	☐
4. Feeding …………………………	☐	☐	☐	☐	☐
5. Sheep health ……………………..	☐	☐	☐	☐	☐

Other (specify)

6. _____ ☐ ☐ ☐ ☐ ☐

5. Type of housing
   (Tick one or more)

1. Kraal ☐

2. None ☐

Other (specify)

3. _____ ☐

6. Supplementation regime
   (Tick as appropriate)

1. Lucerne hay …………….. ☐
3. Home-made ration ……….. ☐
4. Crushed grain ……………. ☐
5. Whole grain ……………… ☐

Other (specify)

6. _____ ☐

7. Mating system

1. Artificial insemination ☐

Other (specify)

3. _____ ☐

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SHEEP   Health   Page 4/5

1. Access to veterinary services
   (Tick as appropriate)

1. Government vet.   ☐
2. Private vet.   ☐
3. Veterinary drug supplier   ☐
4. Extension service   ☐
5. None   ☐

Other (specify)

6. _____   ☐

2. Prevalent diseases that occur on farm
   (i.e. diseases that are seen by farmer in his sheep)

   If none tick this box   ☐

Local name or symptoms of disease   Are animals treated when sick?
(Rank, most common first)

                              Code *   Yes   No   Treatment given (if known)   Code *

1. _____   ☐   ☐   ☐   _____   ☐
2. _____   ☐   ☐   ☐   _____   ☐
3. _____   ☐   ☐   ☐   _____   ☐
4. _____   ☐   ☐   ☐   _____   ☐
5. _____   ☐   ☐   ☐   _____   ☐

*(codes to be entered later from lists of diseases and treatments)

3. Vaccination/preventive treatments given

   If none tick this box   ☐

Local name or symptoms of disease   Done   Done when
                                 Code *   routinely   need arises
                                          (Tick as appropriate)

1. _____   ☐   ☐   ☐
2. _____   ☐   ☐   ☐
3. _____   ☐   ☐   ☐
4. _____   ☐   ☐   ☐
5. _____   ☐   ☐   ☐

*(code to be entered later from list of diseases)

4. Ectoparasite control

                    Done when   Done   *If done routinely specify how often*
   Method   need arises   routinely

       (Tick)   dry   wet   dry   wet   dry season   wet season
                   season   season

                ☐
                ☐   ☐   ☐   ☐   ☐   ☐   ☐   ☐
                ☐
                                                      ☐

                ☐   ☐   ☐   ☐   ☐   ☐   ☐   ☐

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SHEEP　　　Entries/exits/culling　　Page 6

1. Numbers of entries within last 12 months
   (Enter X in a box if not known, 0 if answer is none)

Adults
Males　　Females

1. Bred ……………
2. Bought …………
3. Donated/gift …...
4. Exhanged/lent …

3. Sale outlet *(if sold in last 12 months)*

Were sheep sold?　Yes　☐　No ☐

If yes tick one　　1. Sold at auction

or more boxes.　　2. Sold to butcher
　　　　　　　　　3. Sold privately
　　　　　　　　　4. Sold to abattoir

　　　　　　　　Other (specify)

　　5. _____

Selling price
Are you making profit?　　　　　　Y | N
If not why?

2. Numbers of exits within last 12 months
   (Enter X in a box if not known, 0 if answer is none)

Adults
Males　　Females

1. Died ………….
2. Sold …………..
3. Slaughtered …..
4. Exchanged/lent
5. Donated/gift …
6. Stolen ………...

4. Reasons for culling / disposal

Ask as open question and tick any answers given in first

*half of box, one or more boxes to be ticked. Then rank
top three by writing in second half of box 1 for
primary reason for culling, 2 for second and 3 for third.*

Males　　　Females

1. Size ………………………
2. Conformation / shape ……
3. Colour ……………………
4. Temperament …………….
5. Health ……………………
6. Body condition ………….
7. Performance …………….
8. Old age …………………..
9. Poor fertility ……………..

Other (specify)

10. _____

11. _____

General Problems

　　　　　　　　　　Y　N

Stock theft　　　　　☐ ☐
If yes, how many get stolen in a year?
How much does theft costs you yearly?
Problem of predators (dogs, jackals, etc)　☐ ☐
How much does predation costs you yearly?
Are there any other major obstacle in your enterprise?
Do you think government has done enough so far in improving the standard of farming in communal areas?

SHEEP   **Breeding**   **Page 7**

1. Primary reason for keeping ram(s)
   (Tick one)

   1. Breeding …………… ☐

   2. Socio-cultural ……… ☐

   Other (specify)

   3. _____ ☐

2. Reasons for choice of ram(s) for breeding
   If breeding not done proceed to next page.

   Ask an open question and tick any reason for

   choice

   considered in first half of box, one or more boxes to be
   ticked. Then rank top three by writing in second half of box
   1 for primary reason for choice, 2 for second and 3 for third.

