Investigating the diet selection and genetic variation of small ruminants in a dryland pastoral system in South Africa

by

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DECLARATION

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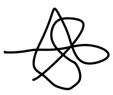

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ABSTRACT

Small ruminants found in pastoral dryland systems face many challenges regarding constant environmental and climate changes. These variable environments are home to many pastoralists who use the natural resources to sustain their livestock. Due to the prevailing environmental changes, these pastoralists require various adaptation strategies for the survival of their small ruminants. Adaptation is vital for all pastoralists globally, especially those living in semi-arid to arid regions as these areas are badly impacted by climate change. Farming with small ruminants that are able to constantly adapt to variable environments are a long-term and low cost resource strategy for farmers in these areas.

Drought is a recurring challenge that farmers in dryland systems have to cope with and small ruminants are forced to adapt to food and water available to them as drought affects their survival, reproduction and production. This is because drought affects the environment directly as rainfall has an impact on all forage and water resources found in drylands. Thus available forage and the utilisation of this resource by small ruminants is essential for sheep and goat farmers who depend on these animals for their livelihoods.

This thesis sets out to establish sheep and goat breeds found in a dryland pastoral system in South Africa focussing on their genetic differences and their diet selection during a drought period. The study was carried out in the 582 634 ha Steinkopf communal area located in the semi-arid to arid region of Namaqualand in South Africa. The dominant land use in this area is livestock farming where farmers utilise two biomes for grazing.

Using mitochondrial DNA, genetic differences were investigated in small ruminants found in Steinkopf. The small ruminants that were studied were the Boer goats, Swakara sheep (Karakul) and cross-bred sheep. These were the most commonly farmed small ruminants in this area. Genetic differences and diversity found within the small ruminants in this area supports their ability to adapt to drought and changing environments. Diet selection of these

small ruminants were assessed using direct forage observation during this drought period in both the Succulent and Nama Karoo biomes.

Findings of the study indicate that small ruminants during a drought period will largely forage on what is available to them. Boer goats changed their diets from browser to grazers in the different biomes while sheep remained grazers in both biomes. This suggests that these animals are well adapted to changing forage availability and will adjust their feeding behaviours accordingly. Succulent plant species were utilised by all small ruminants and this can be regarded as new knowledge for small ruminants in dryland systems. Succulent species play a role in the diets of small ruminants in the Steinkopf rangeland and these animals have adapted traits that allow them to eat plants that contain high levels of phenolics and tannins, which show their high adaptability to this area. This study also revealed that indigenous and locally bred sheep in this area are crucial resources for livestock farming in this area. Swakara sheep in this area showed a low level of genetic variation while cross-bred sheep and the Boer goat had significant variation. With a long tradition of breeding small ruminants in the Steinkopf communal area that suit changing conditions, livestock keepers have accumulated detailed knowledge of their animals.

Recommendations from this study were to do further studies regarding genetic variation within the cross-bred sheep as this information will be useful for breeding programs in dryland areas and it will add to the small ruminant genetics in South Africa. Because this study was conducted in a drought period, I recommend that diet selection should be observed during a regular wet and dry period as this would indicate how these animals adapt to what forage is available to them. These studies can act as management strategies for herders as it can provide information on how to use the natural resources sustainably.

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CHAPTER ONE: GENERAL INTRODUCTION

1.1 Background

Globally, there is evidence of changing environments particularly due to climate change and land degradation (Pott, 1996; Potts, 1998; Grove, 2011; Potts, 2013; Bullinaria, 2018). These changes affect the world in different ways but mostly have a big impact on communities living off natural resources. For many of these nature-based communities, environmental changes essentially affects the livelihood of those who practice livestock farming in arid environments. Due to the prevailing environmental changes, these pastoralists require various adaptation strategies for the survival of their livestock.

Africa's history of climate variability and change has already forced pastoralists to adapt and taught them that mixed species farming is an optimal approach to livestock survival. However, these livestock species and breeds need to be environmentally adapted to issues such as frequent drought periods, hot temperatures, vegetation changes and variable and uncertain climate. Small stock is replacing cattle in many parts of Africa as cattle are identified as a threat to environments that are vulnerable to climate change (Jones and Maroge 2010). In the arid rangelands of Namaqualand in South Africa, small stock farming with mixed species is dominant due to the long history of pastoral traditions in the area but also because of a changing and diverse environment and rangeland management systems (Roux et al., 1981).

The introduction of breeds such as the Meat master in the Namaqualand region has allowed for more diverse genetic material within herds, which can maximise meat quality. However, the quality and quantity of available forage to livestock is one of the main factors that contribute to the production success of a flock. Different breeds forage differently thus having breeds that can change their diets when forage availability changes is important for free ranging livestock found in heterogeneous landscapes.

This thesis sets out to explore sheep and goat breeds found in the Steinkopf dryland pastoral system focussing on their genetic make-up and their diet selection during a drought period. These small-scale farmers are faced with many challenges such as climate change, land degradation, vegetation loss and drought being its more recent event. All of these issues affect livestock production, which directly threatens their livelihoods if they cannot adapt their farming system.

1.2 Livestock production in a global context

The livestock sector accounts for more than 40 % of the agricultural gross domestic products and is an important land-use to the world as it provides almost one-third of the protein intake for humans (FAO, 2009). The demand for livestock products is expanding due to the rapid growing human population and even more so in developing countries (Thornton and Gerber, 2010). The majority of African countries are reliant on agriculture as the main upkeep for their economies, thus making agriculture the largest domestic producer on the continent (Hussein et al., 2008).

Livestock farming operates under a wide range of environmental conditions and is the dominant land use on 41% of the earth's surface which consist of subtropical and tropical drylands, mountainous and high altitude zones and semi-arid to arid regions (FAO, 2009). These areas are home to many rural communities that are dependent on livestock farming to maintain their livelihoods. Most of these communities are situated in harsh environmental climates such as semi-arid to arid areas (FAO, 2009). Not only is the rapid increase in human population influencing livestock production, environmental factors such as climate change is affecting livestock production. The increasing change in climatic conditions is expected to affect livestock in these areas by making them more vulnerable when there is increasing temperatures and little to no rainfall (Rust and Rust, 2013).

1.3 Livestock farming in semi-arid regions

Semi-arid regions are climatically stressed with high temperatures, low rainfalls and long dry seasons and rainfall uncertainty (New, 2015). These regions are dynamic with high primary productivity in the wet seasons and low primary productivity in the dry seasons (New, 2015). Approximately 65% of South Africa's rangelands are in the semi-arid or arid areas and these areas are characterised by low annual rainfall, often less than 500 mm, decreasing as you move west (Snyman, 1998). Due to seasonal and multi-year droughts experienced within these areas, the most extensive agricultural activity is livestock farming with mainly sheep, goats, cattle and ostriches and different breeds of each species (Snyman, 1998).

In South Africa, there are two main livestock farming systems, these include commercial and communal (pastoral) systems. Commercial farms are privately owned and the main aim of these farms are to maximise production. Pastoralism is practiced on communal areas that are not privately owned. For these communities, farming with animals is not only for production, but serves other socio-economic purposes such as a saving mechanism which allows farmers to acquire other necessities in time of need (Samuels, 2006). In South Africa, communal rangelands are often perceived to be overgrazed, degraded, unproductive and overstocked (Lamprey, 1983). When these systems are compared with commercial farming areas, pastoralism is seen as unsustainable (de Bruyn, 1998). However, pastoral areas globally, including South Africa, are resource poor, consequently these farmers are faced with many challenges including climate change and environmental change such as land degradation. The literature on pastoralism is uneven with studies suggesting that pastoralism can be seen as a "problem" or a "crisis" with regards to what farmers experience or what this farming system is said to cause (FAO, 2001). A study conducted by Ward et al., 1998, showed that communal farming in Namibia is not more destructive to the natural environment than commercial farming where soil and vegetation parameters did not differ in communal and commercial areas. Communal farmers are adaptable and knowledgeable about the land that they utilise. These farmers have and are still using their Local Ecological Knowledge (LEK) to adapt to climate change (Nyong et al., 2007; Egeru, 2012; Samuels et al., 2018). These farmers have to balance their understanding of pasture, rainfall, disease, political insecurity and national boundaries with access to markets and infrastructure (FAO, 2001).

Climate change is a challenge to future livelihood strategies practiced by communal farmers, specifically those communities that are currently vulnerable (Bohle et al., 1994). Communities in drylands such as Namaqualand in South Africa are vulnerable to climate change. About 27% of the land in this region is under communal tenure (Rohde et al., 2002) and livestock farming is one of the main uses on these communal rangelands. This area has harsh and variable climate, as a result, making access to resources difficult. Pastoralists practice mobility to find accessible resources such as water and forage (Samuels et al., 2007; 2013; 2019). Pastoralists in Namaqualand have been using this mechanism to alleviate the threat of drought and to avoid the worst effects of natural stress (Samuels, 2006). Namaqualand is prone to frequent drought periods and these droughts usually last for a few successive years (Kelso & Vogel, 2007). As drought conditions worsen it essentially influences livestock productivity. Farmers try and counter these challenges by alleviating the pressure drought has on their livelihood by investing in hardier livestock breeds as well as diversification of these (Escarcha et al., 2018).

Most of the small ruminants farmed in drylands have low metabolic requirements and are able to reduce metabolism and endure the efficient use of water (Silanikove, 2000). This is an important trait to have in these drought prone areas. However, drought affects livestock growth, appetite, health, immune functions and the quality of livestock products directly (Hahn & Mader, 1997; Mader et al., 2009; Gaughan, 2012). Drought impacts on livestock include amongst others heat stress which alters the physiological and behavioural function of livestock, decrease in reproduction performance, livestock deaths which is highest in pastoral systems and directly affecting their welfare (Escarcha et al., 2018). Livestock breeds in drought prone areas need to be resilient and there is considerable genetic variability in domestic livestock, and characteristics such as ability to withstand temperature extremes, drought and diseases. The utilisation of different livestock breeds is essential in developing resilience to climate catastrophes and longer-term climate change (Thornton & Herrero, 2014).

1.4 Livestock breeds in semi-arid areas

Semi-arid areas have a high concentration of small ruminants and are the most prominent livestock units. Small stock animals include different breeds of goats and sheep. Small stock farmers commonly allow for mixed grazing to occur between goat and sheep because these two species have interspecific dietary similarities but in different proportions (Bartolome et al., 1998). According to Animut and Goetsch (2008), the advantages of multi-species herds having different forage preferences is to utilise land that contains a diversity of plant species.

South Africa depends on indigenous developed small stock breeds as they are beneficial genetic resources by which they developed many adaptive traits to respond to pressures in their environment (Soma et al., 2012). Sheep breeds such as the Dorper were locally bred in South Africa as a tough, non-wooled mutton breed that produced excellent meat and milk. This breed demonstrates hardiness to adapt to harsh climate conditions resulting in a popular sheep breed throughout South Africa and the rest of the world (Brand, 2000). Another example includes the Swakara (South Western Karakul) sheep breed. This breed is hardy and well adapted to hot and cold, dry climate conditions and is the most important sheep used in the production of high quality pelts (Näsholm & Eythorsdottir, 2011). Even though this sheep is not indigenous to Southern Africa, it has been locally developed making it a strong adaptable breed in Southern Africa where pelts are produced in Namibia, South Africa and Botswana (Martins & Peters, 1992b). The Boer goat is an outstanding breed that is shaped by its environment and is farmed globally in a wide variety of climates and grazing conditions (Erasmus, 2000). It is one of the hardiest breeds that has a great ability for adaptation including harsh arid conditions (Erasmus, 2000).

Local breeds are important in semi-arid areas thus the replacement and dilution of locally adapted breeds is and will result in a loss of these breeds (FAO, 2007). This potential loss will essentially affect the global food crisis as well as meeting challenges for the future (Jabbar et al., 1999). The preservation of genetic variability for animal production under harsh conditions is important because the majority of animal production occurs in unfavourable regions (Rognoni, 1980). The upkeep of the livelihoods in these regions need to be maintained through the conservation of genetic variability.

1.5 Importance of genetic diversity in livestock

The diversification of livestock breeds which has developed over thousands of years plays a major role in livestock production as we see it today. The long history of natural and human selection, genetic drift, inbreeding and cross-breeding gave rise to the diversity in breeds found within all livestock species today (FAO, 2007). A breed is generally associated with a certain ecological zone, geographic area and farming system (Hall et al., 2017). Breeds are moulded by their environments and by introducing livestock into new surroundings they are faced with natural and cultural challenges (Brand, 2000). These pressures influence livestock breeds to succeed or fail thus new breeds will emerge and replace primitive breeds (Brand, 2000). Breeds that are indigenous or locally bred will be beneficial because of the unique combinations of adaptive traits which allows them to endure harsh climate conditions, enhance meat production, and tolerate various diseases and are able to reproduce and survive for a long period of time (Peters et al., 2010).

The development of breeds goes through specific selection guidelines and are important genetic resources. Livestock breeds are important genetic resources as they have developed adaptive traits that best suit their production needs which allows them the ability to survive, produce and reproduce (Soma et al., 2012). Genetically diverse livestock breeds are essential for the future of livestock production (Hall and Bradley, 1995). Animals that have a diverse genetic make-up have a better chance in meeting future challenges. These challenges include environmental change, emerging diseases, human nutritional requirements as well as a change in the market (FAO, 2007). Livestock contributes to the agro-ecosystems on which production takes place and is evidently important for food security (FAO, 2007).

Genetic diversity within livestock breeds is also important in terms of livestock management. There are over a thousand genetically diverse breeds of domestic animals which have adapted to diverse environments as well as human needs (Jabbar et al., 1999). Animal genetics is important to sustain productivity and the livelihood of people (Jabbar et al., 1999). The increasing loss of genetic diversity will essentially reduce the ability to adapt to change.

Genetic variability can be lost through a number of reasons. These threats include crossbreeding, inbreeding within a population, loss of habitat, disease, neglect and unsustainable breeding management (FAO, 2007). Inbreeding causes high mortality rates, low fecundity, reduces mating ability, and gives rise to slower growth rates and developmental defects (Lacy, 1997). These negative outbreaks essentially affect livestock production.

Semi-arid rural communities that depend on livestock farming rely on genetic diversity that are flexible and resistant. Livestock that undergo genetic modification through breeding systems such as cross breeding allow for sustaining and improving livelihoods of the rural communities. Methods to improve genetic variation include crossbreeding “local breeds” with “improved breeds”. This has a positive impact due to the heterosis which is expressed in a crossbred animal

(Anderson, 2003). Crossing breeds within a region is another option and is recommended for farmers in semi-arid areas.

Livestock breeds in drylands are adapted to the variable climate and harsh environments, such as degradation of vegetation. Livestock rely on the natural resources in these areas and the unfavourable conditions due to changing climate and degradation has a massive impact on forage availability and the quality and quantity of the natural fodder. Livestock species and breeds have co-evolved in semi-arid to arid systems therefore are adapting to prevalent climate. Indigenous and locally developed breeds have over time developed unique combinations of adaptive traits to best respond to pressures of their local environment. Indigenous sheep of Kenya for example, are important to resource-poor pastoralists because over time have adapted to harsh climate conditions such as drought and diseases (Muigai et al., 2009). However, the variability of climate conditions influences the forage resources available to these small ruminants in these pastoral systems.

1.6 Foraging selection and preference of livestock

Foraging plays an important role in the survival, growth and reproductive success of an animal. Different foraging behaviours can be explained by the optimal foraging theory (De Boer & Prins, 1989). This theory begins with an optimal diet, which are choices made by an animal. These choices should essentially be those that give the greatest foraging success where the costs do not exceed the benefits. Grazing animals, such as herbivores, face many challenges in natural forging environments. They require a sufficient trade-off where adequate amounts of nutrients ensure that their welfare is not negatively affected. The optimal diet for herbivores requires them to select food items on sensory and nutritional properties (De Boer & Prins, 1989). These properties allow them to obtain a mixture of foods which they either ingest or reject.

Generally, if an animal is faced with a variety of food items, it will prefer to eat some and avoid others. Preferences are due largely to the palatability and availability of the food items. Palatability is defined as “characteristics or conditions that stimulate a selective response by an animal” (Barroso et al., 1995). In semi-arid ecosystems, biological resources, such as plant biomass, go through periods of high and low quality and availability which is mainly influenced by rainfall events (Schwinning et al., 2004). Seasonal shortages of available natural feed are considered to be the most detrimental constraint to livestock production (Ngwa et al., 2000).

Some livestock species are selective in what they eat and there are different factors that influence their choices. Factors such as seasonality, nutritional value, the distance the plant is from a water point, palatability, associated species as well as how long they spend in a particular habitat in the wet and dry season affects the diet choice (Arnold, 1964; Botha, 2012). Diet selection is a complex behavioural act that is not only influenced by environmental factors but can be influenced by the chemical impairment of taste, smell and touch (Krueger et al., 1974). A study conducted by Krueger et al., (1974), found that taste was the primary sense used by sheep for diet selection. Different livestock species may also have unique morphological, physiological and behavioural traits dictated by its genetic make-up that guide a particular feeding strategy or their exploitation of the available food items (Barroso et al., 1995).

Seasonality changes grazing activities because the amount of forage available to grazing animals depends on the season (Schlecht et al., 2006). Plants consumed by herbivores provide a source of nutrients to the foraging animal but can also contain defences which can prevent herbivory (Duncan et al., 2006). These defences are primarily chemical and physical mechanisms (Cheeke, 1994). Physical defences include spines, thrones and leaf hairs, whereas chemical defences are toxic substances that protect the plants and have a negative effect on herbivores (Cheeke, 1994). Herbivores must therefore balance the rewards of the food items with their negative defences when selecting food items (Duncan et al., 2006).

Semi-arid rangelands in South Africa are seen as heterogeneous landscapes with high temporal and spatial plant variability allowing livestock to make complex food consumption choices (Desmet, 2007). Samuels et al., (2016), show how the management (herding and free-ranging) of different species of livestock herds influences their feeding ecology during the wet and dry seasons in a semi-arid shrubland.

Studies have shown that during drought periods farmers adapt their grazing patterns and management in general. Samuels (2006), found that herders in Namaqualand guide their livestock to higher elevations, as they perceive vegetation and the quality of this vegetation to be better in the mountains. Herders and farmers must continually adjust their practices in order to cope with environmental and climate variable (Scoones, 1992). Namaqualand is projected to change due to changing climate where biomes such as the Succulent Karoo will become more arid (Bourne et al., 2012). This result will affect the local farming community in many ways. Other studies have looked at diet selection in the Succulent Karoo biome (Milton & Hoffman, 1994; Hendricks et al., 2002; Samuels et al., 2016a), however, this study explored the genetic diversity of livestock breeds in this dryland system and assess their diet selection between biomes during a drought period.

1.7 Research aims and questions

The overarching aims of this study were to evaluate diet selection of different small ruminant species and breeds in the semi-arid to arid Steinkopf pastoral rangeland in the Northern Cape province. Furthermore, this study aimed to assess whether genetic variability of these small ruminants plays an important role in forage intake in a dryland pastoral system. This study attempted to answer the following questions;

1) What is the breadth in genetic differences of small ruminant herds found in the Steinkopf dryland pastoral system?

2) What is the nature of the diets of herded small ruminants under meteorological drought conditions?
3) How do the diets of genetically diverse small ruminants compare?

1.8 Significance of this Study

In South Africa, ruminants are found on 80% of the land available to agriculture. Cattle, sheep and goat production constitute between 25-30% of the total agriculture in South Africa. The small stock sector produces 12% of sheep and 67% of goats in the country (Ogunkoya, 2014). The small-scale farming sector is prominent in rural areas where these farmers depend on livestock products for food as these areas are customary to unemployment and poverty (Mandleni, 2011). As a result of climate change, farmers in the Namaqualand area have been struggling with low productivity. Climate change is expected to alter the intensity of droughts in South Africa therefore understanding how small-scale farmers cope with resource use in these climate conditions is important.

This low productivity in this region was influenced by the harsh recurring drought which started in 2015. Small ruminants were faced with many problems during this drought period where the availability of forage changed during the wet season, which was affected by a significant drop in rainfall that was well below the long-term average. These animals had to adapt to what forage was available to them. The adaptability of these livestock breeds allowed for farmers to sustain their livelihoods by having herds surviving during this harsh time. Evidence based on climate adaptable livestock breeds and species in these areas are what could be done to improve productivity and enhance the potential for income for small- scale farmers in Namaqualand is thus a necessity.

