RANGELAND UTILIZATION BY CATTLE IN THE LOWER KUISEB RIVER AREA,
NAMIB DESERT, NAMIBIA

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# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>LIST OF TABLES</td>
<td>4</td>
</tr>
<tr>
<td>ACKNOWLEDGEMENTS</td>
<td>6</td>
</tr>
<tr>
<td>DECLARATION</td>
<td>7</td>
</tr>
<tr>
<td>ABSTRACT</td>
<td>8</td>
</tr>
<tr>
<td>CHAPTER 1</td>
<td>9</td>
</tr>
<tr>
<td><strong>INTRODUCTION</strong></td>
<td></td>
</tr>
<tr>
<td>1.1. Background of the study</td>
<td>9</td>
</tr>
<tr>
<td>1.2. Statement of the problem</td>
<td>11</td>
</tr>
<tr>
<td>1.3. Objectives of the study</td>
<td>11</td>
</tr>
<tr>
<td>1.3.1. The general objective</td>
<td>11</td>
</tr>
<tr>
<td>1.3.2. Specific objectives</td>
<td>11</td>
</tr>
<tr>
<td>1.4. Hypotheses</td>
<td>12</td>
</tr>
<tr>
<td>1.5. Significance of the study</td>
<td>12</td>
</tr>
<tr>
<td>3.3. Population and Sample size</td>
<td>29</td>
</tr>
<tr>
<td>3.4. Research instruments</td>
<td>30</td>
</tr>
<tr>
<td>3.4.1. Africa Wildlife tracking (AWT) GPS collars</td>
<td>30</td>
</tr>
<tr>
<td>3.4.2. Suzuki Gypsy 1.3i 4x4 Bakkie 2014</td>
<td>31</td>
</tr>
<tr>
<td>3.4.3. Yagi Antennae</td>
<td>31</td>
</tr>
<tr>
<td>3.4.4. African Wildlife Tracking, Version 05.03 Ultra high frequency (UHF) Transceiver</td>
<td>31</td>
</tr>
<tr>
<td>3.4.5. The ASUS field laptop</td>
<td>32</td>
</tr>
<tr>
<td>3.4.6. Ultra–Optec fully coated 8x21 binoculars</td>
<td>32</td>
</tr>
<tr>
<td>3.5. Research Procedure</td>
<td>32</td>
</tr>
<tr>
<td>3.5.1. Tracking habitat selection by cattle in the lower Kuiseb River</td>
<td>32</td>
</tr>
<tr>
<td>3.5.2. Determining cattle foraging behaviour in relation to air temperature</td>
<td>33</td>
</tr>
<tr>
<td>3.6. Data analysis</td>
<td>35</td>
</tr>
<tr>
<td>3.6.1. Habitat selection by cattle in the lower Kuiseb River area</td>
<td>35</td>
</tr>
<tr>
<td>3.6.2. Cattle foraging behaviour in relation to air temperature</td>
<td>36</td>
</tr>
<tr>
<td><strong>CHAPTER 4</strong></td>
<td>37</td>
</tr>
<tr>
<td><strong>RESULTS</strong></td>
<td>37</td>
</tr>
</tbody>
</table>
LIST OF TABLES

Table 1: Data acquisition performance of each African Wildlife Tracking UHF–GPS enabled collar from 09 April–30 June 2018.

Figure 1: The study area along the lower Kuiseb River around Gobabeb Research and Training Centre in the Namib Desert, Namibia..........................................................27

Figure 2: Settlements in the lower Kuiseb River area, where the research study was conducted. ........28

Figure 3: The nine cows that were initially fitted with GPS collars .....................................................30

Figure 4: Field Materials used during the study ..............................................................................35

Figure 5: Overall frequency of time spent by cattle in each habitat in lower Kuiseb River area settlements before and after rainfall (P < 0.05)............................................................................................................38

Figure 6: Movement of cattle (collar tags 2478 and 2479) at Homeb in the lower Kuiseb before (09 April–24 May, in Red) and after rainfall (25 May–30 June, in Blue) ..............................................39

Figure 7: Cattle movement (collar tags 2481 and 2482) at Natap in the lower Kuiseb before (09 April–24 May, in Red) and after rainfall (25 May–30 June, in Blue) ................................................39

Figure 8: Cattle movement (collar tags 2485 and 2486) at Klipneus in the lower Kuiseb before (09 April–24 May, in Red) and after rainfall (25 May–30 June, in Blue) .................................................................40

Figure 9: Frequency of time spent at each habitat within settlements in the lower Kuiseb River, between 09 April and 30 June 2018 (P < 0.05)..................................................................................................................41

Figure 10: Daily movement distance of cattle in the lower Kuiseb River before (09 April–24 May) and after rainfall (25 May–30 June) during 2018 (P > 0.05). .........................................................................................42

Figure 11: Proportion of time spent feeding by 6 cattle in the lower Kuiseb in relation to air temperature. .............................................................................................................................................43

Figure 12: Temperature difference (Collar temperature–weather station air temperature) as a function of habitat assemblages (P < 0.05)........................................................................................................44

Figure 13: Accessible Faidherbia albida pods in the Kuiseb River .......................................................45

Figure 14: Cattle in the inter–dunes before rainfall .............................................................................46

Figure 15: The inter–dune rangeland after rainfall (note the third cow from the left with a collar)........47

Figure 16: Cattle seeking shade in the Kuiseb River .........................................................................48
DEDICATION

I would like to dedicate this research study to my family and friends who encouraged me in pursuing my career.
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Lastly, I would like to thank my family and friends for supporting me throughout my career, and for always encouraging me to further my studies.
DECLARATION

I, Eric Shiningayamwe, hereby declare that this study is a true reflection of my own research, and that this work has not been submitted for a degree in any other institution of higher education.