   1. Size ………………………….. ☐☐
   2. Conformation/shape ………… ☐☐
   3. Colour ……………………… ☐☐
   4. Temperament ……………….. ☐☐
   5. Performance ………………… ☐☐
   6. Availability (no choice) ……... ☐☐

   Other (specify)

   7. _____ ☐☐

3. Mating

(Tick one or   1. Uncontrolled …. ☐
more boxes)   2. Hand mating ….. ☐
                   3. Group mating …. ☐

       Other (specify)

       4. _____ ☐

4. Source and breed(s) of ram(s) used in the household

Breed name(s) *(specify if known – crosses can be included.)*

	Breed 1 Common name	Code*	**Breed 2** Common name	Code*
Tick one or more boxes				
1. Own ram (bred) ☐	_____	☐☐	_____	☐☐
2. Own ram (bought) ☐	_____	☐☐	_____	☐☐
3. Ram donated ☐	_____	☐☐	_____	☐☐
4. Ram borrowed ☐	_____	☐☐	_____	☐☐
5. Unknown Ram ☐	_____	☐☐	_____	☐☐

*(code to be entered from list of breeds – use first box only if pure breed, two boxes
if ram is a crossed breed)

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SHEEP

Breed/age/sex structure (pure breeds)

Number of pure breeds * | 0 | 1 | 2 | 3 | 4 | 5 | *(tick)*

* If crossing of two breeds has resulted in a genotype that is recognised and maintained as a breed, then count this as a separate breed and include it on this form. If no pure breeds tick 0 in box and complete section on mixed crosses form. If more than two pure breeds, third breed can be entered on mixed crosses form.

BREED 1   **Code** [ ]
(from list of breeds)

1. Common breed name _____

Local breed name _____

2. Trend within flock *(tick one)*

Increasing [ ]   Decreasing [ ]
Stable [ ]   Unknown [ ]

3. Numbers of adult sheep

Male [ ]   Female [ ]

4. Number of lambs

Average number of lambs per breeding season [ ]

Breeding season every [ ] months

4. Origin/source of breed

1. Inherited [ ]
2. Communal area farm [ ]   ** specify location if known*
3. Commercial farm * [ ]   _____
4. Market * [ ]

5. Quality of traits perceived by owner
(Ask each question and for each trait tick one box, poor average, good, no opinion)

Poor	Average	Good	No opinion/ not important	
[ ]	[ ]	[ ]	[ ]	.... 1. Size ....
[ ]	[ ]	[ ]	[ ]	.... 2. Conformation / shape ....
[ ]	[ ]	[ ]	[ ]	.... 3. Mothering ability......
[ ]	[ ]	[ ]	[ ]	.... 4. Disease tolerance ....
[ ]	[ ]	[ ]	[ ]	.... 5. Drought tolerance ....
[ ]	[ ]	[ ]	[ ]	............6. Heat tolerance ....
[ ]	[ ]	[ ]	[ ]	.... 7. Temperament ....
[ ]	[ ]	[ ]	[ ]	.... 8. Control of flies ....
[ ]	[ ]	[ ]	[ ]	.... 9. Numbers ....
[ ]	[ ]	[ ]	[ ]	.... 10. Meat taste/quality ....
[ ]	[ ]	[ ]	[ ]	.... 11. Growth rate ....
[ ]	[ ]	[ ]	[ ]	.... 12. Fertility ....
[ ]	[ ]	[ ]	[ ]	.... 13. Foraging ability ....

Other (specify)

[ ]   [ ]   [ ]   [ ]   .... 14. _____

BREED 2   **Code** [ ]
(from list of breeds)

1. Common breed name _____

Local breed name _____

2. Trend within flock *(tick one)*

Increasing [ ]   Decreasing [ ]
Stable [ ]   Unknown [ ]

3. Numbers of adult sheep

Male [ ]   Female [ ]

4. Number of lambs

Average number of lambs per breeding season [ ]

Breeding season every [ ] months

4. Origin/source of breed

1. Inherited [ ]
2. Communal area farm [ ]   ** specify location if known*
3. Commercial farm * [ ]   _____
4. Market * [ ]

5. Quality of traits perceived by owner
(Ask each question and for each trait tick one box, poor, average, good, no opinion)

Poor	Average	Good	No opinion/ not important
[ ]	[ ]	[ ]	[ ]
[ ]	[ ]	[ ]	[ ]
[ ]	[ ]	[ ]	[ ]
[ ]	[ ]	[ ]	[ ]
[ ]	[ ]	[ ]	[ ]
[ ]	[ ]	[ ]	[ ]
[ ]	[ ]	[ ]	[ ]
[ ]	[ ]	[ ]	[ ]
[ ]	[ ]	[ ]	[ ]
[ ]	[ ]	[ ]	[ ]
[ ]	[ ]	[ ]	[ ]
[ ]	[ ]	[ ]	[ ]
[ ]	[ ]	[ ]	[ ]

[ ]   [ ]   [ ]   [ ]

SHEEP   Breed/age/sex structure (mixed crosses)   Page 9

This form is also designed for a third pure breed. If there is a fourth pure breed this should be included under mixed crosses and ranked 1; likewise a fifth breed would be ranked 2.