1.9 Thesis structure

This thesis comprises of five chapters of which the two data chapters are in journal article format. Information such as study area is repeated in the two data chapters.

Chapter one: Introduction

This chapter introduces the key concepts which this thesis integrates. The chapter gives background to different factors related to livestock farming such as diet selection of small ruminants and livestock breed types. This is followed by the research problem, research aim and research questions.

Chapter two: Study area

This chapter describes the geographical location, climate, vegetation and the major land use which is livestock farming in the Steinkopf communal rangeland. Livestock farming and the methods of this practice is discussed as well as the history of livestock farming in this area.

Chapter three: Genetic variation between small ruminants found in a semi –arid pastoral rangeland in South Africa**.** This chapter investigates what local sheep breeds are being farmed as well as quantify genetic variation with in the local sheep and goat breed populations in a semi-arid pastoral rangeland in South Africa.

Chapter four: Diet selection and preferences of small ruminants during drought conditions in a dryland pastoral system in South Africa. This chapter specifically investigates the availability of forage, the nature of diet selection and the role livestock breeds and biome play in forage preferences.

Chapter five: Study synthesis and recommendations

This chapter synthesizes the main findings of the thesis and embeds them within the general literature on the genetic diversity and diet selection of small ruminants in semi-arid environments.

CHAPTER TWO: STUDY AREA

2.1 Location

The Steinkopf communal area is 582 634 hectares in size and is located in Namaqualand, in the Northern Cape Province in South Africa. It is situated 50 kilometres north from the major administrative town of Springbok and is positioned in the Nama-Khoi Local Municipality (Fig.2.1). Steinkopf is one of the six former coloured missionary stations created during the British administration in the early 1800s to ensure a measure of protection of their traditional grazing lands from being exploited by the colonial farmers (Cousins et al., 2007; Hongslo et al., 2009). Steinkopf has a number of human settlements which include Goodhouse Henkries, Ikosis, Wyam, Gladkop and Bulletrap.

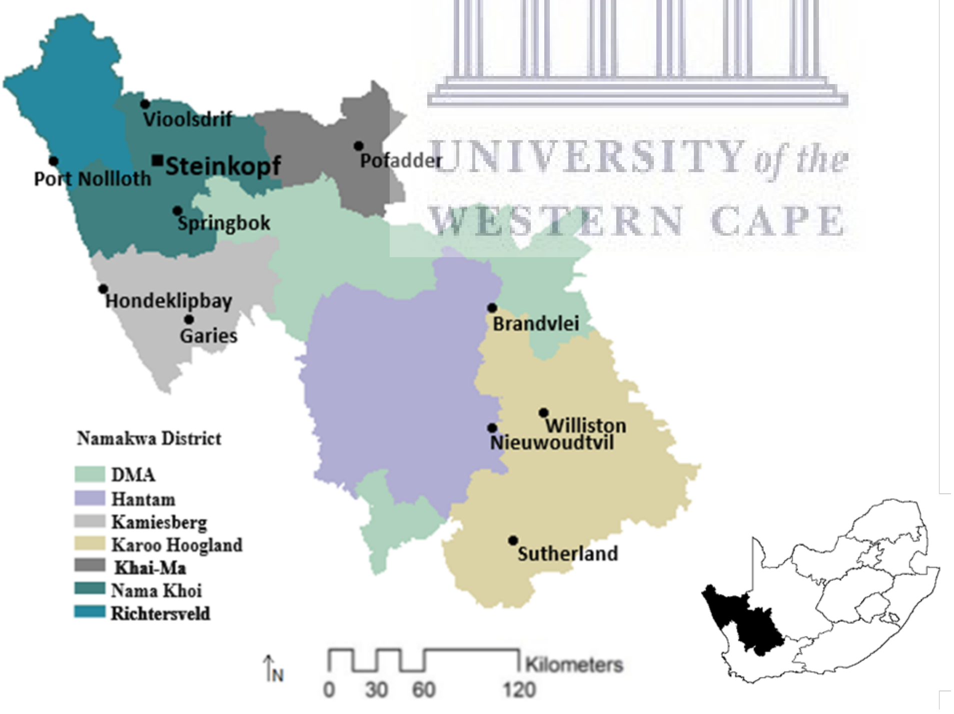


Fig.2.1: Location of Steinkopf in Namakwa District Municipality, Northern Cape.

2.2 Climate

The climate of Steinkopf is divided into winter rainfall in the west and a summer rainfall area in the east known as Bushmanland. More than half of the Steinkopf communal area receives winter-rainfall. The mean annual precipitation ranges between 100-200mm, decreasing from west to east (Mucina and Rutherford, 2006). During winter, there is an increase in fog and dew which contributes to the west-east moisture gradient. The fog and dew are a vital source of moisture for the vegetation, specifically the rare succulent shrubs. This moisture aids in the regeneration of plants in disturbed ecosystems (Matimati et al., 2013). The summers are hot and winters are cold, with a large difference between seasons. The maximum summer temperature can reach up to 39.4°C and the minimum temperature can reach -1.4°C (South African Weather Service 2012). The average maximum winter temperature is 21.1°C and the average minimum temperature is 10.9°C (South African Weather Service, Unpublished data).

Areas such as Steinkopf have shown a decrease in annual rainfall, which is consistent with future climate change predictions for this region (MacKellar et al., 2007). Midgley and Thuiller, (2007) propose that future climates in Namaqualand will be different to any climate that has occurred there for the last several million years; this is according to bioclimatic models which emphasis the decrease of rainfall.

The Northern Cape Province was declared a drought disaster area in 2015.The duration and severity of the drought lasted until 2018. These recurrent droughts cause water stress and livestock farming is severely affected, especially in the communal areas. The average annual rainfall per month, per year (Fig. 2.2.) indicates that there has been a severe decrease in rainfall from 2015-2016. Semi-arid to arid areas are prone to be affected by droughts due to seasonal and variable precipitation patterns. Drought can be defined by different users as well as the geographical and climatic regime of the region being affected (van Vuuren, 2015). In persistently drier areas such as the Sahelian zone in western Africa, droughts are only gazetted after two or more rainy seasons without rainfall (Oladipo, 1985).

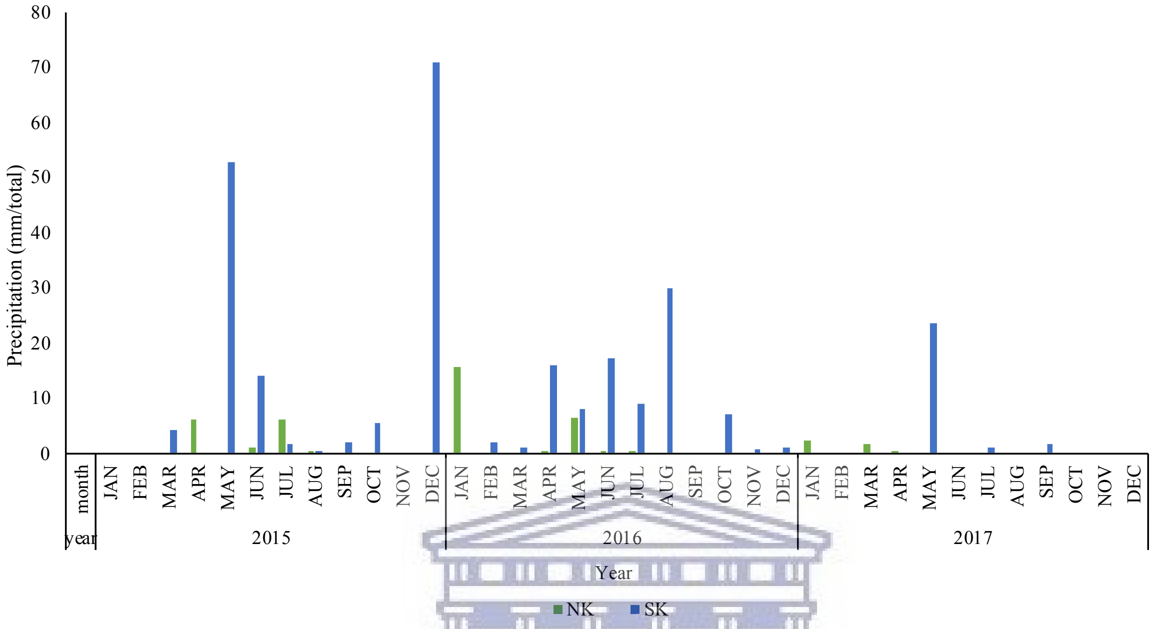


Fig.2.2: Rainfall data for the Steinkopf communal rangeland.

The 2015 drought had an excessive impact on livestock production in Steinkopf, with many farmers forced to slaughter their animals prematurely due to them not being able to survive the harsh climate conditions (Personal. Observation.). In doing so farmers obtain more meat from the animals than if they had to die of emaciation (Western and Finch, 1986). The welfare of the sheep is important at every stage of their development, and under extensive grazing systems this is being compromised by increasing high mortality due to factors such as harsh climate conditions (Fayemi & Muchenje, 2013). Predictions of future decrease in rainfall, and increased drought frequencies and intensities in the winter-rainfall region will thus have a negative impact on the livestock production of agriculturally-dependent communities, such as in Steinkopf (Cousins et al., 2007)

2.3 Vegetation

The vegetation of Steinkopf forms part of the Succulent Karoo, Nama-Karoo and Desert Biomes (Desmet, 2007) (Fig. 2.3.). The Succulent Karoo biome is recognised as a global biodiversity hotspot. According to Myers et al., (2000), a hotspot can be defined as an area featuring exceptional concentrations of endemic species and experiencing exceptional loss of habitats. The Succulent Karoo has more than 4 500 plant species, which is dominated by dwarf succulent shrubs, with 25% consisting of endemic taxa (Desmet, 2007). The growth-form scales are unusual for semi-arid regions with an inadequate amount of tall shrubs, trees and grasses (Cowling et al., 2004). In the wet season, a diverse ephemeral vegetation composed mainly of geophytes make an appearance and are grazed on by livestock. Most of the vegetation falls within the winter rainfall region (Mucina and Rutherford, 2006) and makes up the largest vegetation types in Steinkopf.

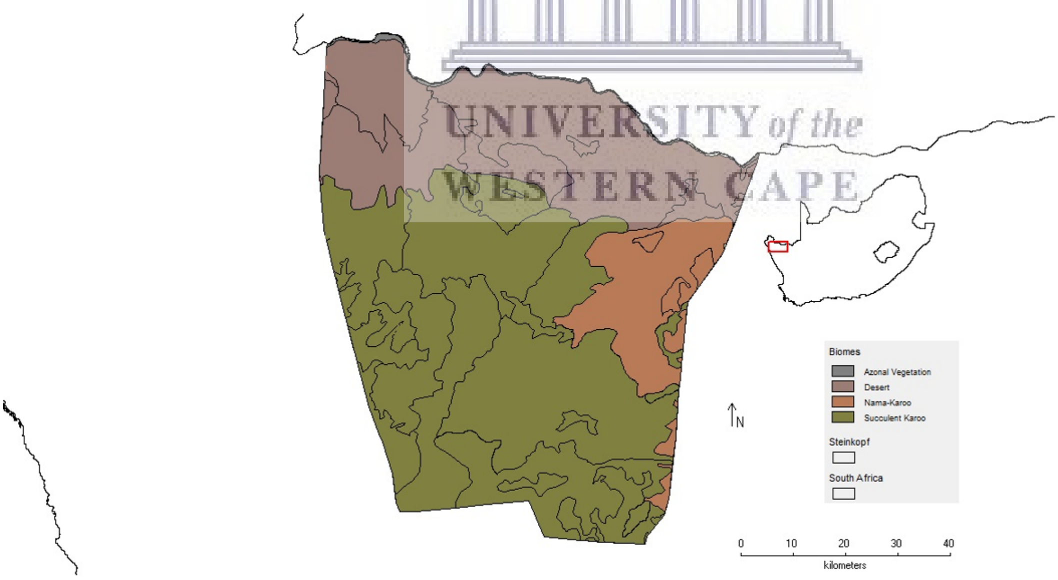


Fig.2.3: Biome distribution map of Steinkopf.

The Nama-Karoo is an arid biome and is a landlocked region. This biome receives most rainfall in the late summer, from December through to April (Rutherford et al., 2006). Namaqualand falls within the Upper Karoo area of the biome and has the highest number of local endemics in the biome at large (Rutherford et al., 2006). The biome has low floristic diversity but has a high diversity of plant form. Growth forms include low dwarf shrubs, grasses, succulents, geophytes and annual forbs (Rutherford et al., 2006). The Nama-Karoo plays a major role in farming in the Steinkopf communal rangeland and the dominant land use is small stock faming. Farmers move their livestock to this biome during the summer months where seasonal grasses are grazed on. However, this biome has suffered considerably from overgrazing, followed by drought, which has changed the vegetation composition (Rutherford et al., 2006).

The desert biome is found in a small area in the northwest of the country located in Namaqualand and stretching to Namibia (Rutherford et al., 2006). Its harsh environmental conditions are more extreme than the Nama-Karoo and Succulent Karoo. There is occasional summer rainfall and high levels of aridity. The mean annual rainfall is 10mm in the west and 70-80mm inland. The desert biome is dominated by annuals (often annual grasses), with drought resistant perennial plants found in more complex habitats within the biome (Desmet, 2007). The desert biome essentially provides grazing resources to livestock and is critical for communal pastoralists in this region. The desert is poorly protected with only 20% of the protected area targets being met.

2.4 The people of Steinkopf

There are currently 10 000 residents in the communal area, of which 596 are registered as small stock farmers (NamaKhoi Local Municipality, 2011). Livestock farming is a tradition of the Nama, and the people of Steinkopf have kept this tradition. The people of Steinkopf keep livestock for various reasons, such as consistent or occasional income, sustenance and savings. The livestock is thus an extremely valuable commodity for the livelihood of the people of Steinkopf. This communal rangeland has approximately 45 000 small stock animals that occupy the land, with an average of each herd being ±150. In this study area, farmers raised two types of livestock - goats and sheep whereas the latter is the most preferred type because of its multiple uses. It is also home to ±900 cattle and hundreds of feral horses and donkeys (Text box 2.0).

Livestock farming: Types and breeds raised in the Steinkopf communal rangeland.

Test box 2.0

Picture A. Boer goat

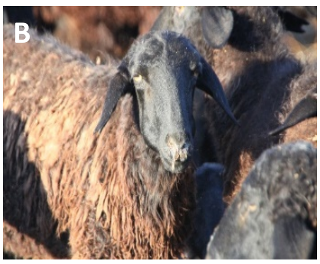
The Boer goat is the only goat breed farmed in Steinkopf. This is an extremely hardy breed that can survive in semi-arid to arid environments. They are well adapted to variable environments such as Steinkopf. Goats are usually kept with sheep and are rarely kept alone. Goat products are not popular amongst the people of Steinkopf hence it is mainly sold to the Kwazulu-Natal market where goat meat and milk are of preference during traditional Zulu ceremonies.

Picture B. Swakara sheep

The Swakara is characterised by their coloured fleece which can be grey, white, brown or the more famously bred, coal black sheep. These sheep are bred for their wool and pelts which has a large contribution to the international fur industry. The wool of the adults is used to make carpets and heavy fabrics however the pelts are the main attraction and the best pelts are obtained from lambs. Steinkopf houses many Swakara farmers which contribute to the Swakara industry whether it be wool or pelt production. According to farmers in Steinkopf, they send their pelts to Namibia, which is the largest producers of Swakara pelts, from here it gets sold under the name Swakara in Denmark.

Picture C. Cross-bred sheep

There are many different sheep breeds found in Steinkopf and all of them are well adapted to the harsh climate conditions. The majority of the sheep found in Steinkopf are cross between breeds such as the Black head Dorper, Swakara, Meat master, Afrikaner, Damara and Persian. The Dorper, Damara and Meat Master sheep are used for meat production however the meat is mainly used for local consumption. Crossing breeds within the region is an extremely effective approach to improving sheep production, reproduction. Each herd has an average of two rams which are mainly Dorpers or newly introduced Meat masters. The rams get rotated within the region by neighbouring herds. The most dominant sheep breeds found in Steinkopf is the Black head Dorper and the Damara.



2.5 Livestock herding practices

2.5.1 Archaeological evidence of small stock herding in Namaqualand

Small stock herding traditions in Namaqualand has been evident from up to 2000 years ago (Webley, 2007). Archaeological research at the Spoegrivier cave in Namaqualand confirms the presence of sheep at 2100 years ago (Sealy & Yates 1994). Between 800 – 360 BP, the co – existence of mixed herds was discovered, where goat and sheep remains were present in the 1983 excavation conducted in Bethelsklip, central Namaqualand (Webley, 1984). Despite the aridity of the region, pastoralism and herding of domestic stock is a tradition that has been kept for thousands of years until present day. There was a change in temperature and aridity throughout the Holocene period and until present, the aridity is however increasing. According to Avery (1992), climate conditions at 2000 years ago were superior to the days where a variety of grasses were present which could have supported the small flocks of sheep.

2.5.2 Transhumance cycle "herd mobility"

As the region became more arid, seasonal transhumance cycle dated as far back as 1661 which was documented by Van Meerhoff's travels to Namaqualand (Moodie, 1959). The extreme environmental factors in these areas forced herders to adopt the transhumance cycle, harsh winters in the Kamiesberg area were so severe that livestock losses were experienced, hence herders moved into more accessible areas such as Bushmanland, which is a summer rainfall area and houses palatable grass species (Mossop, 1931; Webley, 2007). In arid environments mobility is a response to temporal and spatial variability in resources, such as water access and forage availability (McCabe, 2009). Staying close to watering holes were the most common grounds for pastoralists hence movement opened up a window for vegetation away from the watering holes to recover.

2.6 Current herding management strategy

Archaeological evidence and history has confirmed that herding has been practised for millennia in numerous areas in Namaqualand. The communal areas in Namaqualand houses the descendants from Little Namaqua, Steinkopf being one of these rural reserves where the herding strategy has been an on-going management technique used by farmers. The principal economic activity of the early inhabitants as well as the contemporary community of Steinkopf was herding of small stock (goat and sheep) (Carstens, 1961). Mixed farming still constitutes the majority of the farming population in addition new breeds have been introduced and developed to sustain the climate conditions.

Currently in the Steinkopf region, livestock graze in unfenced areas and are always supervised by a herder. Some livestock owners personally herd their livestock whereas some hire herders. Herding is an exhausting process, but according to the local farmers, it is beneficial because it reduces predation, stock theft, and aids with dispersing pressure across the rangeland, as well as contributing to job creation (Salomon et al., 2013). The herders sleep at the stockpost, which includes a kraal for livestock, Khaya (shelter for herder) and a cooking shelter (Fig. 2.4.). Herders can stay in the rangeland for up to six months at a time. Livestock are kept at the stockposts overnight and follow a grazing orbit which returns them back to the stockpost on a daily basis. The grazing routes that the animals walk have a lot to do with where the herder wants them to graze. The majority of the herders in the Steinkopf rangeland have adapted management systems to their own constraints.