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Eric Shiningayamwe

Date: 26/11/2019
ABSTRACT

There is a general lack of information on how cattle utilise the lower Kuiseb River rangelands, their feeding behaviour and how they deal with intense heat. This study aimed at understanding cattle habitat selection (considering that they are free ranging in the absence of a herder), and their foraging behaviour in relation to air temperature along the lower Kuiseb River area in the Walvis Bay Rural Constituency, Erongo Region. The study was carried out at three farmer settlements along the Kuiseb River area through remote sensing technology, where six selected cows were fitted with Global Position System (GPS)–enabled collars, two cattle per site from 09 April 2019 to 30 June 2019. The collars set to ten–minute sampling intervals to track their movement and understand how they select habitats. Soon after the collars were deployed, rare and unpredictable episodic rainfall in the study area allowed the rare opportunity to track cattle movement and behaviour before and after rain events in desert rangeland conditions. Cattle behaviour was interpreted by pairing observed behaviour with collar sensor data for the same animal over ten–minute intervals. Activities were categorised and scored for feeding, resting and walking, which were associated with ambient temperature to understand how cattle behaviour may relate to temperature. Data analysis was done using R, QGIS and SPSS, at 5 % level of confidence. The study revealed that there was a significant difference (P < 0.05) in habitat selection by cattle under dry and wet conditions. The distances over which livestock move to available forage did not significantly differ (P > 0.05) before and after rain, and temperature did not seem to be an important consideration as there was no significant relationship (P > 0.05) between ambient temperature, collar temperature and cattle foraging in the lower Kuiseb River area.

Keywords: Ambient temperature, Foraging behaviour, GPS collars, Habitat selection, lower Kuiseb River area.
CHAPTER 1

INTRODUCTION

1.1. Background of the study

Rangelands provide vital environmental functions and ecosystem services such as forage, shade and protection for livestock worldwide (Scherr et al., 2012). Arid and semi-arid rangelands provide grazing and browsing grounds to livestock in majority of extensive pastoralists (Adler et al., 2004). However, such continuous land support capabilities come with great responsibility in preventing resource depletion which may result in severe land degradation, affecting the production of forage (Lehmann, 2010).

Understanding animal behaviour is not only a crucial aspect in livestock management, but also in sustainable use of range resources, especially the spatial and temporal patterns of habitat use (Senft et al., 1987). Habitat selection and utilization by livestock is influenced by many factors, of which foraging availability and the influence of ambient temperature are most crucial, and must be understood for decent rangeland management (Van Beest et al., 2010). Ambient temperature plays a significant role in influencing livestock movement and behaviour. Animals must regulate their body temperature to be compatible with ambient temperature, while maintaining a constant nutrient intake. Cattle in many regions are affected physiologically and behaviourally to climate change, and this may be worse in hyper-arid environments (Osuji, 1974).

Due to these factors, cattle management practices in dryland areas should be documented and analysed as a basis for adaptation strategies that may best suit the new climatic paradigms expected in the future, without triggering rangeland degradation (Todd & Hoffman, 1999). An introduction
of precision agriculture has emerged, a farming management concept based on observing, measuring and responding to inter– and intra–field variability in animal production using radio–transceivers and position data from the Global Positioning System (GPS) (Zarco–Tejada, Hubbard & Loudjani, 2014). With advances in tracking and GPS technology, bio–loggers are able to observe animal behaviour on a much larger scale than was previously feasible. Information can now be directly, easily and immediately acquired and managed by farmers and researchers (Dimitri & Longland, 2018; Zarco–Tejada et al., 2014). This modern approach challenges traditional methods of investigating livestock behaviour, as they are usually labour–intensive; cause observer fatigue; may alter cattle movement due to observer presence; and are affected by visibility factors when observing at night and in adverse weather conditions (Agouridis et al., 2004).

The Kuiseb River rangeland within the Namib Naukluft National park hosts the Topnaar Nama (≠Aoni), a Khoekhoen group. Since the 14th Century, the Topnaar have been making a living through small stock rearing and the harvesting of !nara (Acanthosicyos horridus) melons (Henschel et al., 2004; Van den Eynden et al., 1992). Cattle are an essential source of food for the Topnaar in the lower Kuiseb area and a contributor to the Namibian economy at large (Lamprey et al. 1974; Miller & Coe, 1993). Because of the limited and sporadic rainfall, forage grass is scarce in the desert, Namib cattle are believed to rely almost entirely on pods from leguminous trees, Faidherbia albida and Vachellia erioloba (Acacia erioloba), as both the pods and the seeds they contain are very nutritious (Eckardt et al., 2013; Moser–Nørgaard & Denich, 2011).