BREED 3   **Code** ☐
    (from list of breeds)

MIXED CROSSES

1. Common breed name _____

    Local breed name _____

1. **Breeds apparently used to produce mixed crosses of chicken in flock** (rank up to four breeds in order of probable influence - use owner's knowledge if known)

    Rank   Code

2. Trend within flock *(tick one)*

Increasing ☐   Decreasing ☐
Stable   Unknown

1. ☐ Common name _____
     Local name _____

2. ☐ Common name _____
     Local name _____

3. ☐ Common name _____
     Local name _____

4. ☐ Common name _____
     Local name _____

3. Number of adult sheep

Male ☐   Female ☐

    or   unknown ☐

4. Number of lambs

Average number of lambs per breeding season ☐

Breeding season ☐ months

4. Origin/source of breed

1. Inherited ☐
2. Communal area farm ☐   * *specify location of known*

3. Commercial farm * ☐ _____
4. Market * ☐

2. Numbers of adult sheep

Male ☐   Female ☐

3. Number of lambs

Average number of lambs per breeding season ☐

Breeding season ☐ months

5. Quality of traits perceived by owner
    (Ask each question and for each trait tick one box, poor, average, good, no opinion)

4. Quality of traits perceived by owner
    (Ask each question and for each trait tick one box, poor, average, good, no opinion)

Poor	Average	Good	No opinion/ not important		Poor	Average	Good	No opinion/ not important
☐	☐	☐	☐	………… 1. Size ……………………….	☐	☐	☐	☐
☐	☐	☐	☐	………… 2. Conformation / shape …….	☐	☐	☐	☐
☐	☐	☐	☐	………… 3. Mothering ability……	☐	☐	☐	☐
☐	☐	☐	☐	………… 4. Disease tolerance ………….	☐	☐	☐	☐
☐	☐	☐	☐	………… 5. Drought tolerance …………	☐	☐	☐	☐
☐	☐	☐	☐	………… 6. Heat tolerance ……………..	☐	☐	☐	☐
☐	☐	☐	☐	………. 7. Temperament ……………...	☐	☐	☐	☐
☐	☐	☐	☐	………. 8. Control of flies……………	☐	☐	☐	☐
☐	☐	☐	☐	…………9. Numbers…………………..	☐	☐	☐	☐
☐	☐	☐	☐	……….. 10. Meat taste/quality …………	☐	☐	☐	☐
☐	☐	☐	☐	……….. 11. Growth rate ………………..	☐	☐	☐	☐
☐	☐	☐	☐	……….. 12. Fertility ………………….	☐	☐	☐	☐
☐	☐	☐	☐	……….. 13. Foraging ability ………..	☐	☐	☐	☐

Other (specify)

| ☐ | ☐ | ☐ | ☐ | ……….. 14. _____ | ☐ | ☐ | ☐ | ☐ |

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SHEEP   **Phenotypic description**   **Page 10**

IF MORE THAN ONE PURE BREED SELECT ONE BREED.

1. **Breed common name** _____   **Code** [ ] *(from list of breeds)*

2. **Colour** *Enter number(s) from colour chart. Complete more than one portion of triple or double box if sheep have more than one colour, main colour first; second colour second; third colour third; first box only if uniform. Rank in order of frequency of colour combinations in flock.*

	Rank	Males	Females			*Rank*	M	F			*Rank*	M	F
Wool	1.				Hair colour	1.					1.		
	2.					2.				Horns	2.		
	3.					3.					3.		
	4.												
	5.												

	Rank	M	F			*Rank*	M	F			*Rank*	M	F
	1.				Mouth	1.				Lambs	1.		
	2.					2.					2.		
						3.					3.		

3. **Tail type**   M   F

   (1 or more ticks allowed)
   1. Thin
   2. Flat rump
   3. Thick base
   4. Fat

   Present [ ]   Density   Full [ ]
   Absent [ ]   Sparse [ ]

4. **Head features**   <u>Comb</u>   1. Single   M [ ]   F [ ]   <u>Comb size</u>   1.   Small   M [ ]   F [ ]

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(1 or more ticks allowed)

2. Pea ☐ ☐
3. Rose ☐ ☐
4. V-shaped ☐ ☐
5. Walnut ☐ ☐
6. Absent ☐ ☐

2. Medium ☐ ☐
3. Large ☐ ☐

	M	F
Wattles Present	☐	☐
Absent	☐	☐

		M	F
Beak	Short	☐	☐
	Medium	☐	☐
	Long	☐	☐

Beak	Hooked	☐
	Straight	☐

		M	F
Earlobes	Small	☐	☐
	Large	☐	☐

5. Legs

		M	F
Length	Short	☐	☐
	Medium	☐	☐
	Long	☐	☐

Feathers	Present	☐
	Absent	☐

Spur size	Rudimentory	☐
	Medium	☐
	Long	☐

Number of toes / digits ☐

6. Body

		M	F
Frame	Small	☐	☐
	Medium	☐	☐
	Large	☐	☐

Shape	Blocky/compact	☐
	Angular/tallish	☐

7. Tail

Length	Short	☐
	Medium	☐
	Long	☐

8. Eggs

Shell colour *(1 or more ticks allowed)*

1. White ☐
2. Brown ☐
3. Tinted ☐
4. Light brown ☐
5. Reddish ☐
6. Red spotted ☐

7. Other _____ ☐

Size
1. Small ☐
2. Medium ☐
3. Large ☐
4. Mixed ☐

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Table 1 Selected sites for rangeland condition scoring for communal and small-scale farmers