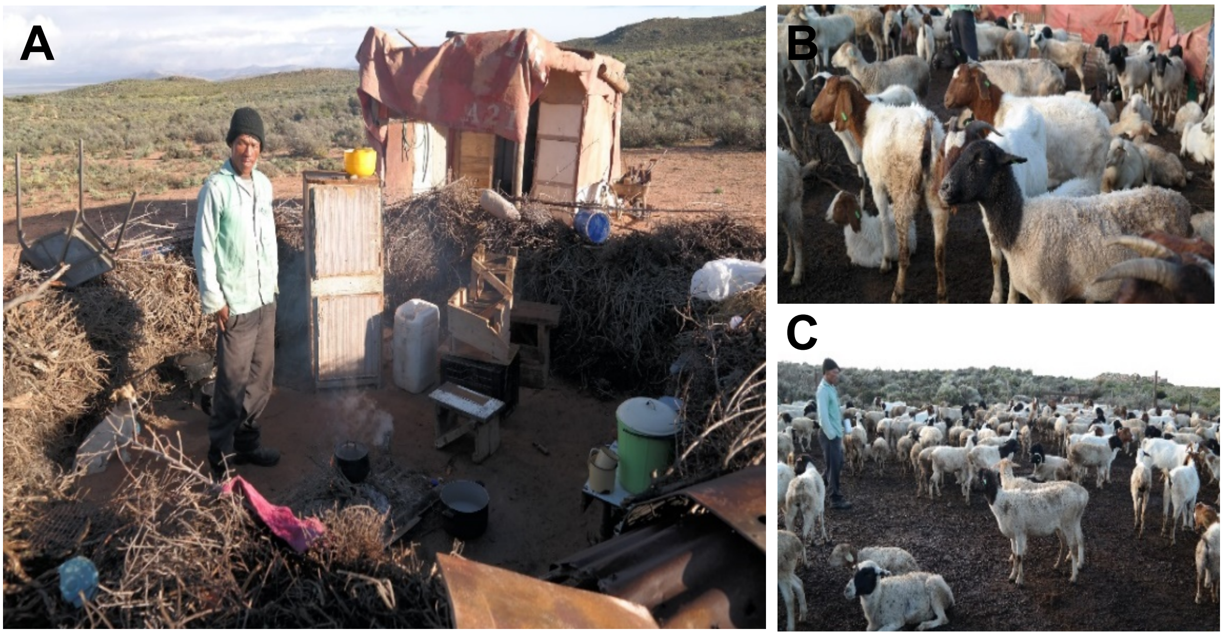


Fig.2.4: Herders' surroundings. (A) The cooking shelter and Khaya. (B and C) the stockpost or "Kraal".

CHAPTER THREE:
ASSESSMENT OF GENETIC DIVERSITY OF SMALL RUMINANTS IN A DRYLAND PASTORAL SYSTEM IN SOUTH AFRICA

Abstract

Genetic diversity of small ruminants is essential for livestock farming systems especially in vulnerable regions such as drylands where environments are constantly changing. It is with desire to preserve genetic diversity of small ruminants in drylands as they possess traits that give rise to adaptations to changing climatic and environmental conditions. Farming with small ruminants such as sheep and goat is the main land-use in drylands in Africa. This study was conducted to explore the genetic diversity and differences within small ruminants found in the dryland pastoral system of Steinkopf in South Africa. Mitochondrial DNA analyses of Swakara sheep, cross-bred sheep and Boer goats were studied to determine the genetic differences and phylogenetic relationships between these small ruminants. Results showed that there is high genetic diversity within the cross-bred sheep and Boer goat herds but low genetic diversity within the Swakara population. Understanding the genetic diversity of small ruminants in the Steinkopf pastoral system is important as the climate and environment are constantly changing. Thus, it is essential to put in place management strategies that would ensure the survival of small-scale farming in this region despite the harsh effects of climate change in present and future times.

Keywords: sheep, goat, genetic diversity, dryland, mitochondrial DNA

3.1 Introduction

Livestock farming is practiced throughout the world where breeds and species differ according to the climate, environment and production systems. Livestock farming in South Africa is a significant contributor to food security and both commercial and communal farming systems provide many economic and social attributes to local communities and the country as a whole (Meissner et al., 2013). In South Africa, livestock production is the dominant land use on roughly 69% of agricultural land and most of these rangelands could be considered semi-arid. Semi-arid areas are climatically stressed environments with high temperatures and low rainfall, and are particularly vulnerable to climate change and catastrophic events such as frequent droughts (Vetter, 2009). Because of increasing temperatures in general and decreasing precipitation in some areas, the livestock sector has been severely affected in these semi-arid regions of South Africa. Large-scale livestock mortalities occur more frequently, the overall condition of rangelands are decreasing which in turn affect livestock health and many farmers have become extinct in recent years (Sweet, 1998; Varadan & Kumar, 2014; Ntombela, 2017).

Unpredictable and variable climate conditions have made farmers selective in what livestock species and breeds to keep. Livestock such as sheep and goat are generally found in regions where temperature is high and climate is harsh (Dwyer, 2009). More than 50% of sheep and goat breeds are adapted to arid areas (FAO 2006b). Indigenous sheep and goat breeds constitute over 95% of the small ruminant population of Africa (Rege 1994). Popular sheep breeds found in the challenging rangelands of Kenya include the Red Maasai and East African fat tailed. These breeds are very important to recourse-poor farmers and pastoralists as they possess traits that allow them to survive where they are constantly faced with challenges of persistent droughts, diseases, and conflict of poor nutrition (Muigai et al., 2009). The Red Massai sheep in Kenya, which can walk long distances in search of forage, adapt to harsh environments and unique traits like being resistant to gastrointestinal parasites, which increase their importance to farmers and pastoralists (Baker et al., 1999; Muigai et al., 2009). South Africa itself has an exceptional pool of indigenous livestock, which have developed adaptive traits to best respond to pressures of local environments (Kruger, 2015). South African breeds such as the Dorper sheep, is well known for its hardiness and adaptation to dry and extensive veld conditions, these characteristics has led to global distribution of the breed for small and large scale meat farming (Brand, 2000). The Boer goat is another South African breed that is farmed globally. This breed is seen to be one of the hardiest small stock breeds in the world and is encounter in a variety of climates (Malan, 2000). The importance of adapted indigenous and local small ruminants are important in South African rangelands as it is seen as a tool for sustainability (Scholtz et al., 2013).

Local breeds play a huge role in small-scale farming because little to no income is used for the survival, production and reproduction of the breeds e.g. a cost for additional feed and medicine (Molotsi et al., 2017). Their broad genetic variability enables them to survive stressful conditions thus embracing survival, resilience and efficiency in both economic and environmental stress (FAO, 2006b). Conserving local and indigenous breeds are thus important for sustaining livestock farming in harsh environments (Rege & Gibson, 2003; Wollny, 2003; Hoffman, 2010).

The increasing loss of genetic diversity will essentially reduce the ability to adapt to change and genetic variability can be lost. Threats that can cause a loss of genetic variability include crossbreeding, inbreeding within a population, loss of habitat, disease, neglect and unsustainable breeding management (The state of agricultural biodiversity in the livestock sector, 2007). Inbreeding causes high mortality rates, low fecundity, reduces mating ability, and gives rise to slower growth rates and developmental defects (Lacy 1997). These negative impacts essentially affect livestock production. The importance of genetic diversity is required to meet current production needs in many different environments and aid in genetic improvement, which is essential for food security (Notter, 2004).

Methods to improve genetic variation include crossbreeding "local breeds" with "improved breeds"; this has a positive impact due to the heterosis, which is expressed in a crossbred animal (Anderson, 2003). Crossing breeds within a region is another option and is recommended for farmers in semi-arid areas. Several studies have assessed genetic diversity in small ruminants in pastoral systems globally (Muigai et al., 2009; Al-Atiyat et al., 2014; Naqvi et al., 2017; Phyu et al., 2017). Also several studies have investigated genetic diversity of small ruminants in South Africa in production and experimental system (Kunene et al., 2009; Peter et al., 2010; Visser et al., 2014; Selepe et al., 2018). However, there have been no studies focusing on genetic diversity of small ruminants in dryland pastoral systems in South Africa. The aim of this study was to investigate what local and indigenous sheep breeds are being farmed as well as quantify genetic variation within and between the local sheep and goat breed populations in a dryland pastoral system in South Africa.

3.2 Study Area

The study was conducted in the Steinkopf communal rangeland (-28.84° S and -29.66° S latitude and 17.58°E and 18.37°E longitude), situated in the arid and semi-arid Namaqualand region of South Africa and is approximately 582 634 hectares in size. The dominant land use in this region is livestock farming. This communal rangeland has approximately 50 000 small stock animals (goat and sheep) that occupy the rangeland and rely on the natural vegetation for forage, with an average of each herd being ±150. Many different sheep breeds that occupy the land as well as the Boer goat. Most of the sheep are cross-bred with the exception to purebred Swakara herds. The Swakara is characterised by their coloured fleece, which can be grey, white, brown or the more famously bred, coal black sheep. Steinkopf houses many Swakara farmers which contribute to the Swakara industry whether it be wool or pelt production. There are many different sheep breeds found in Steinkopf and all of them are well adapted to the harsh climate conditions. The majority of the sheep found in Steinkopf are crossed between breeds such as the Black head

Dorper, Swakara, Meat master, Afrikaner, Damara and Persian (Textbox 2.0. found in Chapter 2). Morphological differences can be seen in Appendix 1.

Farmers cross breeds to get the best and adaptable traits in their herds to survive the harsh environmental and climate conditions. Each farmer in this region own only one or two rams that are either brought in from other areas or are locally from the rangeland, however these farmers rotate rams between herds to increase fecundity, genetic variation and to prevent inbreeding. Generally, famers raise goat and sheep where sheep is most preferred due to the multiple uses they provide such as meat, wool and pelts. The majority of herds found in this rangeland are mixed species of goat and cross-bred sheep however Swakara sheep are usually farmed on their own.

3.3 Methods and materials

3.3.1 Small ruminants and sampling procedure

Hair follicles (collected from female live animals) from 30 different cross-bred sheep, purebred Swakara sheep and purebred Boer goats were collected from nine herds of mixed small ruminants in August 2017. Random sampling was done to allow each female an equal chance to be chosen and as such providing reputable representation of the herd. We sampled a subset of the samples that were collected from different herds to randomize our samples.

3.3.2 DNA extraction and PCR procedure

Total DNA was extracted from hair follicles using the NucleoSpin® Tissue Kit (Macherey-Nagel GmbH & Co. KG, Düren, Germany) according to the manufacturer instructions. DNA quality and quantity estimation by agarose gel electrophoresis was conducted and successful samples were then stored at -20 ˚until further processing. Specimen DNA was amplified via Polymerase Chain Reaction (PCR) using primers designed to amplify 395 pairs (bp)of the cytochrome-b, GLUA (5’- TGA CT TGAA RAA CCA YCG TTG -3’) and GLUJ (5’- CCC TCA GAA TGA TAT TTG TCC TCA -3’).

All PCR reactions were optimized and carried out using 25µl reaction volumes. The PCR reaction solution of 25 µl consisted of 6 µl H2O, 10 µl amplicon (Taq and $MgCl^2$), 2 µl forward primer, 2 µl reverse primer and 5 µl sample. To produce a negative sample, one tube consisted of only the PCR mix and no sample was added. The PCR thermal cycle for the Cyt-b sequence was [94 °C for 4 min], 30 × [(94 °C for 30 s), (50 °C for 30 s), (72 °C for 30 s)] and [72 °C for 10 min], [hold at 12°C]. After amplification 5µl of the PCR product were tested for success using 2% gels. The remainder of the PCR product was purified and sequenced through Bigdye chemistry at CAF of Stellenbosch University.

3.3.3 Sequences and alignment

Sequences were authenticated on GENBANK using the BLASTIN tool (https://blast.ncbi.nlm.nih.gov/Blast.cgi). All sequences were aligned and edited using BIOEDIT SEQUENCE ALIGNMENT EDITOR v.7.0.5 (Hall, 1999).

3.3.4 Statistical analyses

Phylogenetic relationships among individual small ruminants were inferred using maximum parsimony (MP) in PAUP*v4 (Swofford 2002). A neighbour joining tree was created in PAUP*v4 (Swofford 2002) and visualized with the program FIGTREE v1.4.4

The haplotypes (h), haplotype diversity (Hd), nucleotide diversity (π), pairwise nucleotide differences (k) and the number of polymorphic sits (S) were calculated for all small ruminants using DNASP v. 5.10.1 (Rozas et al., 2010). An AMOVA in ARELEQUIN v.3.5.1.2 (Excoffier et al., 1992) was used to determine the genetic divergence (fixation index *Fst*) between small ruminants.

3.4 Results

3.4.1 Genetic differences between small ruminants using Mitochondria gene

A total of 22 sequences were analysed (cross-bred (n) = 8, Swakara (n)= 8, Goat (n)= 6) Genetic divergence is seen within the different small ruminants where (Table 3.1 Sequence diversity within different small ruminants ranged from 0.42% for cross-bred sheep to 3.67% for Swakara. Sequence divergence between small ruminants ranged from 0.48% for Swakara + cross-bred to 11.90 % for cross-bred sheep + Boer goat (Table 3.1).

Table 3.1: Pair- wise genetic divergence within and between the described small ruminants at the mtDNA level.

	(%± SD)
Sequence divergence within Swakara	3.67 ± 0.19
Sequence divergence within Cross-bred	0.42 ± 0.00
Sequence divergence within Goat	2.28 ± 0.03
Sequence divergence between Swakara X Cross-bred	0.48 ± 0.00
Sequence divergence between Swakara X Goat	7.94 ± 0.04
Sequence divergence between Cross-bred X Goat	11.90 ± 0.05

The neighbour-joining analyses of the small ruminants revealed the existence of at least two monophyletic lineages (Fig.3.1.) However, there is an obvious outlier (CB7) which has a significant genetic distance from the two lineages. The two lineages support the morphological distinction between the small ruminants. This tree supports the genetic distances found in (Table 3.1.).

3.4.2 Genetic relationships and phylogenetic analysis

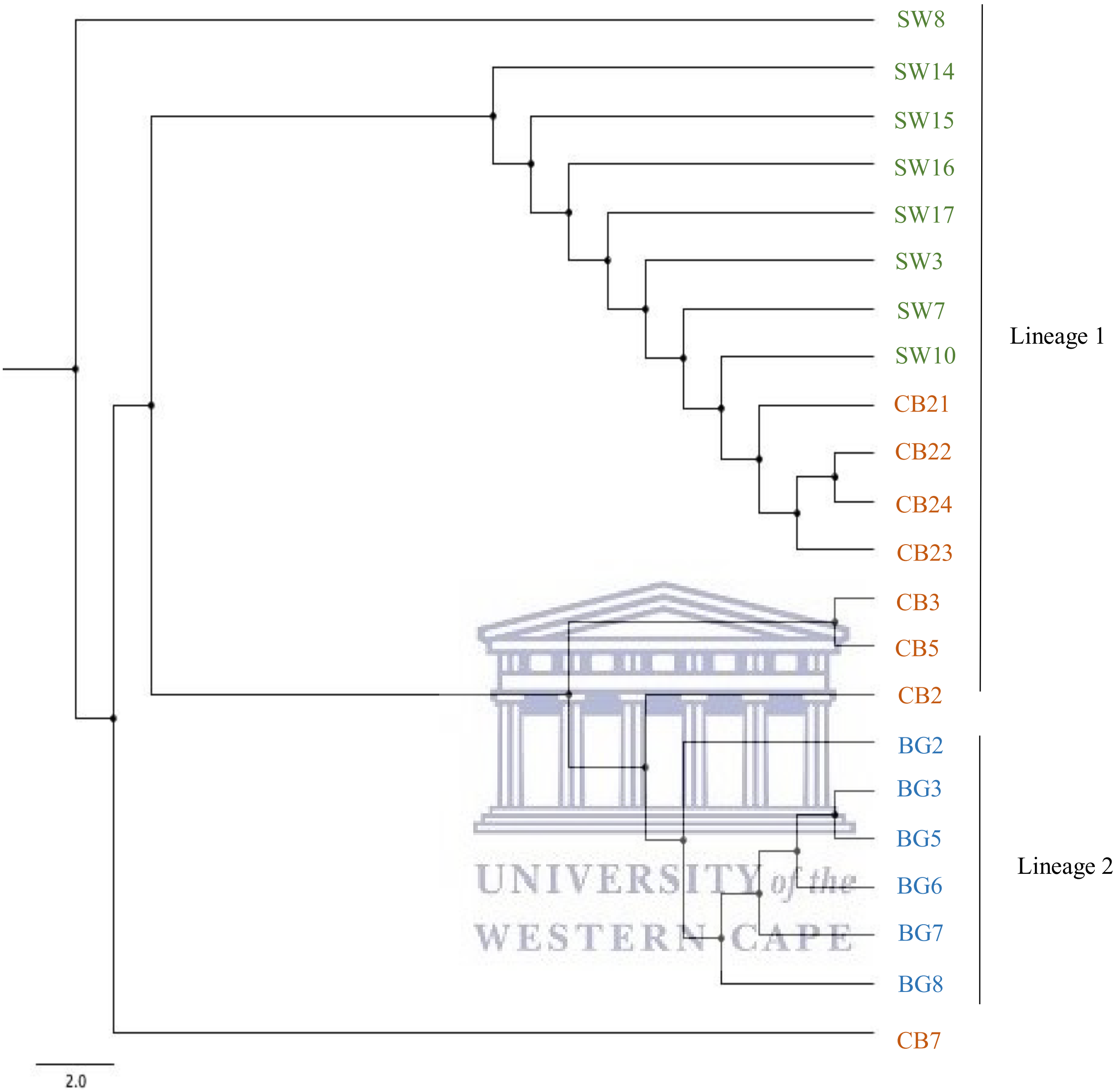


Fig.3.1: Neighbour-joining phylogeny indicating the two major clades of small ruminants. Lineage 1 represents the sheep and Lineage 2 represents the Boer goat. (CB= cross-bred sheep, SW= Swakara sheep, BG= Boer goat).

Within all tested small ruminants, the haplotype diversity and average number of pairwise differences were 0.81 and 23.35, respectively. The haplotype diversity in cross-bred sheep was 0.93 with K: 18.96. The haplotype diversity for the Boer goat ranged from 0.60 with an average number of pairwise differences K: 9.00. On the other hand, the haplotype diversity in Swakara sheep ranged from 0.25 with an average number of pairwise differences K: 0.25.

The results show that the Swakara sheep possess the lowest nucleotide diversity than cross-bred sheep and Boer goat where it ranged from 0.00 in Swakara to 0.05 for cross-bred sheep. Total nucleotide diversity of 0.06 for the three tested small ruminants where shown (Fig.3.2.).

Table 3.2: Genetic diversity measures of small ruminants found in the Steinkopf pastoral rangeland.

Population	**No. of sequences (N)**	**No. of polymorphic sites (S)**	**No. of haplotypes (H)**	**Haplotype diversity (HD)**	**Average number of pairwise differences (K)**	**Nucleotide diversity (π)**
Swakara	8	1	2	0.25	0.25	0.00
Cross- bred	8	74	6	0.93	18.96	0.05
Boer goat	6	27	3	0.60	9.00	0.02
Total	22	116	9	0.81	23.35	0.06

Pairwise values (*Fst*) for small ruminants show high genetic differentiation between Swakara and Boer goat (P= 0.75) and Cross-bred and Boer goat (P= 0.57) but no difference between Swakara and Cross-bred sheep (P= 0.01). F-statistics supports the genetic differences found between small ruminants where both sheep breeds had a significant difference to the goat but no difference between each other, which is presented in (Fig.3.1.).

3.5 Discussion

3.5.1 Genetic differences between small ruminants

The current study provides genetic data to support the genetic differences within the small ruminant population in the Steinkopf communal area. The differences within and between small ruminants varied as different species were compared. The high genetic divergence at the mtDNA level within purebred Swakara and within purebred goat suggests that these small ruminants have diversified as opposed to the cross-breed sheep which shows low genetic divergence (Table 3.1.). Swakara sheep in this region have been bred using different rams regularly, some rams being brought in from Namibia. The Boer goat is an indigenous breed to this area and like the Swakara; a number of male goats are regularly used for breeding purposes (Personal. Observation.). Cross- bred sheep in this region have been bred using rams that are rotated from herd to herd, this breeding mechanism has been in use for many generations and as a result, these sheep appear morphologically highly diverse but possess low genetic divergence (Table 3.1.).

Differences between small ruminants had a similar result where there was a high divergence between species but a low divergence between cross-bred and Swakara sheep (Table 3.1.). The low divergence between sheep indicate that there has been cross breeding between Swakara and cross-bred sheep, this supports the morphological traits seen in different herds in this area (Appendix 1.). This result is supported by the low *Fst* value indicating that sheep found in this area are genetically similar. However, a cross-bred outlier (CB7) seen in (Fig. 3.1.) indicates a significant genetic distance from the other cross-bred sheep. This individual displays such differences from the two lineages confirming it was crossed with a different ram not from the area. Bringing in exotic or commercial breeds that are not indigenous to the area can lead to genetic erosion if not introduced correctly (Molotsi et al. 2017). Farmers need to ensure that the accumulation of deleterious loci is limited this will lead to the loss of adaptive traits that are important for survival, especially in low production small holder systems (Molotsi et al. 2017).