However, little is known about how cattle utilise the lower Kuiseb rangeland, their feeding behaviour, and how they deal with intense heat, even though the Topnaar communities have reared cattle in that area for centuries (Lamprey et al. 1974). This gap in knowledge affects cattle management practices and analysis as a basis for adaptation strategies, hence this study was aimed
at providing information using GPS collars to understand cattle habitat selection and their foraging behaviour in relation to ambient temperature along the Lower Kuiseb River.

1.2. Statement of the problem

The Topnaar home area is classified as hyper–arid, characterised by sporadic events of average precipitation that range between 5–18 mm (Eckardt et al., 2013) and average temperatures that range between 11.2 ºC – 29.7 ºC. Little is known about how cattle survive in the desert with such climatic conditions, the lack of information on free ranging cattle behaviour as to how they utilize the rangeland, how ambient temperature affects animal foraging behaviour make it difficult to understand and manage both the livestock and the range on which they depend. The fact that cattle in the lower Kuiseb River area are free ranging also makes them highly vulnerable to theft and predation.

1.3. Objectives of the study

1.3.1. The general objective

The general objective of this study is to determine the utilisation (movement and feeding pattern) of rangeland habitats along the lower Kuiseb River area by cattle.

1.3.2. Specific objectives

1) To determine habitat selection and foraging grounds preferred by cattle in the lower Kuiseb River area during drier and wetter conditions.

2) To determine cattle behaviour in relation to ambient air temperature in the lower Kuiseb River area in order to determine how temperature affects foraging behaviour.
1.4. Hypotheses

1. Habitat selection by cattle in the lower Kuiseb River area changes in dry and wet conditions

2. Ambient temperature has a significant effect on foraging behaviour by cattle in the lower Kuiseb River area.

1.5. Significance of the study

Livestock management practice in the lower Kuiseb, particularly cattle is to range freely without herding. Cattle may respond freely to environmental and ecosystem level influences as they range across the landscape. Topnaar farmers expressed interest in understanding the factors that drive livestock movement and foraging patterns, in order to better manage their herds.

According to Moser–Nørgaard & Denich (2011), livestock in the lower Kuiseb River area feed on the *V. erioloba* and *F. albida* pods throughout the year (these plant species alternate in flowering and pod production) to supplement or completely comprise their diet, despite cattle being natural grazers. Livestock are therefore not solely reliant on ephemeral grasses that may occur on the gravel and inter-dune plains of the Namib Desert after sporadic rainfalls, they have become tolerant to the environment challenges, by taking advantage of the vegetation in the river.

Since their feeding behaviour has adapted to the resources of the lower Kuiseb River area, it is possible that cattle may have adjusted other behaviour or movement to utilise different resource availabilities in habitats associated with three very distinct ecosystems – the riverine woodland along the ephemeral Kuiseb River; the gravel plains to the north of the River; and the inter–dune plains of the Namib Sand Sea to the south. Each of these ecosystems may offer different services
throughout the year, and cause livestock to utilise them to different degrees, thus the area offered the opportunity to study the movement patterns and habitat selection of desert inhabiting cattle.

This study used telemetry to understand livestock habitat selection and foraging behaviour, it is a new concept in the lower Kuiseb River area and Namibia as a whole. This study used GPS collars to understand the free ranging cattle behaviour in the lower Kuiseb River area. Tracking these cattle using the GPS technology will provide reliable information to the Topnaar farmers and researchers, information such as movement patterns, foraging sites, preferred habitats, foraging behaviour and cattle response to the ever–fluctuating climate of the Namib desert. Tracking these cattle will also indirectly provide information that will assist the Topnaar farmers in avoiding theft and understanding the rangeland better.

The introduction of GPS technology in Namibia, as successful as it is in the lower Kuiseb River area can be used in other areas to understand the movement, habitat selection and influence of temperature on animals elsewhere in Namibia.

1.6. Limitation of the study

Despite the fact that a large amount of data were gathered during this study by using GPS collars and can be used to understand diverse phenomenon about cattle behaviour and perhaps function, this study is only limited to understand habitat selection, activity and the effect of air temperature to cattle in the Namib Desert (lower Kuiseb River area). This study cannot explain other important aspects such as how much forage is available for cattle and their preference; the annual amount of forage and water intake by cattle; the duration of grass growth and mortality; differences or similarities in behaviour between types of cattle breeds; daily mass gain and growth of the cattle that were studied; or individual behaviour and instinct of all cattle in the lower Kuiseb River area.
This study cannot be used to infer cattle behaviour and their response to air temperature in other parts of the country either, as ecosystems are complex and climatic conditions in different areas may result in different behavioural responses and rangeland utilisation patterns, however the technology of using GPS collars can be applied anywhere.
CHAPTER 2

LITERATURE REVIEW

2.1. Habitat selection by livestock

Habitat selection is a hierarchical process involving a series of innate and learned behavioural decisions made by an animal about what habitat it would use at different scales of the environment (Hutto, 1985). Rosenzweig (1981) proposed that habitat selection was generated by foraging decisions such as forage quality and quantity, but that foraging is only one behaviour driving habitat selection as specific habitats may be selected for availability of cover and resting or denning sites, but that each of these may vary seasonally. Hilden (1965) categorized the differences between proximate and ultimate factors, where reproductive success and survival of the species are the ultimate reasons that influence a species to select a specific habitat. Proximate factors are cues used by an individual animal to determine the suitability of a site, including the specific vegetation composition within a desired habitat. The ability for habitat choices to persist is governed by ultimate factors such as forage availability, shelter, and avoiding predators (Litvaitis, 2000).