Farms	GPS coordinates		Season	District
Farm 1				Karoo
Camp 1	32˚45'29.77"S 22°29'56.37"E	;	Wet-season	Karoo
Camp 2	32˚45'28.94"S 22°31'08.56"E	;	Wet-season	Karoo
Farm 2				
Camp 1	32˚18'02.41"S 22°37'41.83"E	;	Wet season	
Camp 2	32˚18'02.13"S 22°37'35.70"E	;	Wet season	
Farm 3				West Coast
Camp 1	31˚38'06.14"S 18°13'48.66"E	;	Dry season	
Camp 2	31˚36'48.11"S 18°15'01.80"E	;	Dry season	

Farm 4			
Camp 1	31°36'37.55"S	;	Dry season
	18°17'34.70"E		
Camp 2	31°36'26.73"S	;	Dry season
	18°15'32.02"E		
Farm 5			
Camp 1	31°41'58.34"S	;	Dry season
	18°15'36.32"E		
Camp 2	31°41'38.35"S	;	Dry season
	18°15'21.94"E		
Farm 6			
Camp 1	31°40'21.30"S	;	Dry season
	18°15'06.96"E		
Camp 2	31°37'54.07"S	;	Dry season
	18°16'13.02"E		

Table 2 Age in years vs Bodyweight

Age	N Obs	Mean	Std Dev	Std Error	Minimum	Maximum
1	96	43.15789	10.21036	2.342417	27	67
2	162	51.2763	6.778568	0.583406	36	73.5
4	164	54.9042	6.929737	0.579494	38.2	76
6	348	58.53901	8.400915	0.467439	39	88
8	272	59.52571	7.79831	0.498216	40.5	84
9	65	56.93617	8.107603	1.182616	39	77

Table 3 Body condition score vs bodyweight

BCS	N Obs	Mean	Std Dev	Std Error	Minimum	Maximum
1	6	46.91667	7.241662	2.956396	40	56
2	76	54.64844	7.869814	0.983727	39	76
2.5	145	53.70417	5.986854	0.546523	40	74
3	414	56.37394	8.692202	0.462639	27	83
3.5	193	61.06204	7.538735	0.644078	42.5	88
4	102	62.74667	9.233229	1.066162	41	85
4.5	3	76	2.645751	1.527525	74	79

Table 4 Analysis of maximum likelihood estimates for sources of income

Analysis of Maximum Likelihood Estimates sources of income					
Parameters	DF	Estimate	Standard Error	Wald Chi-Square	P-value
Intercept 1:1	1	-2.298	0.834	7.594	0.0059
Intercept 2:2	1	-0.253	0.768	0.1085	0.7418
Intercept 3:3	1	0.193	0.769	0.0629	0.8020
Intercept 4:4	1	2.115	0.855	6.1201	0.0134
Farmsize	1	-0.0003	0.0003	1.5614	0.2115
Sheep	1	-0.0012	0.0015	0.5984	0.4392
District E	1	-0.339	0.6322	0.2878	0.5917
District K	1	0.777	0.6316	1.5117	0.2189
Wealth 2	1	-0.410	0.3405	1.4514	0.2283
Gender 1	1	1.282	0.6568	3.8075	0.0510
Ownership 1	1	-0.708	0.4252	2.7729	0.0959
Ownership 2	1	1.472	0.5940	6.1447	0.0132

Table 5 Analysis of maximum likelihood estimates for sale outlets

Analysis of Maximum likelihood estimates for sale outlets					
Parameter	DF	Estimate	SE	Wald Chi square	P-value
Intercept 1:1	1	-0.915	0.931	0.9657	0.326
Intercept 2:2	1	0.185	0.945	0.0384	0.8446
Intercept 3:3	1	3.589	1.167	9.4489	0.0021
farmsize	1	-0.0008	0.0004	3.409	0.0648
District E	1	1.031	0.749	1.892	0.169
District K	1	-0.974	0.742	1.725	0.1891
Age 1	1	-3.197	1.351	5.599	0.0180
Age 2	1	0.934	1.248	0.559	0.4545
Age 3	1	-1.645	1.138	2.089	0.1483
Age 4	1	2.462	0.908	7.350	0.0067
Age 5	1	-0.425	0.959	0.196	0.6577
Owner 1	1	-2.228	0.712	9.796	0.0017
Owner 2	1	3.017	0.993	9.236	0.0024