Indigenous breeds have traits that are crucial for the survival and reproduction of the herd, these breeds may be no use to commercial interest but have huge value in changing environments such as arid environments (FAO, 2009). A study undertaken by Cloete et al., 2013 found that the indigenous Namaqua Afrikaner sheep had a significantly lower tick count on the udders and hind legs as opposed to the commercially developed SA Mutton Merino and Dorper. This suggest that the indigenous Namaqua Afrikaner would be more robust than the other two breeds in natural pasture regarding tick resistance. This trait is important to have amongst small stock herds in parasite prone environments such as drylands. Indigenous and locally developed sheep breeds are therefore an important asset because of the unique combinations of adaptive traits that developed to respond effectively to the pressures of the local environment (Buduram, 2004). Examples of well-developed local breeds in South Africa are the Dorper, the Boer goat and the most recent breed, the Meatmaster (Malan, 2000; Buduram, 2004; Peters et al., 2010). According to indigenous knowledge and morphological traits shown in the Appendix 1, the Dorper, Meatmaster, Afrikaner and Damara sheep breeds have been used in the cross-bred breeding pool in the Steinkopf area with Dorper being the dominant breed in most herds. Maintaining this genetic diversity within these adaptive breeds in a dryland system is an important and cheap adaptation mechanism for farmers in environments that are prone to changing conditions (Thornton et al., 2010).

3.5.2 Genetic diversity within small ruminants

The high diversity for cross-bred sheep seen in Table 3.2. shows that all individuals that were examined in this study are different from each other. This can also be seen for the Boer goat however, for Swakara sheep, the diversity is low which means that all individuals are genetically the same indicting inbreeding. Low genetic diversity in small ruminant populations can inhibit adaptation in changing environments such as drylands. Emerging diseases due to climate change is a huge threat to livestock populations as they can be directly linked to mortality (Gray et al., 2009; Jones & Thornton 2009; Mude et al., 2010). Animal genetic diversity has allowed farmers to select livestock breeds or develop new breeds in response to environmental change and threats and disease. Low genetic diversity in populations will develop the incapability to adapt these changes (Anya & Ayuk, 2011). Even though the Swakara sheep in Steinkopf possess traits that allow them to survive in harsh climate and environmental conditions, it is important to preserve these traits by reducing inbreeding. Farmers in Steinkopf need to be aware of the vulnerability of the Swakara population as these sheep are of economic value.

The high diversity found within cross-bred and Boer goat shows that they are able to adapt to changing climate because there is variation found within their genetic makeup. Small ruminants in the Steinkopf communal rangeland possess heat tolerant traits, as they are able to reproduce and survive in these harsh dryland conditions. Sheep and goat breeds found in Mediterranean regions appear to be less susceptible to heat stress than other domestic species (Renaudeau et al., 2012). However, animals reared in hot dryland environments are subjected to more than one stress at a time; heat stress and nutritional stress are usually the two stresses that occur simultaneously (Sejian et al., 2010). Heat stress is known to alter the physiology of livestock, reduce reproduction and increase mortality (Hoffman, 2010). Such exposure of sheep and goats to heat stress evokes a series of drastic changes in the biological functions, which include a decrease in feed intake efficiency and utilization of forage (Marai et al., 2007).

3.6 Conclusion

The recorded high genetic distance between Swakara and Boer goat and Boer goat and cross-bred is reasonable and expected because these are different species. The low genetic distances between Swakara and cross-bred indicate high genetic similarity between the sheep found in the Steinkopf pastoral rangeland. Even though Swakara sheep are purebred, they still share a large amount of genetic information with the cross-bred sheep.

Genetically adaptable breeds of small ruminants are important in dryland systems (Bradford & Berger, 1988; Omondi et al., 2008; Hoffmann, 2010; Richkowsky et al., 2010). The data revealed in this study shows the diversity between these different small ruminants found in Steinkopf. With long tradition of breeding small ruminants in the Steinkopf communal area that suit changing conditions, livestock keepers have accumulated detailed knowledge of their animals. This knowledge has allowed them to develop breeding plans that ensure gene flow and genetic diversity throughout the rangeland. Conserving these adaptable genetic traits is important for the survival of the small ruminants.

CHAPTER FOUR:
DIET SELECTION AND PREFERENCE OF SMALL RUMINANTS DURING DROUGHT CONDITIONS IN A DRYLAND PASTORAL SYSTEM IN SOUTH AFRICA

Abstract

Semi-arid and arid areas are prone to droughts which are frequent occurrences in South Africa's drylands. Droughts can alter plant species availability thus influencing the of forage for livestock. The availability and quality of forage drive livestock production, especially among pastoral herds who mainly rely on the natural rangeland to sustain themselves. The overall aim of this study was to determine the forage selection of cross-bred sheep, pure-bred Swakara sheep (*Ovis aries*) and Boer goats (*Capra hircus*) in a herded system, during the 2016-2017 drought period in the Nama Karoo and Succulent Karoo biomes in Namaqualand, South Africa. The study specifically investigated the (1) availability of forage for small ruminants, (2) nature of diet selection of different small ruminants and how it varied between the two biomes, and (3) the role livestock species, breeds and biome play in forage preferences. We established diet selection, preference and dietary overlap by using direct observation of livestock grazing in the rangeland. Results indicate that availability of forage influence diet selection and preferences of all small ruminants. There was a high dietary overlap between cross-bred and Swakara sheep irrespective of the biomes. Sheep are described as near ground level foragers in the Succulent Karoo consuming mainly on low-growing annual herbs, indicating an overdependence to this forage resource when it became available. Goats were primarily typical browsers in the Succulent Karoo biome where shrubs were dominant, but they together with the sheep were considered grazers in the Nama Karoo biome where grasses were dominant. Moreover, all small ruminants in this study generally showed non-selective grazing tendencies, which offers an important grazing management tool to ensure that specific rangeland resources are not over exploited. We conclude by arguing that herding and the mixture of different livestock species by pastoralists is an effective strategy for

better use of rangelands with herbaceous and woody plants strategy plants and thus an important risk mitigation strategy during drought periods.

Keywords: Diet selection, drought, forage availability, rangeland, small ruminants, Namaqualand.

4.1 Introduction

Livestock farming is the principal land-use in semi-arid to arid areas globally (Koohafkan and Stewart, 2008). This is due to the high climatic variability which influences rangeland resources, making it the best suited land use to make optimal use of available resources (Illius et al., 2000). Since these dryland areas are climatically stressed with temperature extremes, long dry seasons and rainfall uncertainty, farmers have to choose livestock species that are able to survive and can be farmed productively (New, 2015). Small ruminants are mostly farmed in these areas because they can cope well with harsh climatic conditions and sparse vegetation (Degen et al., 2002). These harsh climatic conditions have allowed African pastoralists to adapt their livestock management to the variety of climates across the continent (Seo and Mendelsohn, 2008). Strategies such as herding and farming with mixed herds of small ruminants have allowed pastoralists in semi-arid to arid areas to rely on their livestock as a source of income (Rust and Rust, 2013).

In South African rangelands, there are two prominent livestock management systems, namely commercial and pastoral farming systems. Commercial farming practices occur mostly on private land whereas pastoralism occurs largely on state and tribal lands and remains the backbone of most rural communities (Cousins, 1999). Pastoralists depend on their livestock products such as meat, wool and milk for subsistence, profit and employment (Samuels, 2006).

Agriculture is used in 80% of the land surface of South Africa, 11% of this land is arable and the remaining land is used for livestock and/or game farming (Goldblatt, 2010). These rangelands can be described as heterogeneous landscapes that are high in spatial and temporal variability in plant diversity and forage production (Desmet, 2007), which gives pastoralists opportunities to explore a range of grazing sites for their livestock across the landscape and between seasons (Samuels et al., 2013).

The variability and unpredictability in plant production result in changes in the quality and quantity of available forage which affect the productivity of livestock (Abusuwar & Ahmed, 2010; Amary, 2016). However, livestock species have evolved various mechanisms for coping and adapting to changing forage quantity and quality. In Kenya for example, range sheep are described as intermediate feeders because of the high diversity of forage in their diets, and this is a mechanism used to cope with the seasonal variation in quality and quantity of feed (Holechek, 1984). This mechanism is a result of the "animal-season-environment" interaction by which the environment determines the availability of forage while season determines the quality and quantity (Kassilly, 2002).

Drought, which is a common phenomenon in drylands, can trigger plant compositional changes thus influencing forage availability for small ruminants (Finch et al., 2016). Drought is defined here as "A prolonged period of below average precipitation (usually lower than 70%), which creates a natural shortage of available water" (van Vuuren, 2015). A study conducted by Fynn and O'Connor, (2000) indicated that the 1991-1992 drought that occurred in the semi-arid bushveld in South Africa changed the botanical composition drastically which resulted in a critical food shortage for cattle. Food shortages for livestock will thus become more severe in areas projected to have increased frequencies and intensities of drought such as the Namaqualand region of South Africa. Farmers would have to find strategies to cope with inevitable droughts as these strategies will essentially aid in the survival of livestock herds. A study conducted by (Scoones, 1992) explored strategies of how farmers from southern Zimbabwe coped and adjusted to the 1982-1984 and 1986-1987 drought conditions by moving their livestock to alternative grazing areas.

Several studies have assessed foraging tendencies and diet selection of multiple livestock species in semi-arid to arid areas under free-range and herding systems (Genin et al., 1994; Bartolome et al., 1998; Ngwa et al., 2000; Pisani et al., 2000; Hendricks et al., 2002; Samuels et al., 2016a). In a herding system, goats are predominantly browsers with a preference for shrubs and sheep being predominantly grazers albeit the same landscape at the same time (Samuels et al., 2016a). However, depending on the forage available to these livestock seasonally, animals show that they can adapt their forage selection throughout the year by becoming intermediate feeders or completely switch their diet (Migongo-bake and Hansen 1987; Pfister et al., 1988; Kam et al., 2012; Samuels et al., 2016a). However in free-range grazing systems, livestock largely tend to exhibit selective grazing (Botha et al., 1983; Els, 2000a).

While most of these studies were done during normal rainfall periods, no other study has assessed diet selection of small ruminant breeds and species in the same herded system under drought conditions in South Africa. As such, this study was undertaken to answer the following questions: (1) what is available for herded small ruminants to forage in the Succulent Karoo and Nama Karoo biomes under meteorological drought conditions?, (2) what is the nature of diet selection of different small ruminants and how does it vary between the Succulent Karoo and Nama Karoo biomes?, and (3) what role do livestock species and breeds play in forage preference in both biomes under drought conditions?

4.2 Study area

The study was conducted in the Steinkopf communal rangeland located between (-28.84° S and -29.66° S latitude and 17.58°E and 18.37°E longitude), situated in the arid and semi-arid Namaqualand region of South Africa. This area is approximately 582 634 hectares in size and has several human settlements where grazing is the main land-use concentrated around those villages. This study focuses on regions of the Succulent Karoo and Nama Karoo biomes which together constitutes by far the largest area used for livestock farming in the Steinkopf communal rangeland. The Succulent Karoo receives winter rainfall and the Nama Karoo receives summer rainfall (South African Weather Service, Unpub. data).

During the study period and the preceding year, precipitation in the winter rainfall area varied (2015 = 80.8 mm, 2016 = 161.8 mm, and 2017 = 27.1 mm; South African Weather Service, Unpub. Data) (Fig 4.1.). The total annual rainfall in the summer rainfall area during the study period and preceding year was 13.2 mm in 2015 and 23.4 mm in 2016 and 4 mm in 2017 (South African Weather Service, Unpub. data) (Fig. 4.1.). Therefore, the Northern Cape Province, which Steinkopf forms part of, was declared a drought disaster in 2015 and the duration of the drought extended beyond 2017.

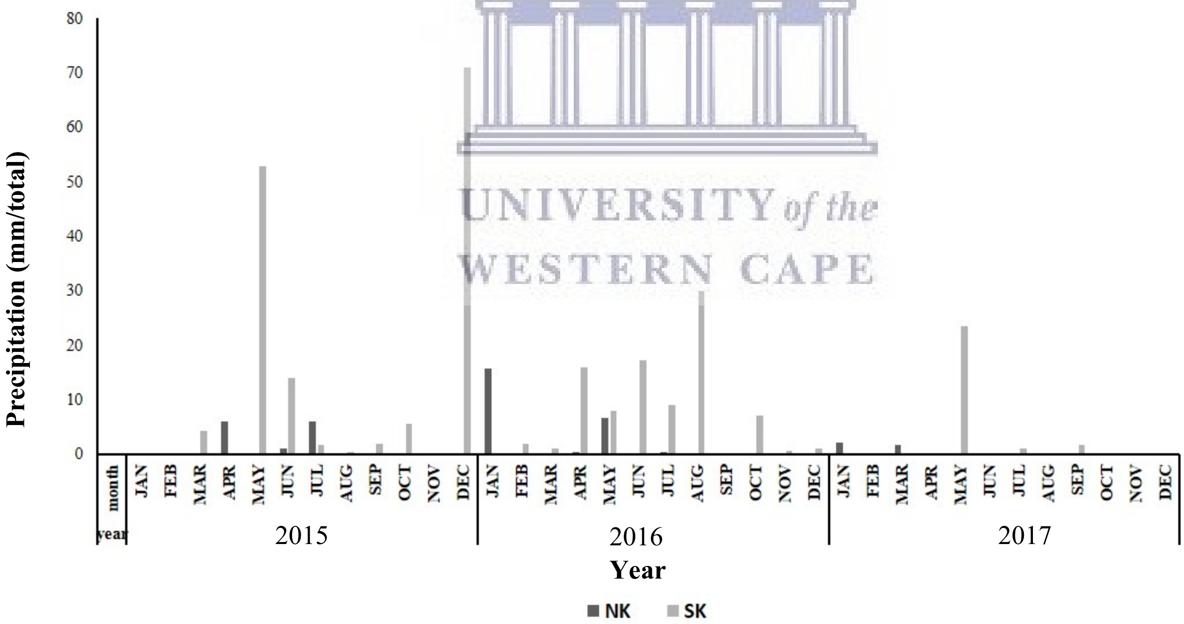


Fig.4.1. Rainfall during the study period for regions of the Succulent and Nama Karoo biomes forming part of the Steinkopf communal rangeland.

The Succulent Karoo biome is known for its floral diversity and is recognised as a global biodiversity hotspot (Cowling et al., 2004). In this biome small ruminants graze mainly on the

Namaqualand Blomveld vegetation type, which is dominated by dwarf succulent and non-succulent shrubs of which Aizoaceae and Asteraceae species are particularly prominent (Mucina and Rutherford, 2006). In the Nama Karoo biome, small ruminants graze mainly on the Bushmanland Arid Grassland vegetation type which is dominated by grasses such as *Stipagrostis* species (Mucina and Rutherford, 2006). The Nama Karoo landscape is characterised by inselbergs which provide refuge for species that are not able to grow on the surrounding plains and these include palatable perennial species (Burke, 2002).

In the Steinkopf communal rangeland there are approximately 50 000 small ruminants (sheep and goats) but about 900 large stock (cattle, horses and donkeys) that rely on the natural vegetation for forage. Generally, pastoralists raise goats and sheep, with sheep being the preferred species because of the more variable products they provide such as meat, wool and pelts. In Steinkopf, small ruminants are kept in temporary and semi-permanent stockposts where they are corralled overnight to prevent stock theft and predation. These herds follow a grazing orbit in which they return to the stockpost every night after visiting the water point. Small ruminant herds are managed by herders who decide on the targeted grazing area and then allow the herds to graze freely. Herders practice seasonal transhumance and move from the Succulent Karoo to the Nama Karoo in early summer and usually return after the first winter rains.

4.3. Methods and materials

4.3.1 Assessing diet composition in livestock

Diet selection was observed in Boer goats (*Capra hircus*), and mixed breeds of sheep (*Ovis aries*), representing crosses between mutton breeds such as the black head Dorper, Meat master, Afrikaner, Damara and Persian, and purebred Swakara (formerly known as Karakul) sheep farmed for their pelts, during the drought periods in both the Nama and Succulent Karoo biomes. The feeding observations for the Succulent Karoo for cross-bred sheep was conducted in August 2016, and Boer goat and Swakara observations were conducted during August 2017. All the observations for the Nama Karoo were conducted in February 2017. We followed 12 cross-bred sheep, five Swakara sheep and five Boer goat herds in the Succulent Karoo and five cross-bred sheep, five Swakara sheep and five Boer goat herds in the Nama Karoo. The herd sizes ranged between 70-900 animals of mostly mixed species and two herds composed of sheep only. Direct feeding observations were conducted by a research team of rangeland ecology postgraduate students and co-authors. The method used was discussed and standardized to Samuels et al., 2016a.

Goat and sheep herds were followed at different times of the day, between 09:00-10:00 in the morning until they return to the corral in the late afternoon. The presence of the observers did not affect the foraging behavior of these animals as they are always supervised by a herder. Small ruminants could be approached within five meters without disturbing their behaviour. Diet selection was observed in five-minute feeding bouts. For each feeding bout, an adult female was randomly selected as a focal animal to represent the entire herd, however the focal animal could change within the duration of the five minutes. A new focal animal was selected for each feeding bout. Ten feeding bouts were completed for each herd with intervals of 10-30 minutes between each bouts (Samuels et al., 2016a). Plant species that were selected or avoided but within 2 m on either side of the focal animal were identified. These plants species were recorded on a cell phone recorder and later transcribed (Hendricks et al., 2002).

Diet selection was quantified based on whether an individual plant was grazed only. Plant species were identified in the field, and for unidentified plants, voucher specimens were collected and later identified. A list was compiled from the 2-m-plant samples of all the available plant species found in the rangeland that small ruminants encountered. Plant species were then grouped into six plant functional types, (annual grasses, perennial non-succulent trees, perennial non-succulent shrubs, perennial leaf succulent shrubs, perennial stem succulent shrubs and annual herbs) (Anderson and Hoffman, 2011). Low growing annual herbs could not be identified to species level and were therefore grouped as ‘annual herbs’.

4.3.2 Data analysis

Diet selection for each plant species and plant functional type was calculated as a percentage of the plant in the total diet of a small ruminant. Species abundance was calculated as a percentage of the total plant canopy cover in the rangeland. Canopy cover was calculated by dividing each plant functional type by the grand total of all plant functional types found in the rangeland and was relative to the total of all feeding bouts. Cover differs between all herds that were followed because of different grazing routes and feeding bouts. The average of all feeding bouts represent the canopy cover.

Forage preferences were determined for each plant species and functional types based on Ivelev’s forage ratio (Ivlev, 1961; Samuels et al., 2016a): $E_i = \mathrm{r_i}/\mathrm{P_i}$). The Ivlev’s forage ratio compares the relative availability of plant species in the environment ($\mathrm{P_i}$) and their relative utilization in the diet ($\mathrm{r_i}$). Plant species that constitute a large proportion of the diet than that of the available plant species are considered preferred (Lechowics, 1982).

4.3.3 Statistical analysis

Separate data matrices of the plant functional types available to and selected by the small ruminants were produced using preference percentages data. The percentage composition data were log (X+1) transformed to reduce skewness. Patterns of variation within and between small ruminants in each biome on the composition of available and selected plant functional types were visualized with Principle Component Analysis (PCA) using CANOCO (ter Braak and Šmilauer, 2012). A permutation multivariate analysis of variance (PERMANOVA) test (999 permutations) based on Euclidean distances (ED) was conducted to assess the differences in available and selected diet composition in both biomes and between small ruminants. A distance-based (ED) test for homogeneity of multivariate dispersions (PERMDISP) was conducted to test the differences in heterogeneity of plant functional types available in both biomes. SIMPER (similarity percentages) was used to evaluate the contributions of plant functional types to observed differences in forage availability and selection. All three tests were conducted in PRIMER 6 (Clarke and Gorley, 2006). Distances among samples between the composition of available and selected plant functional types were quantified using ED, calculated for each small ruminant species or breed, to assess the dissimilarity between diet availability and diet selection in both biomes. A two-way ANOVA within a general linear model was conducted using Genstat 18 (VSN International, 2015) to test the effect of herd type, biome, and their interaction, on the dissimilarity (ED) between the composition of forage available and that selected by animals.