Models of population dynamics often assume that individuals have perfect knowledge about habitat qualities and accordingly that animals settle in the best habitats available. Many studies of dispersal have focused on the movements of individuals away from a site, but knowledge on settlement decisions is still scarce. Although energy gain in ungulates can theoretically be maximised at relatively low biomass densities of food, time and digestibility constraints may cause herbivores to seek patches of greater biomass density (Bergman et al., 2001). Certain species may therefore choose to forage high quality vegetation and others may find that energy is best
maximised with large quantities of lower quantity food. The forage maturation hypothesis predicts that herbivores will seek out resources of intermediate age in order to avoid patches of low biomass or those that are fully mature and thus of low quality (Hebblewhite et al., 2009).

In regions where vegetation biomass may be minimal and dispersed, livestock may be forced to walk greater distances to find patches that support their food intake requirements. According to Leichenko & O'Brien (2002), in drought years forage and water become limiting for livestock, hence their populations decline either through the effects of reduced reproduction, starvation–induced mortality or migrations. Drought years also cause drastic changes in vegetation cover due to severe lack of available moisture, resulting in massive loss of livestock (Leichenko & O'Brien, 2002). With the Namib Desert being an extremely dry area, with sporadic events of rainfall and without grazing reserves, it is quite challenging for pastoralists to farm and survive under environmental conditions that resemble permanent drought (Kyuma et al., 2016).

However, cattle tend to graze or browse various types of forage according to the rangeland where they are kept. Ortega, Castillo & Ravita (1999) found that cattle in deciduous forests browse on shrub and tree pods during and after rainfall, and browse on leaf litter before rainfall. A study by Ego, Mbuvi & Kibet (2003) showed that cattle can entirely browse during dry periods before rainfall, provided the forage has the nutrients required by the animals.

Smith et al. (1992), who did a study on habitat selection and distribution patterns of grazing cattle along an ephemeral channel, suggested that the reasons for habitat selection and differential utilization of forage within habitats provide a basis for grazing management and range improvement planning. Emphasis on grazing influences on vegetation and channels in riparian zones, water quality, and dispersed pollution have intensified the need to understand these
processes (Kauffman & Krueger, 1984). Some studies saw that cattle prefer perennial stream riparian zones over upland range sites, and that forage quality and abundance and water availability are important factors leading to selection of riparian habitats (Pinchak et al. 1991; Roath & Krueger, 1982; Ames, 1978).

2.2. Cattle responses to intense air temperature

Like most mammals, cattle function best in specific temperature ranges, which depends on the type or breed of cattle. Below or beyond those ranges results in physiological stress. Heat stress is one of the most critical challenges for cattle in dryland areas. Heat stress occurs when an animal has troubles in getting rid of its surplus body heat and maintaining a constant body temperature. It is believed to be caused by two sets of factors: 1) an animal’s metabolism and physical activity that generate heat load, and 2) specific environmental factors such as air temperature, relative humidity, wind speed and solar radiation that affect the dissipation of heat (Mader et al., 2006). Heat stress adversely affects dairy producers both economically, traditionally and ethically by reducing milk production, beef production, fertility rates and by impairing animal welfare (de Andrade Ferrazza et al., 2017; St–Pierre et al., 2003).

Normal body temperature is maintained by matching heat production with heat losses to the environment. When the amount of heat produced by cattle exceeds the amount released to the environment the body temperature of the cattle rises. The cattle respond physiologically by reducing activities that produce heat such as feed intake, milk yield and exercise; and increasing those that shed heat such as sweating, increased respiration and salivation (Vermunt & Tranter, 2011). Some responses of cattle to heat stress, such as increased respiratory rate and panting, may actually increase heat production in their bodies. Thus, with increasing heat loads the cow
experiences more distress, eventually with life threatening consequences. Cattle calving during daylight hours in hot climates, with direct exposure to solar radiation, are particularly vulnerable to heat stress and hyperthermia, especially those suffering from hypocalcaemia in which the control of body temperature by natural mechanisms is greatly reduced (Vermunt & Tranter, 2011). Dalcin et al. (2016) showed that dairy cattle in Brazil tend to experience moderate heat stress at which point they struggle to regulate their body temperatures above 28 degrees Celsius (28º C), and extreme heat stress above 30º C.

Despite wide fluctuations in environmental temperature, cattle are normally capable of maintaining a relatively constant body temperature that is between 38.4 and 39.0ºC, which is essential to preserve a huge number of biochemical reactions and physiological processes that takes place with normal metabolism (West, 2003). As environmental temperatures increase, certain thermoregulatory responses that are designed to stabilise body temperature are initiated. These responses include reduced feed intake; decreased activity and increased drinking, shade or wind seeking; and increased peripheral blood flow, sweating and panting (Vermunt & Tranter, 2011). However, these thermoregulatory activities may not be sufficient to maintain a normal body temperature during periods when ambient air temperature and humidity are particularly high.