Table 5 Analysis of maximum likelihood estimates for sale outlets

Table 6. List of significant SNP with chromosome-wise significance of P < 0.0005

SNP	CHR	Position (bp)	P-value	Nearest gene		Gene name
				Name	BP	
OAR2_218456860.1	2	218,456,860	0.00048	LOC101109682	218,875,431 - 218,876,300	Protein potassium-transporting ATPase alpha chain 2-like
OAR3_23303598.1	3	23,303,598	0.00005	TRNAC-ACA TRNAW-CCA	23,212,077 - 23,212,149 23,549,786 - 23,549,857	Transfer RNA cysteine (anticodon ACA) Transfer RNA tryptophan (anticodon CCA)
OAR3_84974488.1	3	84,974,488	0.00008	LOC101123202	89,840,447 - 89,842,243	Protein envelope glycoprotein like
OAR3_213627286.1	3	213,627,286	0.00038	TRIB2	21,433,432 - 21,461,996	Tribbles pseudokinase2
s75058.1	4	98,721,454	0.00018	AGBL3	98,659,832 - 98,763,986	ATP/GTP binding protein-like 3
s56605.1	4	118,637,266	0.00028	PTPRN2/	118,111,951 - 118,577,925	Protein tyrosine phosphatase, receptor type, N polypeptide 2
OAR4_119012773.1	4	119,012,773	0.00046	VIPR2	119,039,321 - 119,109,023	Vasoactive intestinal peptide receptor2
OAR5_89563589.1	5	89,563,589	0.00006	GDF9 LOC10112010	41,839,600 - 41,845,359 89,941,245 - 89,943,167	Growth differentiation factor 9 Protein envelope glycoprotein-like
OAR5_102547933.1	5	102,547,933	0.00038	TRNAC-GCA	101,950,656 - 101,950,727	Transfer RNA cysteine (anticodon GCA)
OAR6_19690807.1	6	19,690,807	0.00047	INTS12 BMPR1B	19,605,926 - 19,635,196 29,361,995 - 29,587,033	Integration complex subunit Bone morphogenetic protein receptor, type 1B
OAR8_11038693.1	8	11,038,693	0.00046	ECHDC1	11,087,194 - 11,121,190	Ethylmalonyl-CoA decarboxylase 1

OAR11_30478578.1	11	30,478,578	0.00034	LOC101114791	30,312,220	-	Kelch repeat and BTB domain-containing protein 4
					30,315,257		
OAR11_32628142.1	11	32,628,142	0.00046	TRIM16	32,555,397	-	Tripartite motif containing 16
					32,585,770		
s65320.1	13	37,481,058	0.00018	OVOL2	37,399,585	-	mRNA ovo0like zinc finger 2
					37,424,537		
				PGFS	43,010,431	-	prostaglandin F synthase 1
				OXT	43,024,893		oxytoxcin/neurophysin I prepropeptide
					51,437,794	-	
					51,438,684		
s45329.1	15	3,423,076	0.00004	PDGFD	3,848,954	-	Platelet derived growth factor D
					4,132,770		
s54837.1	15	25,170,260	0.00050	CADM1	25,193,732	-	Cell adhesion molecule 1
					25,556,301		
OAR15_27259223.1	15	27,259,223	0.00010	PAFAH1B2	27,333,728	-	Platelet-activating factor acetylhydrolase 1b, catalytic subunit 2 (30kDa)
					27,349,403		
				SIK3	27,003,266	-	SIK family kinase 3
					27,120,866		
s22327.1	18	64,004,560	0.00043	WDR25	63,934,652	-	WD repeat domain 25
					64,082,517		
s20231.1	18	65,893,960	0.00008	CINP	65,834,515	-	Cyclin-dependent kinase 2 interacting protein
					65,848,211		
				TECPR2	65,862,065	-	Tectonin beta-propeller repeat containing 2
					65,947,163		
s30508.1	20	14,351,869	0.00002	LRFN2	14,364,975	-	leucine rich repeat and fibronectin type11 domain
					14,408,498		
				FRS3	15,672,307	-	fibroblast growth factor receptor substrate3
					15,680,190		
				SPATS1	17,899,513	-	spermatogenesis associated, serine rich 1
					17,937,057		
OAR20_48109414.1	20	44,188,831	0.00006	EVOLV2	44,198,398	-	EVOVL fatty acid elongase 2
					44,234,231		

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| OAR25_38810834.1 | 25 | 38,810,834 | 0.00018 | *CDHR1* | 38,788,175 – 38,809,445 | Cadherin related family member 1 |
| | | | | *LRIT1* | 38,818,798 – 38,841,222 | Leucine-rich repeat, immunoglobulin-like and transmembrane domains 1 |

Table 7. Significant SNPs using HAPFLK method

SNP marker	Chromosome	Position	P-value	Gene	Name	Gene position	Function
OAR1_116705932.1	1	116.7	6.081	LOC101109936 (FMO3)	Protein dimethylaniline monooxygenase		Oxidative metabolism of drugs and pesticides
s59682.1	1	263,592,923	5.766	LOC101110379	Microtubule-associated protein 1 light chain 3 beta pseudogene	236,550,820-263,551,273	2170 functional associations with biological entities spanning 7 categories, molecular profile, phenotype/trait, disease etc.)
s67374.1	1	286344456	5.059				
s07942.1	2	101348019	4.802	ELP3	Elongator acetyltransferase complex subunit 3	101,285,814-101,411,627	Catalytic subunit of the histone acetyltransferase elongator complex, which contributes to transcript elongation and also regulates maturation of projection neurons

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OAR3_163532819.1	3	163532819	5.453	DNAJC14 GDF11	DNAJ heat shock protein family (Hsp40) member C14 Growth differentiation factor 11	163,362,541-163,369,564 163,428,386-163,437,813	Highly conserved proteins, play a role in translation, folding, unfolding, translocation and degradation. Also known as bone morphogenetic protein 11 – myostatin homologous and acts as an inhibitor of nerve tissue growth. Also controls tissue size during muscular and neural development.
OAR3_228963091.1	3	228963091	5.432	RABL2B	RAB, member of RAS oncogene family-like 2B	224,245,620 – 224,261,805	Plays a role in GTPase activity that have manifold functions in diseases
s13763.1	3	237076621	5.104				
OAR4_95728129.1	4	95728129	5.539	PLXNA4	Plexin A4	95,790,004 – 96,204,100	Plays a role in axon guidance in the developing nervous system
OAR5_41052610.1	5	41052610	5.543	STK 11	Serine/threonine kinase 11	41,052,535 – 41,068,369	Regulates cell polarity and functions as a tumor suppressor. Associated with the