4.4. Results

4.4.1 Forage availability

There was a clear separation between plant functional types available to small ruminants in the Succulent Karoo and Nama Karoo. The first axis of the PCA (Fig. 4.2.) represented the majority (74.2%) of the variability in available plant functional types and depicted the large difference between biomes. The second axis, far less important component (9.9%), was associated with variability in the composition of available plant functional within biomes. The composition of the available forage differed significantly between biomes (pseudo-F = 50.89, p = 0.0001) but all small ruminants had a similar dietary composition available overall (pseudo-F = 1.46, p = 0.1824) and in each biome (Biome x Herd: pseudo-F= 1.37, p = 0.2144). The available forage was on average significantly more heterogenous (pseudo-F = 38.19, p = 0.001) in the Nama Karoo than in the Succulent Karoo (Mean dispersion: NK = 2.854, SK = 1.320) but equally homogenous among herd types (pseudo-F = 1.44, p = 0.508). Furthermore, within the same biome, herds between and within the same species and breeds also had different forage available to them as a result of the different grazing routes herders take and the different feeding bouts (Supplementary TB1 and TB2 Appendix 2 & 3). The dispersion of the available forage was on average significantly more variable in the Nama Karoo than in the Succulent Karoo (Mean dispersion: NK = 2.854, SK = 1.320). Perennial and annual grasses were the plant functional types more available to livestock in the Nama Karoo than the Succulent Karoo, whereas perennial stem succulent shrubs, annual herbs and perennial non-succulent shrubs were most in the Succulent Karoo (Fig. 4.2.). Perennial grasses contributed 64.12% and succulent shrubs a further 21.21 % to the difference in available diet composition between biomes. Together these two plant functional types explained >85% of the biome difference in the composition of the forage available to animals in the different herds.

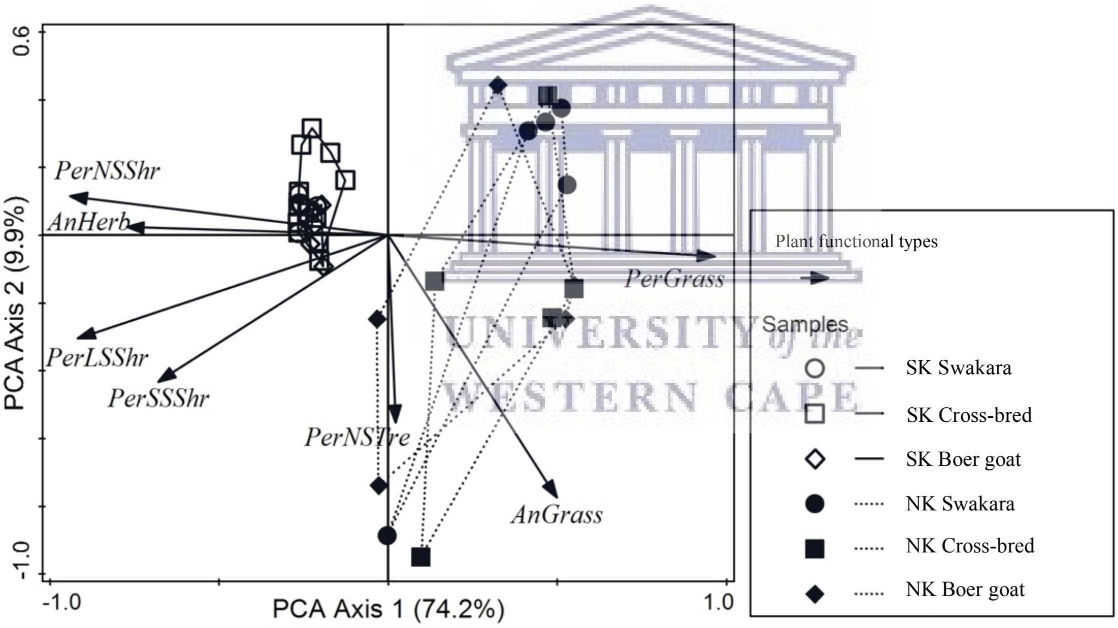


Fig.4.2: The first two axes of a principal component analysis (PCA) of the available plant functional types composition in the Nama Karoo (NK) and Succulent Karoo (SK). *AnGrass* = annual grasses, *AnHerb* = annual herbs, *PerNSTre* = perennial non-succulent trees, *PerNSShr* = perennial non-succulent shrubs, P*erLSShr* = Perennial leaf succulent shrubs, *PerSSShr* = Perennial stem succulents.

The first two axes of a PCA of the percentages of different plant functional types in the diet of different small ruminants (Fig. 4.3.) explained 72.4 % of the total variation in diet composition.

Similar to the pattern in the forage availability data, the diets selected in the Nama Karoo by small ruminants were separated on the first principal component and significantly different, on average (pseudo-F = 33.44, p = 0.0001), from those consumed in the Succulent Karoo (Fig. 4.3.). The small ruminants also differed in their average diet composition across both biomes (pseudo-F = 3.62, p = 0.0005), with a tendency (Biome x Herd: pseudo-F= 1.71, p = 0.0817) for larger dietary differences in the Succulent Karoo (Fig. 4.3.), where Boer goats selected a different diet to the cross-bred and Swakara sheep (p < 0.01). Despite these differences in diet composition, PERMDISP revealed that diets were equally homogenous within the different small ruminant species/breeds (pseudo-F = 1.49, p = 0.335) and biomes (pseudo-F = 2.51, p = 0.170).

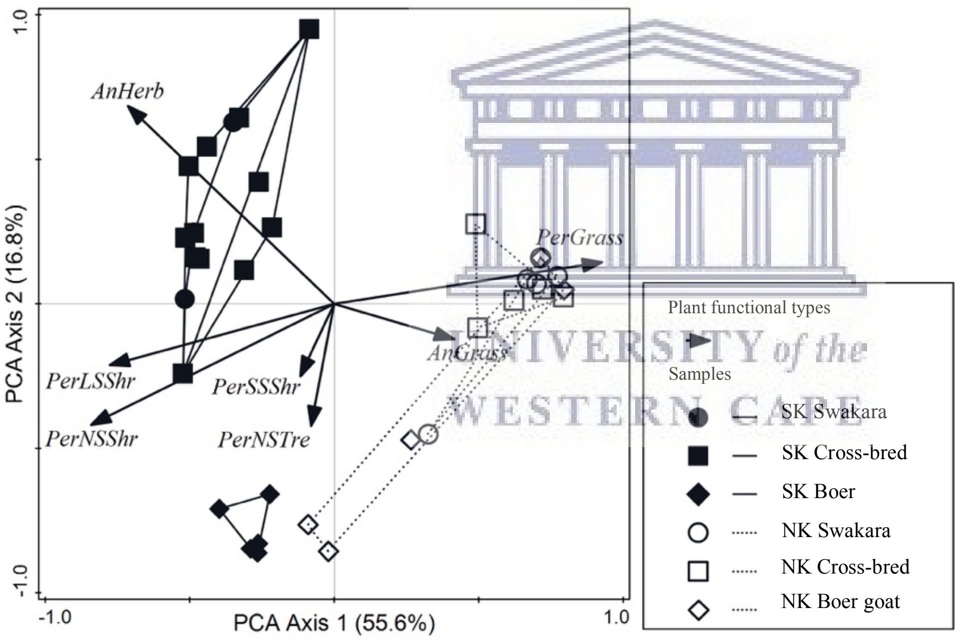


Fig.4.3: The first two axes of a principal component analysis (PCA) of the plant growth form composition of the diet of different types of small ruminants in the Nama Karoo (NK – empty symbols) and Succulent Karoo (SK – filled symbols). See Fig. 4.2 for full names of plant functional types (arrows).

4.4.2 Dietary selection

Livestock in the Succulent Karoo showed a difference in diet niches with goats being predominantly browsers and both sheep breeds foraging mainly on near ground-level vegetation that include grasses and low- growing annual herbs. Boer goats had a high mean percentage of perennial non-succulent shrubs (69.79%) and very few annual herbs (0.43%) in their diet whereas almost half of the diet of Swakara and cross-bred sheep in the Succulent Karoo comprised of annual herbs with lesser amounts of perennial non-succulent shrubs (Swakara = 39%, cross-bred sheep = 26%) (Table 4.1.). In the Succulent Karoo, appreciable amounts of perennial leaf succulents were also consumed by Boer goats (28.51%) and cross-bred sheep (16.34 %) but relatively scarce (<10%) in the diet of Swakara (Table 4.1.).

Diets did not differ significantly ($p > 0.05$) between small ruminants in the Nama Karoo since perennial grasses were the dominant component for all livestock. Perennial grasses made up 84.22% of the Swakara sheep's diet followed by annual grasses at 13.05% (Table 4.1). The cross-bred sheep's diet comprised 62.41% perennial grasses and 31% annual grasses. Perennial grasses made up 53.12% of Boer goats' diet followed by perennial non-succulent shrubs at 14.31% (Table 4.1.).

Table 4.1: Diet selection, forage preferences and cover of plant functional types foraged by small ruminants in the Succulent Karoo (SK) and Nama Karoo (NK) biomes. See Fig. 4.2 for full names of plant functional types.

Biome	Plant Functional types	Cross-bred sheep			Swakara sheep			Boer goat		
		Ri	***Pi***	***Ei***	***Ri***	***Pi***	***Ei***	***Ri***	***Pi***	***Ei***
SK	AnGrass	3.86	1.33	2.90	1.46	0.42	3.44	0.85	0.21	4.00
SK	Herb	52.90	20.88	2.53	49.03	18.07	2.71	0.43	1.32	0.32
SK	PerLSS	16.34	26.98	0.61	9.71	25.72	0.38	28.51	32.60	0.87
SK	PerNSS	25.95	44.87	0.58	39.00	50.10	0.78	69.79	55.19	1.26
SK	PerSSS	0.94	5.93	0.16	0.81	5.69	0.14	0.43	10.68	0.04
NK	AnGrass	31.00	12.31	2.52	13.05	5.68	2.30	19.83	8.96	2.21
NK	PerGrass	62.41	68.87	0.91	84.22	82.45	1.02	53.12	55.14	0.96
NK	Herb	1.44	1.33	1.08	0.00	1.32	0.00	0.14	0.93	0.15
NK	PerLSS	2.27	10.81	0.21	2.10	5.61	0.37	7.08	15.87	0.45
NK	PerNSS	0.41	2.42	0.17	0.46	3.43	0.13	14.31	13.46	1.06
NK	PerSSS	2.47	4.26	0.69	0.58	1.15	0.16	3.40	4.67	0.73
NK	PerNST	0.00	0.00	0.00	0.00	0.35	0.00	2.12	0.98	2.18

The mean ED between the composition of the forage available and that consumed was significantly larger ($F_{1,31} = 4.19$, $p = 0.049$) in the Succulent Karoo (2.37) than in the Nama Karoo (1.61), and this difference in dissimilarity was consistent (Biome x Herd: $F_{2,31} = 0.63$, $p = 0.540$) across all small ruminants (Fig. 4.4.). Different types of breeds and species did not, however, differ in the extent of their mean dietary divergence in both biomes ($F_{2,31} = 0.54$, $p = 0.585$).

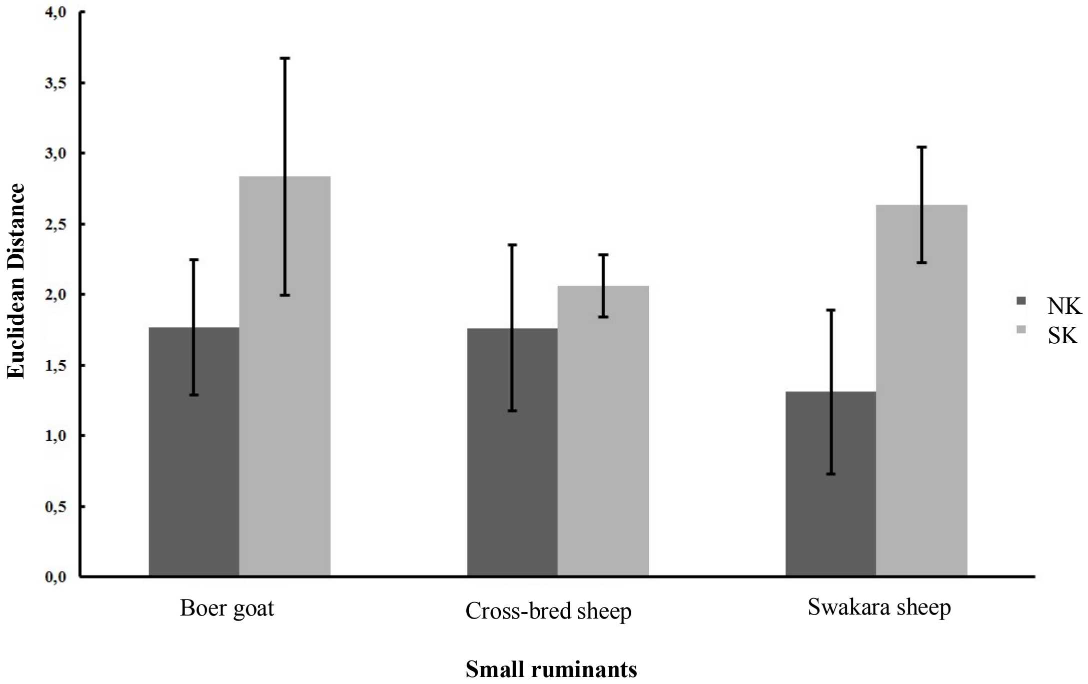


Fig.4.4: Euclidean distance indicating the dissimilarity between the percentage plant functional types available to and selected by small ruminants in the Nama Karoo and Succulent Karoo biome in the Steinkopf communal rangeland. Error bars indicate the standard error of the mean.

4.4.3 Diet preferences

The number of plant taxa that were available to small ruminants in the Succulent Karoo during the study period was 111 of which 30 were consumed. Overall, the different small ruminants preferred a variety of species (Supplementary Table ST1 Appendix 2 & 3). However, preferred species that comprised of more than 10% of the diets of all small ruminants were rare. The preferred species for Swakara was annual herbs ($E_{i=}$ 2.65) and *Pteronia glomerata* ($E_{i=}$ 1.20). The preferred species for cross-bred sheep was annual herbs ($E_{i=}$ 2.89) and for goats the preferred species were *Pteronia glomerata* ($E_{i=}$ 1.62) (PerNSShr), *Ruschia sp.1* ($E_{i=}$1.01) (PerLSShr) and *Searsia incisa* ($E_{i=}$ 2.62) (PerNSShr) (Supplementary Table ST1 Appendix 2 & 3).

There were 61 different plant taxa available to small ruminants in the Nama Karoo and of these, 28 were consumed. All small ruminants adopted the same grazing behavior in the Nama Karoo, spending the majority of their time eating perennial grass species such as *Stipagrostis ciliata*, *Stipagrostis obtusa*, unknown Perennial grass sp. 1, and *Schmidtia kalahariensis*, which is an annual grass species (Supplementary Table ST2 Appendix 2 & 3). These grass species were the most preferred forage and comprised individually more than 10% of the diet of all small ruminants. The preferred species for cross-bred sheep were *S. kalahariensis* (E_i=2.52) (AnGrass) and *S. ciliata* (E_i=1.15) (PerGrass). Preferred species for Swakara were *S. kalahariensis* (E_i=2.30) (AnGrass) and *S. obtusa* (E_i=1.22) (PerGrass). Goats also preferred *S. kalahariensis* (E_i=2.21) (AnGras) and unknown Perennial grass sp. 1" (E_i=1.02) (Supplementary Table ST2 Appendix 3).

4.5. Discussion

4.5.1 Forage availability for small ruminants during drought

Although all small ruminants utilized all forage types available to them during the drought period in both Nama Karoo and Succulent Karoo, they dedicated the majority of their feeding time to certain plant functional types showing different dietary patterns. During 2016, the annual rainfall was between 100-200 mm hence there were more annual herbs present as opposed to 2017. However, the amount of annual herbs available is still less than during a normal rainfall period for the region when this forage type composed up to 66% of total canopy cover (Samuels et al., 2016a). Annual herbs are an indication of the wet season and play a major role in the diets of grazing livestock (Samuels et al., 2016a). A study conducted in the Richtersveld region of Namaqualand indicated that annual herbs act as a supplement in the diets of lactating ewes and kids during the annual spring flowering season (Hendricks, 1994). Thus, during drought periods, these important forage are limited and has implications for livestock growth, and thus productivity of the pastoral system.

4.5.2 Changing diet as dictated by forage availability

During 2017, an absence of annual herbs in the Succulent Karoo forced small ruminants to change their diet to mainly perennial shrubs, which are consumed mainly during the dry summer seasons

(Hendricks et al., 2000; Samuels et al. 2016a). Grova & Bjelland, (1997), also found that goats spent 2.5 times more browsing than grazing when shrub forage was available, but this reversed when shrub forage became scarce and grass and forbs were abundant. The consequence of utilizing dry season forage during drought periods, would lead to overutilization of forage species and a potential shift from palatable to less palatable dominated vegetation in the landscape (Anderson & Hoffman, 2007). Consuming less palatable plant species which are lower in protein content affects growth rates and lactation of ewes (Ben Salem & Smith, 2008).

In the Nama Karoo, all small ruminants were grazers, consuming mostly annual and perennial grasses. These patterns of changing diets based on availability has also been reported in Ngwa et al., (2000), where goat and sheep breeds in northern Cameroon had consistent diet choices during the rainy season. Sheep spent most of their time eating fresh grass and goats consumed the fresh lower layer of browse species. However, due to season changing from wet to dry both sheep and goat foraged on fruits, blossoms and pods in the dry season, unless limited by availability of forage.

4.5.3 Differences in diet selection between small ruminants

In the Succulent Karoo, both sheep breeds can be classified as near ground-level foragers whereas Boer goats, which selected more perennial non-succulent shrubs (such as *Pteronia glomerata* and *Searsia incisa*) and perennial leaf succulents (*Ruschia sp.* and *Cheiridopsis denticulata*) can be classified as browsers (Appendix 2). In the Nama Karoo, all small ruminants *S. kalahariensis*, *S. ciliata* and *S. obtusa* were the main dietary items of all livestock (Fig. 4.3; Appendix 3). Herds of mixed species would thus be beneficial to pastoralists not only in the products derived from them, but also more efficient use of available drought forage resources particularly in the Succulent Karoo.

In the Nama Karoo, Boer goats on occasion also extended their forage to non-succulent trees (*Boscia albitrunca*) (Appendix 3). These non-succulent trees were only found on rocky terrains and inselbergs which suggests that the Boer goats were more flexible in their foraging behavior since the sheep favoured forages on the flatter lowland areas only. Goats generally have high variability in feeding habits in different ecological zones and season variation (Raats, 1997). Their ability to assume a bipedal stance gives them opportunities to reach certain plants or plant parts that other breeds of livestock are not able to do (Bhatta et al., 2001; Dziba et al., 2003). Thus, in general and also found in this study, goats utilize a considerable wider range of plant species than other livestock species (Fraps & Cory, 1940; Ngwa et al., 2000). and this reduces the competition with sheep when they are in the same herd.

The different sheep in the Steinkopf pastoral rangeland, shared a very similar diet in both the Nama Karoo and Succulent Karoo. This is contrary to what has been shown that breeds of sheep have different foraging habits even though their nutritional requirements and digestive systems are similar (Warren et al., 1984; Bartolome et al., 1998; Pfister et al., 1988). (Els, 2000b) shows that three breeds of sheep (Dorper, Swakara and Merino) utilize the most nutritious grass species as the main component of their diets however certain woody species were also utilized but were consumed during different times of the year by each breed. Furthermore, a study conducted by (Degen et al., 2002), showed that Swakara grazing herds in Kazakhstan grazed on the herbaceous species first and once that was grazed out they then selected the woody species followed by soft twigs thus showing selective traits. These studies highlight that Swakara are flexible in forage selection which supports this study indicating that Swakara sheep are opportunist feeders when grazing with other livestock during drought conditions.