The primary sources of environmental heat gain are solar radiation and high ambient air temperature (Vermunt & Tranter, 2011), while wind can lower heat stress by circulating air around the animal and carrying away excess heat. Air temperature, being one of the causes of heat stress, affects foraging behaviour as extra heat accumulates in the body that will lead to physiological responses, such as an increase in respiration rate, sweating and changes in the daily routine activities of animals (Vermunt & Tranter, 2011). The effect of heat stress on cattle has been intensively studied due to the increasing concerns about climate change and animal wellbeing,
with more and more researchers and farmers being interested in heat stress abatement approaches because of its importance to improving cattle husbandry (Wang et al., 2018).

It has been suggested that cattle limit their activity during the hottest part of the day when the ambient temperature is close to their body temperature. According to Perano et al., (2014), an animal that is stressed will seek shade, increase water intake, change their orientation in the sun, and change their feeding patterns to maintain a constant level of food and nutrients. Their behavioural responses depend on how much energy they have to put into foraging or regulating body temperature (Prescott et al., 1994). For example, during the hot temperatures, a cow will seek shade and expend a great deal of energy and water trying to cool itself down, so it will need to consume enough food and water. In order to accommodate this bodily response, the cow may spend the hottest time of day in areas that have access to food, water, and shade then forage more intensively when the temperature drops.

Some results suggest that Bos taurus cattle experience significant physiological changes during exposure to prolonged and continuous high heat and humidity, with alterations persisting for some days after the heat–stress conditions subside, while Bos indicus experience similar but less pronounced physiological changes (Beatty et al., 2006). Colour is also important, as black cattle absorb twice as much heat from the sun compared to white cattle. Size also matters since the release of heat from any object into the environment is proportional to its exposed surface area, with the ratio of surface area to body mass decreasing as overall size increases (McManus et al., 2014). Therefore, large cattle such as adult cows are at a disadvantage of losing excess body heat compared to smaller cattle or calves. Large cattle are also at greater risk of becoming overheated (Vermunt & Tranter, 2011). These considerations often relate to the type and breed of cattle, but are complicated by the fact that the flow of heat away from the animal's body is restricted by high
ambient air temperature, which narrows the thermal gradient between the cow's body and the surrounding air, that is affected by habitat selection and behaviour of cattle.

According to Vermunt & Tranter 2011), Avenues for the dissipation of heat in cattle include non–evaporative and evaporative cooling mechanisms. They also stated that below 10°C, most heat loss from the body occurs by non–evaporative cooling such as conduction, convection and radiation. However, when the temperatures exceed 21°C, evaporative cooling such as evaporation of water from the skin and respiratory tract becomes the predominant mechanism of heat loss in cattle. The evaporation of water from a cattle’s skin is a very effective cooling mechanism, which is enhanced by conditions that promote air movement (e.g. wind), thereby moving water vapour away from the skin. The primary obstacle to evaporative cooling is high relative humidity, which in some environments may be exacerbated by limited air movement. Bos indicus cattle have larger and a greater number of sweat glands than B. taurus cattle; however, actual sweating rates are only slightly higher in the former (Vermunt & Tranter, 2011).

The Namib Desert is drier than the area of these other studies, and food resources are both scarcer and less nutritious, suggesting that Topnaar livestock might experience more thermal stress. It is known that, as temperature rises, livestock are less able to regulate their body temperatures (Thompson et al., 2011) and they lose more water through sweating and panting in order to regulate internal temperatures. Blood pressure also decreases due to vasodilation (the dilation of blood vessels due to thermal expansion). Together, these effects mean that food intake and digestion are less efficient at high temperatures (Thompson et al., 2011). These temperature constraints may be applicable to Topnaar cattle, but additional parameters such as humidity, wind, diet, and water availability must all be considered along with ambient temperature. As the Topnaar cattle are
mostly mixed crossbreeds born and raised within the Namib, it can be expected that their behaviour and foraging may reveal if they have adapted to cope with heat stress in the Namib Desert.