							Peutz-Jeghers syndrome in humans and testicular germ cell tumor
s48233.1	5	95229702	5.112	RGMB	Repulsive guidance molecule family member B	95,304,463 – 95,320,117	BMP coreceptor and sensitizer of BMP signalling, highly expressed in adult dorsal root ganglion
s38754.1	5	108808797	5.137	STARD4	StAR related lipid transfer domain containing 4	107,832,742 – 107,841,096	Cholesterol homeostasis
OAR6_36577984.1	6	36577984	5.318	PKD2	Polycystic kidney disease 2 (autosomal dominant)	36,564,403 – 36,630,798	Controls genetic disorder that causes cysts to grow in the kidneys
OAR6_41192387.1	6	41192387	5.610	TRNAS-GGA	Transfer RNA serine	41,200,559 – 41,200,630	
OAR7_30151280.1	7	30151280	6.202	TMCO5A	Protein transmembrane and coiled-coil domains 5A		Function is unknown
OAR7_99051689.1	7	99.05	6.226	TTC7B	Tetratricopeptide repeat domain 7B		Mutations of this gene causes dermatitis and anemia in mice (Helms et al., 2005)
OAR7_45107055.1	7	45107055	5.437	VPS13C	Vacuolar protein sorting 13 homolog C (S.Cerevisiae)	45,080,689 – 45,260,975	This gene encodes a member of the vacuolar protein sorting-associated 13 gene family. The function in mammals are unknown

OAR7_53371605.1	7	53371605	5.356	UNC13C	UNC-13 homolog C – (C.elegans)	52,649,715 – 53, 333,071	May play a role in vesicle maturation during exocytosis as a target of the diacylglycerol second messenger pathway
s04203.1	8	26713168	5.911	CDK 19	Cyclin-dependant kinase 19	26,592,262 – 26,759,432	Associated with development biology and metabolism pathways. Plays a role with transferase activity, transferring phosphorus containing groups and protein tyrosine kinase activity
OAR9_7947468_X.1	9	7947468	5.211	TRNAC-GCA	Transfer RNA cysteiene (Anti-codon GCA)	7,973,164 – 7,973,235	
s09014.1	9	78982140	5.033	LAPTM4B	Lysosomal protein transmembrane 4 beta	78,987,981 – 79,024,555	Protein coding gene, and is associated with hepatocellular carcinoma (liver cancer). Lysosome is its related pathway.
OAR10_2423211.1	10	2423211	5.009	LOC101104917	60S ribosomal protein L3 pseudogene	2,376,321 – 2, 377,486	Plays a role in protein synthesis. This protein belongs to the L3P family of ribosomal protein L3 pseudogene and is located in the cytoplasm – contributes to tat-mediated transactivation. This is a

							pseudogene and is dispersed throughout the genome.
OAR10_4743855.1	10	4743855	6.294	LOC101121104	Protein chromosome 18 open reading frame, human C15orf40 pseudogene		Protein coding gene
s12145.1	10	84528646	5.450	RAB20	RAB20, member RAS oncogene family	84,520,996 – 84,549,769	Plays a role in maturation and acidification of phagosome that engulfs pathogens such as S.aureus and M.tuberculosis
OAR12_4097445.1	12	4097445	5.035	C12H1orf116	Chromosome 12 open reading frame, human C1orf116	4,098,934 – 4,104,571	Protein coding gene
s16001.1	12	67408377	5.602	SMYD2	SET and MYND domain containing 2	67,363,564 – 67,396,799	Related pathways are chromatin organization and chromatin regulation and acetylation. Also plays a role in P53 binding and protein-lysine-N-methyltransferase activity.
OAR13_51852034.1	13	51852034	5.797	IDH3B	Isocitrate dehydrogenase 3 (NAD+) beta	51,851,424 – 51,856,356	Diseases associated with this gene include idh3b-related retinis pigmentosa and

							retinis pigmentosa 46. Related pathways are metabolism and carbon metabolism.
s51670.1	13	67900809	5.791	TRNAE-UUC	Transfer RNA glutamic acid (anti-codon UUC)	67,566,716 – 67,566,787	
s37081.1	13	79553563	5.470	LOC101120007	Zinc finger protein 64 homolog, isoforms 3 and 4	79,340,612 – 79,478,197	Transcription and DNA-templated
s54638.1	13	84935827	6.526	LOC101102832	Cerebellin-4	82,870,821 – 82,876,344	Involved in regulation of neurexin signalling during synapse development.
OAR14_8026941.1	14	8026941	5.134	HSD17B2	Hydroxysteroid (17-beta) dehydrogenase 2	8,023,082 – 8,121,369	Diseases associated is progesterone resistance and endometriosis of the ovary. Plays a role in oxidoreductase activity and testosterone dehydrogenase (NAD+) activity.
OAR14_38675883.1	14	38675883	6.216	AP1G1 PHLPP2	Adaptor-related protein complex 1, gamma 1 subunit PH domain and leucine rich repeat protein phosphatase 2		Related pathways are immune system and infectious disease. Related pathways are P13K-AKT signalling pathway and P13K/AKT signalling in cancer. Also plays a role in protein/threonine phosphatase activity.