4.6. Conclusion

During the drought period, herded sheep (cross-bred and Swakara) remained grazers when they have an option to graze on grasses and this is consistent with other studies that have shown sheep being grazers during winter rainfall periods (Bartolome et al., 1998; Samuels et al. 2016a). This is also the case when sheep range freely in the rangeland during the active growing season for the vegetation (Pfister et al., 1988; Ngwa et al., 2000). Furthermore, sheep could also become intermediate feeders in herded (Kam et al., 2012) and free-ranging livestock management systems (Genin et al., 1994; Dawson and Ellis, 1995). This flexibility is confirmed during this study when sheep foraged mostly on herbaceous low-growing annual herbs. This study also found that sheep do not become browsers, although this was found in (Shinde et al., 1998; Ngwa et al., 2000) but these were not during a drought period.

Many studies have shown that herded goats are generally browsers (Bartolome et al., 1998; Hendricks et al, 2002; Samuels et al. 2016a) or intermediate feeders (Migongo-Bake and Hansen 1987; Kam et al, 2012) during wet and/or dry season and that they could become grazers when grasses are dominant in the landscape (Pfister et al., 1988). This study during a drought period confirms that goats will change their diets based on forage availability albeit that the nutritious value of plants are generally low during this period. This study also found that selective grazing was not evident although the variety of food options would allow goats to be selective. Thus, forage availability, which is a result of herders moving their livestock between biomes, is key to the management of rangeland resources.

Furthermore, since different livestock species adapt differently to drought, keeping livestock herds of mixed species ensures that there will reduced competition for limited resources and this increases the chances of survival of the herd. This risk management strategy is evident in other pastoral systems such as in the Turkana district in Kenya where pastoralists keep five species of domestic livestock: camel, sheep, goat and donkey because each species have different forage and water requirements (McCabe, 2009). The Boer goat is seen to be one of the hardiest small stock breeds in the world and is encountered in a variety of climates (Malan, 2000). Having drought tolerant livestock breeds is crucial for farming in semi-arid to arid areas. These forage adaptations, coupled with herding, livestock mobility and use of indigenous knowledge (Samuels et al., 2018) in these rangelands, allow pastoralists to adapt to a changing climate (Samuels et al., 2016b).

CHAPTER FIVE: STUDY SYNTHESIS AND RECOMMENDATIONS

5.1 Introduction

Drylands are home to many small ruminants that adapt to the dynamic nature of the environment to survive. The rapid changing climate and environmental conditions affect small ruminant's adaptive capacity as recurring drought periods force livestock to their diet behavior as well as their ability to survive, reproduce and produce. This adaptability of these small ruminants is therefore allowing the survival and continuation of small scale farming in the Steinkopf pastoral rangeland.

Seasonality changes small ruminants feeding behaviors due to the availability of forage. Even though a large amount of studies (Migongo-bake & Hansen 1987; Bartolome et al., 1998; Hendricks et al., 2002; Kam et al., 2012; Samuels et al., 2016a) have shown foraging tendencies and diet selection of multiple livestock species in semi-arid to arid areas under free-range and herding systems, most of these studies were done during normal rainfall periods. However, this study on diet selection was undertaken under drought conditions. Furthermore, this study incorporates genetic diversity of small ruminant species and breeds in this dryland pastoral system.

The aims of this study were to:

1) Determine the breadth in genetic differences of small ruminant herds found in the Steinkopf dryland pastoral system.

2) Assess the nature of the seasonal diets of herded small ruminants under meteorological drought conditions.

3) Compare the diets of genetically diverse small ruminants.

I propose that through the understanding of small ruminants found in drylands and their ability to adapt to changing conditions can have a positive impact on the survival of small scale farmers in the future by allowing them to be prepared for the rapid climate changes. Climate change adaptations by farmers in areas such as Namaqualand is important as bioclimatic models shown by Rutherford et al., (1999) and Thuiller, (2007) indicate that the spatial extent of the Succulent Karoo will be reduced by 2050 and 40% of this biome would be replaced with different vegetation (Bourne et al., 2012). The replacement of vegetation will cause an impact on livestock farmers in this area, as animals are accustomed to present day forages. This area is also predicated to get more arid hence, farmers in this region need to be aware of the weather effects in the immediate and long terms (Ntombela, 2017). The drought period has allowed farmers to understand the challenges they will have with their livestock in the future. Having knowledge about the genetic differences and diets of small ruminants found in this area allows farmers to prepare and adapt for the future challenges that they might face.

This research demonstrated how drought conditions has an impact on the feeding behaviours and adaptation of herded small ruminants found in the Steinkopf pastoral rangeland during changing climate and environmental conditions. Thus, these adaptations allowed herded small ruminants to change their foraging behaviour according to forage availability and biome, which gave us the opportunity to compare diets of small ruminants found in the Steinkopf rangeland during drought conditions. This study also outlined genetic differences and variation of small ruminants found in the Steinkopf rangeland. These differences and variation can be seen as adaptations and resilience, which counters the harsh environmental conditions that they are faced with.

5.2 Small ruminant adaptations and traits during a drought period

Namaqualand has been a victim of recurrent droughts (Cowling et al., 1999). These drought periods have occurred every three to six years during the 19th century (Kelso & Vogel 2007). During the 20th century, there is evidence that droughts have become more intense and widespread in this region (Fauchereau et al., 2003; Hoffman et al., 2009; Davis et al., 2016).

Because the evidence of recurring drought periods dates back to centuries ago, this is an indication that farmers in this region are accustomed to these conditions and have traditionally bred livestock to survive these conditions.

Rainfall is regarded as the main driver of rangeland conditions globally (Debeaudoin, 2001; Fernandez-Gimenez, 2002; Samuels, 2006). Farmers in Steinkopf agree with this and understand that rainfall has an impact on the vegetation dynamics in both the Succulent and Nama Karoo biomes which affects livestock forage. This study found that despite the drought period herded sheep (cross-bred and Swakara) remained grazers when grasses and ephemerals are presented to them. These annuals acted as an important food source for the short duration of the study period for herded sheep. This is consistent with other studies that have shown sheep being grazers during a normal wet season (Bartolome et al., 1998; Samuels et al. 2016a). However, if drought conditions prevail and intensify, these annuals will be absent thus sheep will be forced to only eat woody dicots such as shrubs or succulent shrubs. In normal typical dry season food sources are already scarce and due to the interchangeable adaptation for free ranging sheep to become browsers, it can trigger competition with the Boer goats. Studies have shown sheep to be intermediate feeders in herded (Kam et al., 2012) and free-ranging livestock management systems (Genin et al., 1994; Dawson & Ellis, 1995). However, this study reveals that sheep do not become browsers but remain grazers by foraging on near ground level annuals during a drought period.

The Boer goat is generally a browser (Aucamp, 1976; Schoeman et al., 1997; Erasmus, 2000; Aharon et al., 2007). However like sheep, these small ruminants have the ability to change their diets and become grazers (Migongo-Bake & Hansen 1987; Kam et al., 2012). This study confirms that during a drought period, goats will change their diets based on forage availability albeit that the nutritious value of plants are generally low during this period. This study also found that selective grazing was not evident although the variety of food options would allow goats to be selective. Thus, forage availability, which is a result of herders moving their livestock between biomes, is key to the management of rangeland resources.

This study provides new knowledge of small ruminants having a noticeable preference for succulent plant species during a drought period in both biomes. Succulent species such as *Ruschia sp.* and *Cheiridopsis denticulata* were common in the diets of the small ruminants. Small ruminants had a particular liking for the leaves of both these species, not only the flowers which are higher in nutrition. Succulent plants retain 80% water content, thus small ruminants did not have to stop at a water point at any time during the day for the duration of the study period. Comparing this study to Samuels et al., (2016), herded sheep and goats did not prefer to eat succulent plants during the wet season and did not make up a large portion of their diets. Amary (2016) found that succulent leaves have extremely high tannin and phenolic levels which deters herbivores however the small ruminants in Steinkopf consumed these succulent plants in this drought period.

These small ruminants might have adapted to high secondary compounds in some succulent plants which means its chemical defence is no longer a grazing deterrent. This indicates that these succulent species are a very important in filling food shortages during drought periods and dry summer months when ephemerals are absent. However, all plant species in the diets of small ruminants were not of conservation value but appropriate grazing management strategies should still be in place to avoid the preferred food items from going locally extinct. The conservation status of the Succulent Karoo biome as a whole is very poor with only 3.5% of this area under protection (Driver et al., 2003). The lack of protection is allowing for major land uses, such as livestock farming to be a key factor in the conservation of the biodiversity in the region.

With recurring drought periods, small ruminants were also forced to make use of different plant functional types for forage. This can have an impact on the dry season food reserve especially in

the Nama Karoo biome where ephemerals were absent during the study period. The Nama Karoo is predicted to become part of the Desert biome (Rutherford et al., 1999). This will have major impacts on livestock farming in the Steinkopf region as these farmers practice herd mobility, moving their animals from Succulent to Nama Karoo depending on the active growing season. If the Nama- Karoo becomes part of the Desert biome it is predicted that there will be food shortages for livestock. However, because of the high adaptability of the small ruminants in this region, these animals will continue to adapt to limiting resources and changing climates.
The survival of these animals in this harsh environment is due to the traditional breeding of indigenous small ruminants that are able to deal with current and future climate and environmental conditions. The Boer goat, cross-bred sheep and Swakara sheep hold important animal genetic resources in the Steinkopf pastoral rangeland.

5.3 Recommendation

This research contributes to the knowledge of herded small ruminants found in dryland pastoral systems. To understand their diet selection and how they survive in both the Succulent and Nama-Karoo biome during drought conditions is essential information for livestock farmers in this area. Since this is one of the first studies conducted in the Steinkopf pastoral system, this study has paved the way for follow up studies regarding this topic. Because this study was conducted during a drought period, I recommend similar studies to be conducted during a regular wet and dry season in both biomes as this will provide more information about the foraging behaviour of small ruminants under normal conditions.

These small ruminants play an important role for these farmers as they provide sustenance, cash income, socio-cultural linkages and insurance against risks (Ramsay et al., 1984; Fitzhugh et al., 1992; Lebbie, 1996; Lebbie & Ramsay, 1999). Thus it is important to conserve these breeds as they possess traits that allow them to survive in erratic climate and environmental conditions. I propose further studies should be done on assessing the genetic variation within the cross-bred sheep found in Steinkopf, this information will contribute to the small ruminant animal genetics of South Africa and can be used for breeding programs in drylands. According to Lebbie & Ramsay (1999) smallholder rural farmers are the current custodians of the majority of the indigenous animal genetic resources in sub-Saharan Africa.

Drought is a recurring catastrophe in the Steinkopf pastoral rangeland thus the monitoring of rangeland resources and the use of these resources is necessary for the survival of livestock farming in this area. Understanding the vulnerability of communities such as Steinkopf to climatic and environmental changes and the impacts over time is essential for adaptation strategies regarding livestock management.

REFERENCES

Abusuwar, A., Ahmed, E., 2010. Seasonal variability in nutritive value of ruminant diets under open grazing system in the semi-arid rangeland of Sudan (South Darfur State). Agric. Biol. J. North Am. 1, 243–249. https://doi.org/10.5251/abjna.2010.1.3.243.249

Aharon, H., Henkin, Z., Ungar, E.D., Kababya, D., Baram, H., Perevolotsky., 2007. Foraging behaviour of newly introduced Boer goat breed in a Mediterranean woodland: A research observation. Small Rumin Res. 69, 144-153.

Al-Atiyat, Salameh, N.M., Tabbaa, M.J., Analysis of genetic diversity and differentiation of sheep populations in Jordan. Electronic Journal of Biotechnology 17, 168-173.

Amary, N., 2016. Assessing the quality of forage for livestock in a semi-arid pastoral system in South Africa.

Anderson, P.M.L., Hoffman, M.T., 2011. Grazing response in the vegetation communities of the Kamiesberg, South Africa: Adopting a plant functional type approach. J. Arid Environ. 75, 255–264. https://doi.org/10.1016/j.jaridenv.2010.10.012

Anderson, S., 2003. Animal genetic resources and sustainable livelihoods. Ecol. Econ. 45, 331–339. https://doi.org/10.1016/S0921-8009(03)00088-0

Animut, G., Goetsch, A.L., 2008. Co-grazing of sheep and goats: Benefits and constraints. Small Rumin. Res. 77, 127–145. https://doi.org/10.1016/j.smallrumres.2008.03.012

Anya, M.I., Ayuk, A.A., Genetic diveristy and climate change: Implications for animal production systems in Africa. Asian Journal of Agricultural research. 5, 217-222.

Arnold, G., 1964. Some principles in the investigation of selective grazing. Proceedings Aust. Soc. Anim. Prod. 5, 258–271.

Aucamp, A.J., 1976. The role of the browser in the bushveld of the Eastern Cape. Proceedings of the Annual Congresses of the Grassland Society of Southern Africa. 11, 135-138.

Baker, R.L., Mwamachi, D.M., Audho, J.O., Aduda, E.O., Thorpe, W., 1999. Genetic resistance to gastro-intestinal nematode parasites in Red Maasai, Dorper and Red Maassai X Dorper ewes in the sub-humid tropics. Animal Science 69, 335-344.

Barroso, F.G., Alados, C.L., Boza, J., 1995. Food selection by domestic goats in Mediterranean arid shrublands. J. Arid Environ. 31, 205–217. https://doi.org/10.1006/jare.1995.0061

Bartolome, J., Franch, J., Plaixats, J., Seligman, N.G., 1998. Diet selection by sheep and goats on Mediterranean. J. Range Manag. 51, 383–391.

Ben Salem, H., Smith, T., 2008. Feeding strategies to increase small ruminant production in dry environments. Small Rumin. Res. 77, 174–194. https://doi.org/10.1016/j.smallrumres.2008.03.008

Bhatta, R., Sankhyan, S.K., Shinde, A.K., Verma, D.L., 2001. Seasonal changes in diet selectivity and grazing behaviour of goats on semi-arid rangeland. Indian J. Anim. Sci. 71, 62–65.

Bohle, H.-G., Downing, T.E., Watts, M., 1994. Climate change and social vulnerability. Glob. Environ. Chang. 4, 37–48. https://doi.org/10.1016/0959-3780(94)90020-5

Botha, P., Blom, C.D., Sykes, E., Barnhoorn, A.S.J., 1983. A comparison between the diets of small and large stock on mixed karoo veld. African J. Range Forage Sci. 18, 101–105. https://doi.org/10.1080/00725560.1983.9648993

Botha, P., 2012. Factors influencing the palatability of herbage and species selection by the animal. Grootfontain, Agricultural Development. URL http://gadi.agric.za/articles/Agric/factors.php.

Bourne, A., Donatti, C., Holness, S., Midgley, G., 2012. Climate Change Vulnerability Assessment Cambridgr University Press. https://doi.org/10.1016/C2014-0-02559-2

Bradford, G.E., Berger, Y.M., 1988. Breeding strategies for small ruminants in arid and semi-arid areas. Current Topics in Veterinary Medicine and Animal Science- Increasing small ruminant productivity in semi-arid areas 47, 95-109.

Brand, T.S., 2000. Grazing behaviour and diet selection by Dorper sheep. Small Rumin. Res. 36, 147–158. https://doi.org/10.1016/S0921-4488(99)00158-3

Bullinaria, J.A., 2018. Evolution of learning strategies in changing environments. Cognitive Systems Research, 52 429-449.

Burke, A., 2002. Island - Matrix relationships in Nama Karoo inselberg landscapes. Part I: Do inselbergs provide a refuge for matrix species? Plant Ecol. 160, 79–90. https://doi.org/10.1023/A:1015899729968

Bururam, P., 2004. Genetic characterisation of Southern Africa sheep breeds using DNA markers. MSc. dissertation. Department of Animal, Wildlife and Grassland Sciences. University of the Free State.

Carstens, W., 1961. The Community of Steinkopf: an stenographic study and an analysis of social° hangs in Namaqualand. University of Cape Town.

Cheeke, P.R., 1994. Nutrition and Nutritional Diseases. Am. Coll. Lab. Anim. Med. 321–333.

Clarke, K.R, Gorley, R., 2006. PRIMER v6: user manual/tutorial. Plymouth: PRIMER-E.

Cloete, J.J.E., Cloete, S.W.P., Scholtz, A.J., Hoofman, L.C., 2013. Behaviour response of Namaqua Afrikaner, Dorper and South African Mutton Merino lambs towards humans. South African Journal of Animal Science 43, 16-20.

Cousins, B., 1999. Invisible capital : The contribution of communal rangelands to rural livelihoods in South Africa. Dev. South. Afr. 16, 299–318. https://doi.org/10.1080/03768359908440079

Cousins, B., Hoffman, M.T., Allsopp, N., Rohde, R.F., 2007. A synthesis of sociological and biological perspectives on sustainable land use in Namaqualand. J. Arid Environ. 70, 834–846. https://doi.org/10.1016/j.jaridenv.2007.04.002

Cowling, R.M., Esler, K.J., Rundel, P.W., 1999. Namaqualand, South Africa- an overview of a unique winter-rainfall desert ecosystem. Plant Ecology. 142, 3-21.

Cowling, R.M., Knight, A.T., Faith, D.P., Ferrier, S., Lombard, A.T., Driver, A., Rouget, M., Maze, K., Desmet, P.G., 2004. Nature conservation requires more than a passion for species. Conserv. Biol. 18, 1674–1676. https://doi.org/10.1111/j.1523-1739.2004.00296.x

Davis, C.L., Hoffman, M.T., Roberts, W., 2016. Recent trends in the climate of Namaqualand, a megadiverse arid region of South Africa. Recent trends in climate of Namaqualand, South Africa 1-9.

Dawson, T.J., Ellis, B.A., Diets of mammalian herbivores in Australian arid, hilly schrublands: Seasonal effects on overlap between euros (hill kangaroos), sheep and feral goats, and on dietary niche breadths and electivities. Journal of Arid Environments 34, 491-506.

De Boer, W.F., Prins, H.H.T., 1989. Decisions of cattle herdsmen in Burkina Faso and optimal foraging models. Hum. Ecol. 17, 445–464. https://doi.org/10.1007/BF00889500

de Bruyn, T.D., 1998. The condition, productivity and sustainability of communally grazed rangelands in the central Eastern Cape Province. Res. Train. Strateg. goat Prod. Syst. South Africa. Proc. a Work. Hogsback, South Africa, 18–27.

Debeaudoin, L.M.C., 2001. Livestock farming practices in a communal rangeland, Leliefontein, Namaqualand. MSc. University of the Western Cape, Cape Town.

Degen, A.A., Benjamin, R.W., Abdraimov, S.A., Sarbasov, T.I., 2002. Browse selection by Karakul sheep in relation to plant composition and estimated metabolizable energy content. J. Agric. Sci. 139, 353–358. https://doi.org/10.1017/S0021859602002551

Desmet, P.G., 2007. Namaqualand-A brief overview of the physical and floristic environment. J. Arid Environ. 70, 570–587. https://doi.org/10.1016/j.jaridenv.2006.11.019

Driver, A., Desmet, P., Rouget., M., Cowling., R., Maze., K., 2003. Succulent Karoo Ecosystem Plan: Biodiversity component. Cape conservation unit technical report, Cape Town.

Duncan, A.J., Ginane, C., Elston, D.A., Kunaver, A., Gordon, I.J., 2006. How do herbivores trade-off the positive and negative consequences of diet selection decisions ? Anim. Behav.

71, 93–99. https://doi.org/10.1016/j.anbehav.2005.03.035

Dwyer, C., 2009. The ethnology of domestic animals: an introductory text, modular tests No. Ed. 2, ref 12. 161-176, Wallingford, UK

Dziba, L.E., Scogings, P.F., Gordon, I.J., Raats, J.G., 2003. The feeding height preferences of two goat breeds fed Grewia occidentalis L. (Tiliaceae) in the Eastern Cape, South Africa. Small Rumin. Res. 47, 31–38. https://doi.org/10.1016/S0921-4488(02)00234-1

Egeru, A., 2012. Role of indigenous knowledge in climate change adaptation: A case study of the Teso sub-region, Eastern Uganda. Indian J. Tradit. Knowl. 11, 217–224. https://doi.org/DOI unavailable

Els, J.F., 2000a. Diet selection of four free raning breeds of smallstock I: chemical composition. Ministry of Agriculture, water and rural development. Namibia 2–4.