2.3. Method of studying animal movement and foraging behaviour

Many researchers have successfully used global positioning systems (GPS) and telemetry in general to monitor wildlife and livestock mobility, activity and behaviour (Moen et al., 1996; Rutter et al., 1997; Turner et al., 2000; Schlecht et al., 2004; Agouridis et al., 2005; Ungar et al., 2005). The application of GPS tracking has resulted in much improved accuracy and reliability, as opposed to traditional methods, like those employed by Namibian herders, who use direct observation method in determining behaviour of livestock and being only applicable during daylight period (Barroso et al., 2000). Direct observation has proven to require considerable labour and the presence of an observer can modify animal behaviour at any stage (Papachristou et al., 2005; El Aich et al., 2007). GPS collars offer new capabilities for objective measurements to study how spatial and temporal distribution of livestock arise due to factors such as grazing system, landscape, aspect location, forage type, hide colour, health status, and ambient conditions. Within livestock production, GPS loggers have been utilised to monitor the grazing, browsing, lying and standing behaviour (Rutter et al., 1997), to track beef cattle in intensively managed grazing systems (Udal, 1998; Turner et al., 2000) and to study movement distances of livestock (Ungar et al., 2005). Behavioural actions of cattle such as resting, grazing, and walking were correctly inferred when investigators incorporated tip switch data with the distance between successive GPS locations (Ungar et al., 2005). GPS–enabled collars were also more precise than the Very High Frequency (VHF) variable pulse sensor collars when distinguishing between periods of inactivity and activity in white–tailed deer (Coulombe et al., 2006). To best understand cattle behaviour, it
is recommended to observe females, due to the fact that they are more influential and play a bigger role in a herd (Bouissou et al., 2001; Shahhosseini, 2013).

Telemetry does however have challenges, despite the progress brought by satellite telemetry techniques. The data is restricted to those parameters being measured at the time of transmission. Earlier GPS tracking devices and techniques have been criticised due to the potential for considerable bias from signal modulation (Lindzey & Meslow, 1977; Singer et al., 1981) and signal interference caused by the environment between the animal and the antenna (Galster et al., 2001). Kooyman & Kooyman (1995) found that signals get lost when the animal with the sender attached is below cover. Some investigators used the distance between consecutive GPS points per unit time to measure velocity and to infer activity (Nelson & Sargeant 2008; White et al. 2010). However, cloud cover, vegetative cover, topography, and the orientation of the collar can reduce GPS fix rates by 50% (Hulbert & French, 2001; Di Orio et al., 2003, D'Eon & Delparte, 2005; Jiang et al., 2008; Mattisson et al., 2010). This substantially affects location accuracy and results in underestimating movement in active animals and overestimating that of stationary animals (Ganskopp & Johnson, 2007). Likewise, because animals seldom move in straight lines for significant periods of time, distances between GPS locations are likely to be underestimated unless fixes are recorded frequently. High fix rates however tend to decrease the lifespan of collar batteries, so collar users must balance location frequency with the duration and purpose of their study (Matthews et al., 2013). Location–dependent errors can contribute to inaccuracies when calculating energy budgets or estimating habitat utilisation (Gaylord, 2013).

The orientation of GPS collars when a tip switch is incorporated to determine animal activity or action, can be challenging to interpret. Actions are defined by the roll, pitch and yaw rotations from an initial collar position. The roll, pitch and yaw rotation matrices transform a vector (such
as the earth's gravitational field vector) under a rotation of the coordinate system by angles $\phi$ about the $x$, $y$ and $z$ axes, respectively. This interpretation requires an understanding of trigonometry and algebra (Pedley, 2013).
CHAPTER 3

RESEARCH METHODS

3.1. Description of the study area

3.1.1. Location, extent & land–use

The study took place at the lower Kuiseb River area (15.0415° East, 23.5618° South), which is found in the Namib Desert and part of Namib Naukluft National Park. According to Kok (1996), the Kuiseb River has a length of 440km extending from the Khomas Hochland region, through the Namib and into the Atlantic Ocean. Despite the Kuiseb River area being in the National park, there are currently 14 settlements located along the lower Kuiseb River area, beginning from Homeb settlement down south to Rooibank up north, housing approximately 350–380 “Topnaar people” (who are part of an indigenous tribe belonging to the Nama (Werner, 2003). The number of Topnaar living in the Kuiseb valley has fluctuated over the years, but records suggest that it has never been a very large number, there were difficulties conducting surveys due to migration and because some community members are not permanent residents. The Topnaars are believed to have been living along the Kuiseb for more than 300 years, surviving on the vegetation of the river for livestock farming (especially small stock) and the !Nara plant for subsistence and earning little income (Budack, 1977).

3.1.2. Geology, Soils and Physical features

The lower Kuiseb River area is characterised by three ecosystems: Gravel plains; Kuiseb River riverine woodland; and the Namib Sand Sea.
The gravel plain habitat is characterized by wide expanses of plains (consisting of granites, gneisses, schist’s and quartzite’s), intersected by a network of drainage areas and shallower drainage lines and several inselbergs, which rise 10 to about 200 m above the surrounding plains (Schachtschneider & February, 2010).

The Namib Sand Sea is dominated by large, north–south–trending, complex and linear dunes, the orientation of which is controlled by a bimodal wind regime with a south–westerly wind blowing inland from the South Atlantic Ocean and an easterly “berg” wind that sweeps down the escarpment from the interior (Lancaster, 1989; Seely, 1998 b). Within the Namib Sand Sea are wide, open inter–dune areas between the large linear dunes, where grass species dominate (Seely, 1998 b).

The Kuiseb River supports a dense riparian vegetation of tree species which are usually confined to the riverbed. The riverbed also consists of several granite bedrock compartments filled with sand and alluvium. Flood events, generated in the higher rainfall upper catchment move downstream as flash floods and wash away northward moving dunes while recharging the alluvial aquifers (Ward and von Brunn, 1985).