OAR14_51302860.1	14	51302860	5.680	CEACAM20	Carcino embryonic antigen-related cell adhesion molecule 20	51,380,571 – 51,395,600	Protein coding gene
s41005.1	15	36334303	6.193	SRY	Sex-determining region Y – box 6		Intronless gene encodes a transcription factor that is a member of the high mobility group (HMG)-box family of DNA-binding proteins. This protein is the testis-determining factor (TDF), which initiates male sex determination. Mutations in this gene give rise to XY females with gonadal dysgenesis (Swyer syndrome); translocation of part of the Y chromosome containing this gene to the X chromosome causes XX male syndrome. [provided by RefSeq, Jul 2008]
s75091.1	16	4684035	5.707	DUSP1	Dual specificity phosphatase 1	4,578,597 – 4,581,669	Among its related pathways are MAPK signalling pathway and Immune System. GO annotations related to this gene include phosphatase activity and protein

							tyrosine/serine/threonine phosphatase activity.
s41735.1	16	34825354	5.655	LOC101117109	1-aminocyclopropane-1-caboxylate synthase –like protein 2-like	34,709,010 – 34,710,712	Biosynthetic process
s66037.1	16	76045641	5.218	LOC101112676	Sodium-dependant neutral amino-acid transporter B (0) AT3	71,661,009 – 71,695,124	Amino acid transmembrane transport
OAR18_22628079.1	18	22628079	4.990	TM6SF1	Transmembrane 6 superfamily member 1	22,597,572 – 22,621,723	Protein coding gene, May function as sterol isomerase
OAR19_29949680.1	19	29949680	5.122	EIF4E3	Eukaryotic translation initiation factor 4E family member 3	29,890,032 – 29,934,528	Protein Coding gene. Among its related pathways are Immune System and Interleukin receptor SHC signalling
S01276.1	20	50.71	6.090	EXOC2 IRF4	Exocyst complex component 2 Interferon regulatory factor 4		Protein Coding gene. Among its related pathways are Ras signaling pathway and Organelle biogenesis and maintenance. GO annotations related to this gene include protein kinase binding and Ral GTPase binding.

							A protein coding gene. Related pathways are Immune System and Interleukin receptor SHC signaling.
s67834.1	21	46994392	5.953	SHANK2	SH3 and multiple ankyrin repeat domains 2	46,860,749 – 47,308,546	Related pathways are Neuroscience and Circadian entrainment. GO annotations related to this gene include SH3 domain binding and GKAP/Homer scaffold activity.
OAR22_11674522.1	22	11674522	5.193	KIF20B	Kinesin family member 20B	11,106,788 – 11,183,706	Among its related pathways are Gastric cancer network 1. GO annotations related to this gene include ATPase activity and microtubule motor activity.
s48675.1	22	43604564	5.008	CTBP2	C-terminal binding protein 2		Among its related pathways are Signaling by GPCR and Downstream signaling events of B Cell Receptor (BCR). GO annotations related to this gene include chromatin binding and transcription corepressor activity.

OAR22_46360230.1	22	46360230	5.305	CLRN3	Clarin 3	46,221,487 – 46,238,190	Protein coding gene
s35549.1	23	7810481	5.258	DOK6	Docking protein 6	7,486,798 – 7,762,162	Protein Coding gene. Among its related pathways are Signaling events regulated by Ret tyrosine kinase. GO annotations related to this gene include insulin receptor binding.
OARX_27222920.1	23	27222920	7.141	TRNAS-GGA	Transfer RNA serine (anti-codon GGA)	28,232,247 – 28,232,318	
s46450.1	23	44516757	5.042	LOC 101108009	Heterogenous nuclear ribonucleoproteins A2/B1 pseudogene	44,336,101 – 44,337,153	
OAR25_8308578.1	25	8308578	6.484	GNG4	Guanine nucleotide binding protein (G protein), gamma 4		Protein Coding gene. Among its related pathways are PI3K-Akt signaling pathway and Signaling by GPCR. GO annotations related to this gene include signal transducer activity

| s00745.1 | 25 | 17585973 | 5.016 | C25H10orf107 | Chromosome 25 open reading frame, human C10orf107 | 17,474,909 – 17,634,075 | Function unknown |
| s26517.1 | 25 | 35694641 | 5.516 | SH2D4B | SH2 domain containing 4B | 35,539,285 – 35,615,388 | Protein Coding gene. Diseases associated with SH2D4B include lymphocytic vasculitis. |