Els, J.F., 2000b. Diet selection of of four free ranging breeds of smallstock II: species compostion. Ministry of Agriculture, water and rural development. Namibia 36–38.

Erasmus, J.A., 2000. Adaptation to various environments and resistance to disease of the improved Boer goat. Small Rumin. Res. 36, 179–187. https://doi.org/10.1016/S0921-4488(99)00162-5

Escarcha, J., Lassa, J., Zander, K., 2018. Livestock Under Climate Change: A Systematic Review of Impacts and Adaptation. Climate 6, 54. https://doi.org/10.3390/cli6030054

Excoffier, L., Smouse, P.E., Quattro, J.M., 1992. Analysis of molecular variance inferred from metric distances among DNA haplotypes: application to human mitochondrial DNA restriction data. Genetics, 131, 479-491.

Finch, D.M., Pendleton, R.L., Reeves, M.C., Ott, J.E., Kilkenny, F.F., Butler, J.L., Ott, J.P., Ford, P.L., Runyon, J.B., Kitchen, S.G., 2016. Rangeland drought: Effects, restoration, and adaptation, Effects of Drought on Forests and Rangelands in the United States: A Comprehensive Science Synthesis (US Forest Service Gen. Tech. Report WO-93b)., Chapter: Chapter 8. Washington, DC,.

Fraps, G.S., Cory, V.L., 1940. Composition and utilization of range vegetation of Sutton and Edwards Counties. Bulletin. Texas Agricultural experiment station. College Station, Texas, USA.

Fynn, R.W.S., O'Connor, T.G., 2000. Effect of stocking rate and rainfall on rangeland dynamics and cattle performance in a semi-arid savanna, South Africa. J. Appl. Ecol. 37, 491–507. https://doi.org/10.1046/j.1365-2664.2000.00513.x

FAO., 2001. Pastoralism in the new millennium. Animal Production and Health Paper. No.150. Rome

FAO., 2006b. The state of the World's Animal Genetic Resources for Food and Agriculture- Food aid for security, Food and agriculture organization of the United Nations. Rome.

FAO., 2007. The state of the World's Animal Genetic Resources for Food and Agriculture– in brief, edited by Dafydd Pilling & Barbara Rischkowsky. Rome.

FAO., 2009. Livestock keepers-guardians of biodiversity. Animal Production and Health Paper. No.167. Rome

Fauchereau, N., Trzaska, S., Rouault, M., Richard, Y., 2003. Rainfall variability and changes in southern Africa during the 20th century in the global warming context. Nat Hazards 29, 139-154.

Fayemi, P.O., Muchenje, V., 2013. Maternal slaughter at abattoirs: History, causes, cases and the meat industry. Springerplus 2, 1–7. https://doi.org/10.1186/2193-1801-2-125

Fernandez-Gimenez, M.E., 2000. The role of nomadic Mongolian pastoralists' ecological knowledge in rangeland management. Ecological Applications. 10, 1318-1326.

Fitzhugh, H.A., Ehui, S.K., Lahlou-Kassi., A., 1992. Research strategies for development of animal agriculture. World Animal Rev. 72, 3-13.

Galal, S., Rasoul, F.A., Annous, M.R., Shoat, I., Small Ruminant Breeds of Egypt. In Iñiguez, L., Characterisation of small ruminant breeds in west Asia and North Africa. International centre for agricultural research in dry areas (ICARDA), Aleppo, Syria 2, 196.

Gaughan, J.B., 2012. Environmental Stress and Amelioration in Livestock Production: Basic Principles Involved in Adaption of Livestock to Climate Change. Springer-Verlag Berlin Heidelberg, Belin.

Genin, D., Villca, Z., Abasto, P., Journal, S., May, N., 2018. Diet selection and utilization by llama and sheep in a high altitude-arid rangeland of Bolivia 47, 245–248.

Goldblatt, A., 2010. Agriculture: Facts & Trends South Africa URL. [http://awsassets.wwf.org.za/downloads/facts_brochure_mockup_04_b.pdf].

Gray, J.S., Dautel, H., Estrada-Peña, A., Kahl, O., Lindgren, E., 2009. Effects of Climate Change on Ticks and Tick-Borne Diseases in Europe. Interdisciplinary Perspectives on Infectious Diseases 1-12.

Grove, M., 2011. Speciation, diversity, and mode 1 technologies: The impact of variability selection. Journal of Human Evolution, 61 306-319.

Grova, L., Bjelland, B., 1997. Feeding behaviour of goats in the Valse Thornveld of the Eastern Cape. Combined project in Livestock and Pasture Science. Norway.

Hahn, G., Mader, T., 1997. Heat waves in relation to thermoregulation, feeding behavior and mortality of feedlot cattle, in: R. W. Bottcher and S. J. Hoff, Eds., Vol. 1, American Society of Agricultural Engineers,.Proceedings of the Fifth International Livestock Environment Symposium,. pp. 563–571.

Hall, S.J.G., Bradley, D.G., 1995. Conserving livestock breed biodiversity. Trends Ecol. Evol. 10, 267–270. https://doi.org/10.1016/0169-5347(95)90005-5

Hall, S.J.G., Ruane, J., Hall, S.G., 2017. Society for Conservation Biology Livestock Breeds and Their Conservation : A Global Overview Livestock Breeds and Their Conservation : A Global Overview 7, 815–825.

Hall, T.A., 1999. BioEdit: a user-friendly biological sequence alignment editior and analysis program for Windows 95/98/NT. Oxford University Press 41, 95-98.

Hendricks, H.H., 1994. Ecological studies in a communal farming area: a comparison of Standard Ecological methods and Participatory Rural Appraisal techniques. University of the Western Cape.

Hendricks, H.H., Novellie, P.A., Bond, W.J., Midgley, J.J., 2002. Diet selection of goats in the communally grazed Richtersveld National Park. African J. Range Forage Sci. 19, 1–11. https://doi.org/10.2989/10220110209485769

Hoffman, I., 2010. Climate change and characterisation, breeding and conservation of animal genetic resources. Animal Genetics 41, 32-46.

Hoffman, M.T., Carrick, P.J., Gillson, L., West, A.G., 2009. Drought, climate change and vegetation response in the Succulent Karoo, South Africa. South African Journal of Science 105, 54-60.

Holechek, J.L., 1984. Comparative Contribution of Grasses , Forbs , and Shrubs to the Nutrition of Range Ungulates. Soc. Range Manag. 6, 261–263.

Hongslo, E., Rohde, R., Hoffman, T., 2009. Landscape change and ecological processes in relation to land-use in Namaqualand, South Africa, 1939 to 2005. South African Geogr. J. 91, 63–74. https://doi.org/10.1080/03736245.2009.9725333

Hussein, K., Calvosa C., Roy, R. and the G.E.F.U., 2008. The effects of climate change on small holder farmers in West and Central Africa., in: Published for the 10th Meeting of the Africa Partnership Forum,. Tokyo, Japan.

Illius, A.W., Gordon, I.J., Derry, J.F., Magadzire, Z., Mukungurutse, E., 2000. Environmental variability and productivity of semi-arid grazing systems 1–23.

International, V., 2015. Genstat for Windows 18th Edition. VSN International, Hemel Hempstead, UK. Web page: Genstat.co.uk.

Ivlev, V.S., 1961. Experimental ecology of the feeding of fishes. New York.

Jabbar, M.A., Swallow, B.M., Rege, J.E.O., 1999. Incorporation of farmer knowledge and preferences in designing breeding policy and conservation strategy for domestic animals. Outlook Agric. 28, 239–243. https://doi.org/10.1177/003072709902800407

Jones, P., Maroge, M.J., 2010. Changes in livestock emphasis to help farmers adapt to climate change. South African Society for Agricultural Extension. Conference (44th: 2010: Langebaan, South Africa); SASAE Conference, Langebaan, South Africa.

Jones, P., Thornton, P.K., 2009. Croppers to livestock keepers: livelihood transitions to 2050 in Africa due to climate change. Environmental science & policy 12, 427-437.

Kam, M., El-Meccawi, S., Degen, A., 2012. Foraging behaviour and diet selection of free-ranging sheep and goats in the Negev Desert , Israel. J. Agric. Sci. 379–387. https://doi.org/10.1017/S0021859611000955

Kassilly, F.N., 2002. Forage quality and camel feeding patterns in Central Baringo, Kenya. Livest. Prod. Sci. 78, 175–182. https://doi.org/10.1016/S0301-6226(02)00032-5

Kelso, C., Vogel, C., 2007. The climate of Namaqualand in the nineteenth century. Clim. Change 83, 357–380. https://doi.org/10.1007/s10584-007-9264-1

Koohafkan, P., Stewart, B.A., 2008. Water and cereals in drylands, Water and Cereals in Drylands. The Food and Agriculture Organization of the United Nations and Earthscan. https://doi.org/10.4324/9781849773744

Krueger, W.C., Laycock, W.A., Price, D.A., 1974. Relationships of Taste , Smell , Sight , and Touch to Forage Selection 27, 258–262.

Kruger, L., 2015. Indigenous sheep and goat breeds in South Africa. Farmers weekly. URL: https://www.farmersweekly.co.za/farm-basics/how-to-livestock/indigenous-sheep-and-goat-breeds/

Kunene, N.W., Bezuidenhout, C.C., Nsahlai, I.V., 2009. Genetic and phenotypic diversity in Zulu sheep populations: Implications for exploitation and conservation. Small Ruminant

Research 84, 100-107.

Lacy, R.C., 1997. Importance of Genetic Variation to the Viability of Mammalian Populations. J. Mammal. 78, 320–335. https://doi.org/10.2307/1382885

Lamprey, H.F., 1983. Pastoralism yesterday and today: the over-grazing problem. Ecosyst. world.

Lebbie, S.H.B., 1996. In: Meissner, H.H. (Ed), Food Security in Africa: Challenges, Opportunities and Targets for Animal Production, Proc. of the second all African Conference on Animal Agriculture, 1-4 April 1996, Pretoria, South Africa, 381-396.

Lebbie, S.H.B., Ramsay, B., 1999. A perspective on conservation and management of small ruminant genetic resources in the sub-Saharan Africa. Small Rum Res. 34, 231-247.

MacKellar, N.C., Hewitson, B.C., Tadross, M.A., 2007. Namaqualand's climate: Recent historical changes and future scenarios. J. Arid Environ. 70, 604–614. https://doi.org/10.1016/j.jaridenv.2006.03.024

Mader, T.L., Frank, K.L., Harrington, J.A., Hahn, G.L., Nienaber, J.A., 2009. Potential climate change effects on warm-season livestock production in the Great Plains. Clim. Change 97, 529–541. https://doi.org/10.1007/s10584-009-9615-1

Malan, S.W., 2000. The improved Boer goat. Small Rumin. Res. 36, 165–170. https://doi.org/10.1016/S0921-4488(99)00160-1

Mandleni, B., 2011. Impact of climate change and adaptation on cattle and sheep farming in the Eastern Cape province of South Africa. J. Hum. Ecol. University of South Africa. https://doi.org/10.1080/09709274.2011.11906375

Marai, I.F.M., El-Darawany, A.A., Fadiel, A., Abdel-Hafez, M.A.M., 2007. Physiological traits as affceted by heat stress in sheep- A review. Small Ruminant Research 71, 1-12.

Martins, C., Peters, K.L., 1992. Alternative uses of Karakul sheep for pelt and lamb production in Botswana. II. Pelt prodcution. Small Rumin. Res. 9, 11-19.

Matimati, I., Musil, C.F., Raitt, L., February, E., 2013. Non rainfall moisture interception by dwarf succulents and their relative abundance in an inland arid South African ecosystem. Ecohydrology 6, 818–825. https://doi.org/10.1002/eco.1304

McCabe, T., 2009. Food and the Turkana in Kenya. In Cultural survival.

Meissner, H.H., Scholtz, M.M., Palmer, A.R., 2013. Sustainability of the South African livestock sector towards 2015 Part 1: Worth and impact of the sector. South African Journal of Animal Science 43, 282-297.

Midgley, G.F., Thuiller, W., 2007. Potential vulnerability of Namaqualand plant diversity to anthropogenic climate change. J. Arid Environ. 70, 615–628. https://doi.org/10.1016/j.jaridenv.2006.11.020

Migongo-bake, A.W., Hansen, R.M., Journal, S., Jan, N., 1987. Seasonal Diets of Camels , Cattle , Sheep , and Goats in a Common Range in Eastern Africa. Soc. Range Manag. 40, 76–79.

Milton, S.J., Hoffman, M.T., 1994. The application of state-and-transition models to rangeland research and management in Arid Succulent and Semi-Arid Grassy Karoo, South Africa. African J. Range Forage Sci. 11, 18–26. https://doi.org/10.1080/10220119.1994.9638349

Molotsi, A., Dube, B., Oosting, S., Marandure, T., Mapiye, C.,Cloete, S., Dzama, K., 2017. Genetic traits of relevance to sustainability of smallholder sheep farming systems in South Africa. Sustainability 9, 1-18.

Moodie, D.,1959. The record; or, a series of official papers relative to the condition and treatment of the native tribes of South Africa, part 1, 'Diary kept by Pieter Meerhoff, 18 February 1660)

Mossop, E.E., n.d. Journals of the expeditions of the Honourable Ensign Olaf Bergh [1682 &1683] and Isaq Schrijver [1689]. Van Riebeeck Soc.

Mucina, L., Rutherford, M.C., 2006. The vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19 1–30. https://doi.org/10.1007/s

Mude, A., Chantarat, S., Barrett, A.B., Carter, M.R., Ikegami, M., McPeak, J.G., 2010. Insuring Against Drought-Related Livestock Mortality: Piloting Index Based Livestock Insurance in Northern Kenya. Syracuse University SURFACE. Maxwell school citizenship and public affairs 1-24.

Muigai, A.W.T., Okeyo, A.M., Kwallah, A.K., Mburu, D., Hanotte., 2009. Characterisation of sheep populations of Kenya using microsatellite markers: Implications for conservation and management of indigenous sheep populations. South African Journal of Animal Science 39, 93-96.

Municipality, N.K., n.d. Integrated Development Plan.

Mwacharo, J.M., Kim, E., Ahmed, R., Elbeltagy, Aboul-Naga, A.M., Rischowsky, Rothschild M.F., 2017. Genomic footprints of dryland stress adaptation in Egyption fat-tail sheep and their divergence from East african and wesetrn Asia cohorts. African Archaeological Review 30, 39-50.

Naqvi, A.N., Bukhari, J.F., Vahidi, S.M.F., Utsunomiya, Y.T., Gracia, J.F., Babar,M.E., Lin-Han, J., Pichler, R., Periasamy, K., 2017. Microsatellite based genetic diversity and mitochondrial DNA D-Loop variation in economically important goat breeds of Pakistan. Small Ruminant Research 148, 62-71.

Näsholm, A., Eythorsdottir, E., 2011. Characteristics and utilization of sheep pelts. Small Rumin. Res. 101, 182-187.

New, M., 2015. Are semi-arid regions climate change hot-spots? Evidence from Southern. Adaptations at Scale in Semi- Arid Regions. URL http://www.assar.uct.ac.za/node/471699#sthash.NtlOiINL.dpuf

Ngwa, A.T., Pone, D.K., Mafeni, J.M., 2000. Feed selection and dietary preferences of forage by small ruminants grazing natural pastures in the Sahelian zone of Cameroon. Anim. Feed Sci. Technol. 88, 253–266. https://doi.org/10.1016/S0377-8401(00)00215-7

Norman Myers*, Russell A. Mittermeier[2], Cristina G. Mittermeier[2], G.A.B. da F.& J.K., 2000. Biodiversity hotspots for conservation priorities. Nat. Int. J. Sci. 403, 853–858. https://doi.org/10.1038/35002501

Notter, D.R., 2004. Conservation strategies for animal genetic resources. Commission on genetic resources for food and agriculture. Background study paper 22, 1-13.

Notter, D.R., 1999. The importance of genetic diversity in livestock populations of the future. J. Anim. Sci. 77, 61–69.

Nyong, A., Adesina, F., Osman Elasha, B., 2007. The value of indigenous knowledge in climate change mitigation and adaptation strategies in the African Sahel. Mitig. Adapt. Strateg. Glob. Chang. 12, 787–797. https://doi.org/10.1007/s11027-007-9099-0

Ogunkoya, F.T., 2014. Socio-economic factors that affect livestock numbers: a case study of smallholder cattle and sheep farmers in the Free State province of South Africa. Br. J. Psychiatry. University of South Africa. https://doi.org/10.1192/bjp.205.1.76a

Oladipo, E.O., 1985. A comparative performance analysis of three meteorological drought indices. J. Climatol. 5.

Omondi, I., Baltenweck, I., Drucker, A.G., Obare, G., Zander, K.K., 2008. Economic valuation of sheep genetic resources: implications for sustainable utilization in the Kenyan semi-arid tropics. Tropical Animal Health and Production 40, 615-626.

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 Ruminant Research 90, 101-108.

Peters, G.M., Wiedemann, S.G., Rowley, H. V, Tucker, R.W., 2010. Accounting for water use in Australian red meat production 311–320. https://doi.org/10.1007/s11367-010-0161-x

Pfister, J.A., Malechek, J.C., Balph, D.F., 1988. Foraging Behaviour of Goats and Sheep in the Caatinga of Brazil. J. Appl. Ecol. 25, 379–388.

Phyu, P.P., Pichler, R., Soe, O., Aung, P.P., Than, M., Shamsuddin, M., Diallo, A., Periasamy, K., 2017. Genetic diversity, population structure and phylogeography of Myanmar goats. Small Ruminant Research 148, 33-42.

Pisani, J.M., Distel, R.A., Bontti, E.E., 2000. Diet selection by goats on a semi-arid shrubland in central 103–108.

Potts, R., 1996. Evolution and climate variability. Science 273, 922-923.

Potts, R., 1998. Variability selection in hominid evolution. Evolutionary Anthropology, 7 81-96.

Potts, R., 2013. Hominin evolution in settings of strong environmental variability. Quaternary Science Reviews, 73 1-13.

Raats, J.G., 1997. Feeding behaviour of free range goats. African J. Sci. 18, 34–52.

Ramsay, K.A., Smith, C.H., Geldenhuys, C.P., 1984. The potential of the indigenous veld goat as a meat producer in the traditional developing areas of South Africa. Department of development aid, Pretoria.

Rege, J.E.O., 1994. Indigenous African small ruminants: A case for characterisation and improvement. Small Ruminant Research and devlopment in Africa. Proceedings of the second biennial conference of the African Small Ruminant Research Network AICC, Arusha, Tanzania 7-11 December 1992.

Rege, J.E.O., Gibson, J.P., 2003. Animal genetic resources and economic development: issues in relation to economic valuation. Ecological Economics 45, 319-330.

Renaudeau, D., Collin, A., Yahav, S., de Basilio, V., Gourdine, J.L., Collier, R.J., 2012. Adaptation to hot climate and strategies to alleviate heat stress in livestock production. Animal 6, 707-728.

Richkowsky, B.A., Tibbo, M., Iniguez, L., 2010. Strengthening sustainable use of small ruminant genetic resources in the drylands in the WANA region. International Center for Agricultural Research in the Dry Areas (ICARDA), PO Box 5466, Aleppo, Syria.

Rognoni, G., 1980. Reports from country delegates on animal genetic resources and their conservation. In: Report of the FAO/UNEP technical consultation on animal genetic resources conservation and management. FAO Animal Production and Health paper.

Rohde, R.F., Benjaminsen, T.A., Hoffman, M.T., Cousins, B., Thompson, L., others, 2002. Land reform in Namaqualand: poverty alleviation, stepping stones and'economic units'., Contested resources: challenges to the governance of natural resources in Southern Africa. Papers from the International Symposium, University of the Western Cape, Cape Town, South Africa, 18-20 October 2000.