3.1.3. Climate

The Kuiseb River area is part of the hyper arid system, represented by sporadic rainfall and fluctuating temperature events of the Namib Desert. The lower Kuiseb River area has a sub–tropical climate, with very hot summers and mild winters, it is so unique that rainfall events can occur at different periods of the year, or rainfall events may not occur at all. Several studies have revealed that temperatures in the Kuiseb River area vary unexpectedly all year round, ranging
between 11.2ºC – 29.7ºC annually, and the mean annual rainfall being 18 mm (Eckardt et al., 2013).

Fog from the upwelling of cold water from the Benguela current plays a major role in the ecology of the Namib Desert, by providing as much as 250 days of fog each year (equivalent to 50 mm of water) to living organisms (Seely, 1978a).

### 3.1.4. Flora and Fauna

The Lower Kuiseb River area is comprised of high endemism and biodiversity of flora and fauna that surrounds the three ecosystems (gravel plain, sand dunes and Kuiseb riverine). The gravel plain ecosystem is comprised of scattered *Vachellia erioloba*, *Zygophyllum simplex* and abundant *Stipagrostis* species on the landscape after rainfall events.

The Kuiseb Riverine ecosystem supports a dense riparian vegetation, dominated by tree species such as *Vachellia erioloba*, *Faidherbia albida*, *Euclea pseudebenus* and *Salvadora persica*.

Within the Namib Sand Sea are wide, open inter–dune areas between the large linear dunes, where grass species such as *Stipagrostis species*, *Centropodia glauca* dominate, with *Trianthema hereroensis* and *Acanthosicyos horridus* also on the slopes of the linear dunes (Seely, 1978a).

The Kuiseb river area is also known for its high endemism and diverse fauna. The Namib sand sea is classified as a heritage site under the international union for conservation of nature (IUCN). These ecosystems harbour animals such as diverse Tebreionadae Beetles, side winder Adder, Barking ghecko, White lady spider, Golden mole, Ostrich, Springbock to larger game such as Oryx. The Toopnar people have livestock, having chickens, goats, sheep, donkey and cattle living in the Kuiseb River area (Seely, 1978b).
Figure 1: The study area along the lower Kuiseb River around Gobabeb Research and Training Centre in the Namib Desert, Namibia.
Figure 2: Settlements in the lower Kuiseb River area, where the research study was conducted. The study was carried out in the lower zone of the Kuiseb River, at three Topnaar settlements, namely Homeb, Natab and Klipneus. Small family groups of Topnaar farmers reside at these settlements and most rear livestock (Werner, 2003). Gobabeb Research and Training Centre is a research hub, and hosted this study.

3.2. Research design

This study was a descriptive and quantitative design, as it focused on consecutively gathering numerical data through direct field observation and from GPS enabled collars which were tabulated and transformed into statistical meaning. The data were also used to produce visual aids such as graphs and charts to illustrate results.
3.3. Population and Sample size

The 12 settlements in the lower Kuiseb River area is comprised of 378 cattle, of which 15 are at Homeb, 13 at Natab and 3 Klipneus (the study sites). The study began by collaring a total of nine free-ranging cattle with active GPS collars, three at each of the participating settlements of Homeb, Natab and Klipneus. Only nine cattle were collared, this is due to the costs involved to carry out this study. The nine cattle used in the study were also selected according to the farmer’s willingness, preference and availability.

Cattle in the Kuiseb River area are genetically diverse, of both *Bos indicus* and *Bos taurus* mixed breeds. Most Topnaar cattle cannot be clearly assigned to a specific breed and seems to interbreed freely with no control over which bull breeds with which cows. All selected cattle were female due to the fact that they are more influential and play a bigger role in a herd (Bouissou, 2001; Shahhosseini, 2013). For instance, wild herds are usually based according to a gynocratic model consisting of mothers and young together, and adult males only joining the herd during the reproductive period, so to understand a herd at large it is ideal to target females and calves at nurturing age (Vieira *et al.*, 2012). Only six GPS collars yielded consistent and reliable results over the time-frame for the research study, the other two collars had difficulty connecting with the UHF transceiver which downloads and deletes data on the collar, while one was removed by cattle owner during study period.

All six collared cows were free ranging adults, one had calf. Two cows are white–greyish, and four are brown.
3.4. Research instruments

3.4.1. Africa Wildlife tracking (AWT) GPS collars

Global positioning system (GPS) collars provide an animal tracking and telemetry solution with low power consumption. These collars have a positioning system that collects animal location at a user–specified sampling frequency, and were fitted with optional sensors to measure collar temperature and roll, pitch and yaw. Therefore, that data that were recorded consisted of longitude, latitude, elevation, dilution of precision, time, date, distance, activity, movement, and X, Y and Z values. Data are stored onto non–volatile memory in a secure format, optimising power consumption to extend logger life. The collars incorporated active radio frequency identification transceivers (RF ID) with unique numbers (tags), and have their own power source (typically a

Figure 3: The nine cows that were initially fitted with GPS collars
battery) and are capable of transmitting and receiving data. The GPS collar can store up to 2000 data sets before older data are overwritten with new readings.