Table 8. Significant loci using the Bayescan method

SNP	CHR	BP	FST
s23238.1	1	5,699,676	0.41182
OAR2_128764057.1	2	128,764,057	0.43482
OAR2_217552388.1	2	217,552,388	0.43198
s69477.1	3	81,649,601	0.4624
OAR3_82856188.1	3	82,856,188	0.46232
s05350.1	3	109,965,012	0.47729
OAR3_112822823.1	3	112,822,823	0.41442
OAR3_116028634.1	3	116,028,634	0.49764
OAR3_124569037.1	3	124,569,037	0.56225
OAR3_130491628.1	3	130,491,628	0.57381
OAR3_132622955.1	3	132,622,955	0.42395
OAR3_133356568.1	3	133,356,568	0.53024
OAR3_133503603.1	3	133,503,603	0.45633
OAR3_134032158.1	3	134,032,158	0.46693
OAR3_138331159.1	3	138,331,159	0.43614
OAR3_141586525.1	3	141,586,525	0.4334
OAR3_195793605_X.1	3	195,793,606	0.44239
OAR3_231138606.1	3	231,138,606	0.4257
s43578.1	3	231,769,938	0.51423
s70203.1	4	35,518,370	0.47627
OAR4_71383944.1	4	71,383,944	0.49247
OAR4_92927340.1	4	92,927,340	0.49061
OAR5_2654207.1	5	2,654,207	0.43326
OAR5_6254624.1	5	6,254,624	0.4145
OAR6_10168376.1	6	10,168,376	0.42205
s26384.1	6	38,098,780	0.49082
OAR6_40243862.1	6	40,243,862	0.45216
OAR6_40449774.1	6	40,449,774	0.51359
OAR6_41003295.1	6	41,003,295	0.45453
s17946.1	6	41,384,761	0.46784
OAR6_41558126.1	6	41,558,126	0.44552
OAR6_41709987.1	6	41,709,987	0.48207
OAR6_41768532.1	6	41,768,532	0.48106
OAR6_41850329.1	6	41,850,329	0.49336
OAR6_41877997.1	6	41,877,997	0.50743
OAR6_41925630.1	6	41,925,630	0.46441
OAR6_42094768.1	6	42,094,768	0.46169
OAR6_42247197.1	6	42,247,197	0.46492
OAR6_44237876.1	6	44,237,876	0.47434
s58867.1	6	75,612,613	0.50589
OAR6_76473607.1	6	76,473,607	0.44126
s13781.1	6	76,849,900	0.42053
OAR6_77984215.1	6	77,984,215	0.5146

OAR7_38067420.1	7	38,067,420	0.4468
s11708.1	7	38,467,050	0.46994
OAR7_50418021.1	7	50,418,021	0.44688
OAR7_97378846.1	7	97,378,846	0.47648
OAR9_29949529.1	9	29,949,529	0.47622
OAR9_30006653.1	9	30,006,653	0.51302
OAR9_84099974.1	9	84,099,974	0.44985
s17034.1	10	25,458,242	0.50034
OAR10_27832232.1	10	27,832,232	0.42445
OAR10_27878618.1	10	27,878,618	0.45602
OAR10_28727766.1	10	28,727,766	0.47802
OAR10_28772065.1	10	28,772,065	0.43392
OAR10_29381795.1	10	29,381,795	0.46937
OAR10_29469450.1	10	29,469,450	0.54494
OAR10_29511510.1	10	29,511,510	0.55775
OAR10_29538398.1	10	29,538,398	0.50883
OAR10_29546872.1	10	29,546,872	0.54449
OAR10_29654158.1	10	29,654,158	0.5227
OAR10_29722772.1	10	29,722,772	0.50274
OAR10_29907137.1	10	29,907,137	0.5243
s71004.1	10	31,320,357	0.45038
OAR11_18815864.1	11	18,815,864	0.47069
OAR11_18823250.1	11	18,823,250	0.47101
s52637.1	11	42,641,540	0.53422
s47426.1	13	64,882,378	0.44638
s12884.1	13	67,997,490	0.53228
s29580.1	13	81,764,112	0.46161
OAR13_82845711.1	13	82,845,711	0.49481
s25975.1	13	82,942,440	0.52174
s31035.1	14	13,821,805	0.41648
s26449.1	14	14,396,052	0.44507
s20376.1	14	34,582,995	0.44783
OAR14_68319489.1	14	68,319,489	0.42206
OAR15_12382965.1	15	12,382,965	0.422
s70650.1	16	31,566,533	0.45232
OAR16_33109456.1	16	33,109,456	0.43421
OAR16_34620156.1	16	34,620,156	0.5146
OAR16_34798939.1	16	34,798,939	0.44962
OAR16_35656302.1	16	35,656,302	0.43628
OAR16_42184944.1	16	42,184,944	0.478
s42786.1	16	42,194,575	0.47719
OAR16_42312325.1	16	42,312,325	0.49768
OAR16_42499047.1	16	42,499,047	0.45584
s46382.1	16	42,528,765	0.46148
OAR17_25785256.1	17	25,785,256	0.48467
s18007.1	18	4,450,560	0.42728

s31152.1	18	19,734,572	0.44833
s35737.1	19	32,438,845	0.42679
s34377.1	20	55,380,346	0.47774
s17168.1	23	15,714,376	0.42331
OAR23_39886336.1	23	39,886,336	0.47845
OARX_116720248.1	23	116,720,248	0.48561
OARX_116737201.1	23	116,737,201	0.47681