Roux, P.W., Vorster, M., Zeeman, P.J.L., Wentzel, D., 1981. Stock production in the Karoo region. Proceedings of the annual congresses of the grassland society of Southern Africa 16, 29-35.

Rozas, J., Sánchez-DelBarrio ,J.C., Messeguer, X., Rozas, R., 2010. DnaSP, DNA polymorphism analyses by the coalescent and other methods. Bioinformatics, 19, 2496-2497.

Rust, J.M., Rust, T., 2013. Climate change and livestock production: A review with emphasis on Africa. S. Afr. J. Anim. Sci. 43, 256–267. https://doi.org/10.4314/sajas.v43i3.3

Rutherford, M.C., Powrie, L.W., Schulze, R.E.,1999. Climate change conservation areas of Sout Africa and its potential impact on floristic composition: a first assessment. Diversity and distributions. 5, 253- 262.

Rutherford, M.C., Powrie, L.W., 2006. Biomes and bioregions of southern Africa. In : Mucina , L., Rutherford , M. C. (Eds .), The vegetation of South Africa , Lesotho and and Swaziland.

Salomon, M., Cupido, C., Samuels, I., 2013. The good shepherd: remedying the fencing syndrome. African J. Range Forage Sci. 30, 71–75.

https://doi.org/10.2989/10220119.2013.781064

Samuels, M.I., 2006. Patterns of resource use by livestock during and after drought in a communal rangeland in Namaqualand. J. Arid Environ. University of the Western Cape.

Samuels, M.I., Allsopp, N., Knight, R.S., 2007. Patterns of resource use by livestock during and after drought on the commons of Namaqualand, South Africa. Journal of Arid environments. 70, 728-739.

Samuels, I., Allsopp, N., Hoffman, M.T., 2013. How could herd mobility be used to manage resources and livestock grazing in semi-arid rangeland commons? African J. Range Forage Sci. 30, 85–89. https://doi.org/10.2989/10220119.2013.781063

Samuels, I., Cupido, C., Swarts, M.B., Palmer, A.R., Paulse, J.W., 2016a. Feeding ecology of four livestock species under different management in a semi-arid pastoral system in South Africa. African J. Range Forage Sci. 33, 1–9. https://doi.org/10.2989/10220119.2015.1029972

Samuels, I., Angual, M., Ntombela, K., Katjizeu, E., Cupido, C., Swarts, M., Hambili, E., Knanyala, J., 2016b. Climate change adaptation strategies by pastoralists along an aridity gradient in Southern Africa. In: Proceedings 10th International Rangeland Congres. Saskatoon, Canada, 16-22 July 2016. (Ed A. Iwassa, H., Lardner, A., Schellenberg, M., Willms, W., Larson, K.,) 902-905. (Organiser 10th Rangeland Congress: Saskatoon, Canada.)

Samuels, M.I., Swarts, M.B.V., Schroeder, A., Ntombela. K.P., Cupido, C.F., 2018. Through the lens of a herder: insights into landscape ethno-sociological knowledge on rangelands in Namaqualand. J. Anthropology S. Afr 41, 136-152. DOI:10.1080/23323256.2018.1462091

Samuels, M.I., Allsopp, N., Hoffman, M.T., 2019. Traditional mobile pastoralism in a contemporary semi-arid rangeland in Namaqualand, South Africa. J. Range Ecology and Management 72, 195-203.

Schlecht, E., Hiernaux, P., Kadaouré, I., Hülsebusch, C., Mahler, F., 2006. A spatio-temporal analysis of forage availability and grazing and excretion behaviour of herded and free grazing cattle, sheep and goats in Western Niger. Agric. Ecosyst. Environ. 113, 226–242. https://doi.org/10.1016/j.agee.2005.09.008

Schoeman, S.J., Els, J.F., van Niekerk, M.M., 1997. Variance components of early growth traits in the Boer goat. Small Rumin Res. 26, 15-20.

Scholtz, M.M., Maiwashe, A., Neser, F.W.C., Theunissen, A., Oliver, W.J., Mokolobate, M.C., Hendriks, J., 2013. Livestock breeding for sustainability to mitigate global warming, with the emphasis on developing countries. South African Journal of Science 43, 269-281.

Schwinning, S., Sala, O.E., Loik, M.E., Ehleringer, J.R., 2004. Thresholds, memory, and seasonality: Understanding pulse dynamics in arid/semi-arid ecosystems. Oecologia 141, 191–193. https://doi.org/10.1007/s00442-004-1683-3

Scoones, I., 1992. Coping with drought: Responses of herders and livestock in contrasting savanna environments in Southern Zimbabwe. Hum. Ecol. 20, 293–314. https://doi.org/10.1007/BF00889899

Sejian, V., Maurya, V.P., Naqvi, S.M.K., 2010. Adaptive capability as indicated by endocrine and biochemical responses of Malpura ewes subjected to combined stresses (Thermal and nutritional) in a semi-arid tropical environment. International Journal of Biometeorology 54, 653-661.

Selepe, M.M., Ceccobelli, S., Lasagna, E., Kunene, N.W., 2018. Genetic structure of South African Nguni (Zulu) sheep populations reveals admixture with exotic breeds. PLOS ONE 13.

Seo, S.N., Mendelsohn, R., 2008. Measuring impacts and adaptations to climate change: a structural Ricardian analysis of climate change impacts and adaptations in African agriculture. Agric. Econ. 38, 151–165. https://doi.org/10.1111/j.1574-0862.2007.00289.x

Shinde, A.K., Karim, S.A., Sankhyan, S.K., Bhatta, R., 1998. Seasonal changes in biomass growth and quality and its utilization by sheep on semiarid Cenchrus ciliaris pasture of India. Small Rumin. Res. 30, 29–35.

Silanikove, N., 2000. The physiological basis of adaptation in goats to harsh environments. Small Rumin. Res. 35, 181–193. https://doi.org/10.1016/S0921-4488(99)00096-6

Snyman, H.A., 1998. Dynamics and sustainable utilization of rangeland ecosystems in arid and semi-arid climates of southern Africa. J. Arid Environ. 39, 645–666. https://doi.org/10.1006/jare.1998.0387

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. https://doi.org/10.1016/j.smallrumres.2011.09.041

Sweet, J., 1998. Livestock- coping with drought: Namibia- A Case Study. Grassland group of the crop and grassland service (AGPC) of FAO for the FAO/AGAP electronic conference on "Livestock- Coping with drought". 8 Boyne House, 55 Blackwater road, Eastbourne BN20 7DL, UK.

Swofford, D.L., 2002. PAUP* Phylogenetic Analysis using parsimony (and other methods), Version 4.10. Illinois Natural History Survey, Champaign, Illinois.

ter Braak, C.J.F., Šmilauer, P., 2012. Canoco reference manual and user's guide: software for ordination.

Thornton, P.K., Gerber, P.J., 2010. Climate change and the growth of the livestock sector in developing countries. Mitig. Adapt. Strateg. Glob. Chang. 15, 169–184. https://doi.org/10.1007/s11027-009-9210-9

Thornton, P.K., Herrero, M., 2014. Climate change adaptation in mixed crop-livestock systems in developing countries. Glob. Food Sec. 3, 99–107. https://doi.org/10.1016/j.gfs.2014.02.002

Todd, S.W., Hoffman, M.T., 1999. A fence-line contrast reveals effect of heavy grazing on plant diversity and community composition in Namaqualand, South Africa. Plant Ecology. 142, 169-170.

van Vuuren, L., 2015. Drought management- Stengthening our knowledge armoury. Water Wheel 14. https://doi.org/10.1007/BF02299585

Varadan, R.J., Kumar, P., 2014. Indigenous knowledge about climate change: Validating the perceptions of dryland farmers in Tamil Nadu. Indian Journal of Traditional Knowledge 13, 390-397.

Vetter, S., 2009. Drought, change and resilience in South Africa's arid and semi-arid rangelands. South African Journal of Science 105, 29-33.

Visser, C., Marle-Köster, E.V., 2014. Strategies for the genetic improvement of South African Angora goats. Small Ruminant Research 121, 89-95.

Ward, D., Ngairorue, B.T., Kathena, J., Samuels, R., Ofran, Y., 1998. Land degradation is not a necessary outcome of communal pastoralism in arid Namibia. J. Arid Environ. 40, 357–371. https://doi.org/10.1006/jare.1998.0458

Warren, A.L.E., Ueckert, D.N., Shelton, M., Chamrad, A.D., 1984. Spanish Goat Diets on Mixed-brush Rangeland in the South Texas Plains. J. Range Manag. 37, 340–342

Webley, L., 2007. Archaeological evidence for pastoralist land-use and settlement in Namaqualand over the last 2000 years. J. Arid Environ. 70, 629–640. https://doi.org/10.1016/j.jaridenv.2006.03.009

Webley, L., 1984. Archaeology and ethnoarchaeology in the Leliefontein Reserve and surrounds, Namaqualand. University of Stellenbosch.

Western, D., Finch, V., 1986. Cattle and pastoralism: Survival and production in arid lands. Hum. Ecol. 14, 77–94. https://doi.org/10.1007/BF00889211

Wollny, C.B.A., 2003. The need to conserve farm animal genetic resources in Africa: should policymakers be concerned? Ecological Economics 45 341-351

APPENDICES

Appendix 1

Different morphological features of cross-bred sheep found in the Steinkopf pastoral rangeland in South Africa.

Appendix 2

Supplementary Table ST1. Diet selection and forage preferences of herded livestock during the wet season for the Succulent Karoo biome. E_i = Ivlev's forage ratio included in the study

		E_i			Diet (%)			Cover (%)		
Species	**Plant functional type**	**Cross-bred**	**Swakara**	**Goat**	**Cross-bred**	**Swakara**	**Goat**	**Cross-bred**	**Swakara**	**Goat**
Asparagus juniperoides	PerNSShr	0.29	**2.10**	0.00	0.10	0.16	0.00	0.36	0.08	0.00
Asparagus asparagoides	PerNSShr	0.00	0.70	**5.00**	0.00	0.32	0.21	0.02	0.46	0.04
Calobota sericea	PerNSShr	**1.21**	0.00	**1.67**	0.73	0.00	1.28	0.60	0.38	0.77
Cheiridopsis denticulata	PerLSShr	**1.22**	0.35	**1.01**	4.44	0.32	6.38	3.62	0.92	6.34
Conicosia elongata	PerLSShr	0.23	0.13	0.00	0.52	0.49	0.00	2.29	3.69	0.00
Didelta spinosa	PerNSShr	**1.11**	0.00	0.23	1.72	0.00	0.21	1.55	0.31	0.94
Eriocephalus microphyllus	PerNSShr	0.57	0.72	**1.11**	2.72	5.50	8.72	4.79	7.65	7.83
Euphorbia mauritanica	PerSSShr	0.11	0.15	0.02	0.57	0.81	0.21	5.20	5.34	9.57
Euryops lateriflorus	PerNSShr	**1.35**	**1.40**	**1.67**	0.10	0.16	0.43	0.08	0.12	0.26
Exomis microphylla	PerNSShr	0.37	**1.20**	**1.97**	0.57	1.94	2.77	1.56	1.61	1.40
Galenia africana	PerNSShr	0.09	0.02	0.03	1.10	0.16	0.21	12.00	7.61	7.32
Galenia fruticosa	PerLSShr	0.36	0.58	**1.14**	0.63	1.62	1.70	1.75	2.81	1.49
Annual Grass sp 1.	AnGrass	**2.93**	**3.44**	**4.00**	3.86	1.46	0.85	1.32	0.42	0.21
Hermannia amoena	PerNSShr	**2.38**	0.00	**1.43**	0.63	0.00	0.43	0.26	0.04	0.30
Hermannia disermifolia	PerNSShr	**1.74**	0.00	0.00	1.62	0.00	0.00	0.93	0.00	0.00
Hermannia sp 1.	PerNSShr	0.26	0.37	**1.67**	0.21	0.32	1.91	0.79	0.88	1.15
Lycium amoenum	PerNSShr	**2.02**	0.00	0.00	0.47	0.00	0.00	0.23	0.00	0.00
Lycium cinereum	PerNSShr	0.17	0.15	**2.39**	0.31	0.32	2.34	1.86	2.11	0.98
Lycium light green	PerNSShr	0.00	**2.10**	0.00	0.00	0.16	0.00	0.34	0.08	0.00
Lycium sp 1.	PerNSShr	0.00	**1.58**	**2.86**	0.00	0.49	0.85	0.00	0.31	0.30
Melianthus pectinatus	PerNSShr	0.31	**1.20**	0.00	0.10	0.32	0.00	0.34	0.27	0.43
Monechma sp 1.	PerNSShr	0.00	0.00	**3.33**	0.00	0.00	0.43	0.00	0.00	0.13
Monsonia ciliata	PerLSShr	0.00	0.00	**4.44**	0.00	0.00	1.70	0.06	0.15	0.38
Monsonia herrei	PerLSShr	0.00	0.00	**5.00**	0.00	0.00	0.43	0.00	0.00	0.09
Monsonia salmoniflora	PerLSShr	**3.37**	0.00	0.00	0.05	0.00	0.00	0.02	0.00	0.00
Monsonia spinosa	PerLSShr	0.32	0.28	0.00	0.16	0.32	0.00	0.50	1.15	0.00

Annual herbs (Opslag)	AnHerb	**2.65**	**2.89**	0.42	52.85	49.03	0.43	19.95	16.96	1.02
Pelargonium sp 1.	PerNSShr	0.00	0.00	**5.00**	0.00	0.00	0.21	0.09	0.00	0.04
Pentzia incana	PerNSShr	0.97	**1.33**	**1.40**	3.24	6.47	9.57	3.33	4.88	6.85
Perennial Non Suc sp. 14	PerNSShr	0.00	0.00	**5.00**	0.00	0.00	0.21	0.00	0.00	0.04
Perennial Non Suc sp. 19	PerNSShr	0.00	0.00	**5.00**	0.00	0.00	0.21	0.00	0.00	0.04
Perennial Non Suc sp. 22	PerNSShr	0.00	0.00	**1.88**	0.00	0.00	0.64	0.00	0.00	0.34
Perennial Non Suc sp. 25	PerNSShr	0.00	**4.21**	0.00	0.00	0.32	0.00	0.00	0.08	0.00
Perennial Non Suc sp. 26	PerNSShr	**3.37**	0.00	0.00	0.05	0.00	0.00	0.02	0.00	0.00
Perennial Non Suc sp. 27	PerNSShr	**3.37**	0.00	0.00	0.05	0.00	0.00	0.02	0.00	0.00
Perennial Non Suc sp. 32	PerNSShr	**3.37**	0.00	0.00	0.05	0.00	0.00	0.02	0.00	0.00
Perennial Non Suc sp. 7	PerNSShr	**1.12**	**1.05**	0.00	0.05	0.16	0.00	0.05	0.15	0.00
Pteronia glomerata	PerNSShr	**1.20**	**1.32**	**1.62**	6.63	12.14	15.96	5.53	9.19	9.87
Pteronia incana	PerNSShr	0.62	0.90	0.41	0.78	2.43	1.91	1.25	2.69	4.68
Roepera cordifolia	PerLSShr	0.42	0.47	**1.88**	0.21	0.32	0.64	0.50	0.69	0.34
Roepera sp 1.	PerLSShr	**1.20**	0.60	**5.00**	0.78	0.16	1.06	0.65	0.27	0.21
Ruschia robusta	PerLSShr	0.00	0.00	**1.76**	0.00	0.00	1.28	0.00	0.00	0.72
Ruschia sp 1.	PerLSShr	0.59	0.57	**1.01**	10.08	7.93	16.81	17.02	13.84	16.64
Searsia incisa	PerNSShr	0.00	**2.90**	**2.62**	0.00	3.24	11.91	0.00	1.11	4.55
Searsia undulata	PerNSShr	0.59	0.00	**3.15**	0.57	0.00	3.62	0.98	0.12	1.15
Solanum giftbergense	PerNSShr	**2.41**	0.00	0.00	0.26	0.00	0.00	0.11	0.00	0.00
Tetragonia fruticosa	PerNSShr	0.00	0.00	**2.50**	0.00	0.00	0.21	0.05	0.00	0.09
Thesium lineatum	PerNSShr	0.00	0.00	3.00	0.00	0.00	0.64	0.09	0.15	0.21
Tripteris sinuata	PerNSShr	**1.12**	0.00	0.00	0.10	0.00	0.00	0.09	0.00	0.00
Tylecodon wallichii	PerLSShr	0.12	0.12	0.00	0.10	0.16	0.00	0.85	1.35	3.15
Wiborgia monoptera	PerNSShr	**1.58**	0.60	0.00	0.78	0.16	0.00	0.50	0.27	0.00

Bolded numbers: Preferred plant species

Appendix 3

Supplementary Table ST2. Diet selection and forage preferences of herded livestock during the wet season for the Nama- Karoo biome. E_i = Ivlev's forage ratio included in the study

		E_i			Diet (%)			Cover (%)		
Species	**Plant functional type**	**Cross-bred**	**Swakara**	**Goat**	**Cross-bred**	**Swakara**	**Goat**	**Cross-bred**	**Swakara**	**Goat**
Aasbos	PerLSShr	0.00	0.00	0.00	0.00	0.00	0.00	0.85	0.00	1.02
Almost dead spikey	PerNSShr	0.00	0.00	**1.02**	0.00	0.00	4.96	0.00	0.00	4.88
Aloe sp. 1	PerLSShr	0.00	0.00	0.00	0.00	0.00	0.00	0.31	0.00	0.04
Boscia albitrunca	PerNSShr	0.00	0.00	**2.50**	0.00	0.00	2.12	0.00	0.35	0.85
Cheiridopsis sp.	PerLSShr	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00
Euphorbia gariepina	PerSSShr	0.00	0.00	**1.16**	0.00	0.00	1.13	0.17	0.03	0.98
Perennial Non Suc sp. 2	PerNSShr	0.00	0.00	**1.98**	0.00	0.00	2.69	0.00	0.00	1.36
Mesembryanthemum pseudoschichtianum	PerLSShr	0.00	0.00	0.00	0.00	0.00	0.00	5.80	1.22	1.95
Annual herbs (Opslag)	AnHerb	0.00	0.00	**1.67**	0.00	0.00	0.14	0.00	0.00	0.08
Roepera leptopetala	PerLSShr	0.00	0.00	**1.05**	0.00	0.00	1.70	0.00	0.13	1.61
Perennial Non Suc sp. 3	PerNSShr	0.00	0.00	**2.65**	0.00	0.00	4.96	0.31	0.55	1.87
Annual sp. 2	AnHerb	0.00	0.00	**1.04**	0.00	0.00	0.71	0.00	0.00	0.68
Annual sp. 3	AnHerb	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08
Galenia fruticosa	PerLSShr	0.17	**1.12**	0.44	0.10	2.01	0.57	0.61	1.80	1.27
Monechma sp 2.	PerNSShr	0.25	0.47	**1.00**	0.10	0.27	0.42	0.41	0.58	0.42
Portulacaria fruticulosa	PerLSShr	0.76	0.00	**1.11**	0.21	0.00	0.71	0.27	0.45	0.64
Prosopis mesquite	PerNSShr	**3.02**	0.95	0.00	0.31	0.09	0.00	0.10	0.10	0.00
Roepera sp. 2	PerLSShr	**1.05**	0.00	0.98	0.93	0.00	0.71	0.89	0.48	0.72
Tribulus terrestris	AnHerb	**1.36**	0.00	0.00	1.44	0.00	0.00	1.06	0.55	0.08
Sisyndite spartea	PerSSShr	0.69	0.47	**1.19**	2.47	0.18	2.12	3.58	0.38	1.78
Stipagrostis obtusa	PerGras	0.71	**1.22**	0.89	11.02	64.96	17.42	15.55	53.03	19.57
Stipagrostis ciliata	PerGras	**1.15**	0.73	0.79	19.77	0.91	2.55	17.15	1.25	3.23
Schmidtia kalahariensis	AnGras	**2.52**	**2.30**	**2.21**	31.00	13.05	19.83	12.31	5.68	8.96
Perennial grass sp. 1	PerGras	0.87	0.66	**1.02**	31.62	18.07	33.14	36.17	27.49	32.34

Bolded numbers: Preferred plant species