3.4.2. Suzuki Gypsy 1.3i 4x4 Bakkie 2014

A Gobabeb 4x4 vehicle was used to visit the study sites, and to search for cattle in more remote areas such as the dunes, upstream in the Kuiseb River and on gravel plains. It is a light, small vehicle that can manoeuvre in dense bush as well as through sandy and rocky substrates.

3.4.3. Yagi Antennae

This instrument was used to detect signals from the GPS collars on the cows over a 200–meter range, making it easier to find the cows and for the transceiver to download the data. The Yagi antenna is directional, consisting of multiple parallel elements in a line and a single driven element connected to the transceiver with a coaxial cable.

3.4.4. African Wildlife Tracking, Version 05.03 Ultra high frequency (UHF) Transceiver

It is the device that allows for bi–directional communication with the GPS collar. It was used to find the cattle, and then manage and download data from the active GPS collar. The UHF transceiver also allows the user to configure, download and query the logger on the GPS collars, such as setting time intervals to log GPS locations, download recorded data for specific periods, determining the total number of log entries, and checking the operational status and the settings of a collar.
3.4.5. The ASUS field laptop

The field laptop had a Windows 10 Operating System and specialised, proprietary software from African Wildlife Tracking (the collar manufacturer) to extract encrypted data from the UHF transceiver using a serial cable. The proprietary software also enabled data transformation into comma separated values (CSV) and Microsoft Excel files, which can then be used in other geo-informatics systems (GIS) for interpretation and analysis. The bespoke African Wildlife Tracking program can also be used to map and compute activity of collared animals.

3.4.6. Ultra–Optec fully coated 8x21 binoculars

Binoculars were used to observe cattle activity, and also to search for them when they were far from their usual location. It consists of two telescopes mounted side-by-side and aligned to point in the same direction, with eight times magnification and an objective lens of 21 millimetres diameter.

3.5. Research Procedure

3.5.1. Tracking habitat selection by cattle in the lower Kuiseb River

Before data collecting started, the purpose of the study and that the GPS enabled collars would have negligible negative impacts on their cattle had to be explained to farmers to persuade them to take part and assist in the study. Nine cows which were selected by farmers (by their choice) were initially attached with GPS enabled collars; three cows per site, and were then tested at the beginning and after set up to ensure they were operating correctly. The GPS collars were attached on the cow slightly loose to prevent strangling or stressing it and set to acquire and record the cattle location at 10 minutes intervals, which was used to understand habitat selection of cattle before
and after rainfall. The study began on 09 April 2018 and ended on 30 June 2018. It unexpectedly rained soon after fitting the collars to the cows. Thus, the period 09 April 2018 to 24 May 2018 was categorised as pre–rainfall and 25 May 2018 to 30 June 2018 as post–rainfall.

Although initially nine collars were fitted on cattle, three of the collars failed (one at each site) to connect with the UHF transceiver during data extraction stage [failure to extract data from collars most of the time], therefore only six collars were used for this study.

Location data were stored on board the GPS enabled collar unit and downloaded in the middle and at the end of each month using the UHF transceiver with the Yagi antenna connected. The UHF transceiver together with the Yagi antenna was used to detect or pick up the signal from the collar at a distance of less than 200 meters from a collar, after which it could be used to wirelessly instruct, clear and download data from the collars on the free ranging cows. After data was downloaded from a specific collar, the data from the non–volatile memory on board the GPS collar was cleared to avoid depleting internal space and to avoid overwriting data. After acquiring the encrypted collar data by using the transceiver, it was transferred from the UHF transceiver to the field computer using the bespoke Africa Wildlife Tracking software.

3.5.2. Determining cattle foraging behaviour in relation to air temperature

Each GPS enabled collar included a built–in temperature sensor and an accelerometer sensor, which can be used to determine animal activity, measuring the specific intervals periods that were set for the collars. Calibration of the accelerometer sensor data, which is a tilt sensor recording roll, pitch and yaw angles about the x, y and z axes, consisted of making detailed behavioural observations of captive collared animals and then pairing observed behaviours with collar activity data for the same sampling interval as was done by Gaylord (2013). Collared cows were observed
on the 12th – 15th April 2018 from 09:00 am – 15:00 pm to calibrate and interpret accelerometer data. The actions that were observed were placed into categories and scored for feeding, resting and walking (after Solanki, 2000). The activities were defined as follows:

(1) Feeding – grazing or browsing while walking, or standing and drinking water;

(2) Walking – moving from one place to another without grazing or browsing;

(3) Resting – simply standing and sitting.

The observations revealed that positive “Y” or “pitch” values combined with a “N” movement (meaning not moving) means animal is facing (head) up and is likely to be resting. A negative “Y” or “pitch” value means animal is facing (head) down as when foraging or drinking water (Markham et al., 2008; Ko et al., 2007). Of all the activities, feeding was of most importance to answer the study objective.

Cattle experience heat from the environment through air temperature and solar radiation, especially when in open areas without shade. The ambient air temperature, solar radiation and probably the cow’s body heat contribute to the temperature measured by the collar sensor. Hence weather data were acquired from the weather stations at the Gobabeb Research & Training Center to compare the ambient air temperature to the collar temperature data as a good approximation on what the cattle were experiencing in the environment and how they may respond. Ambient air temperatures at a weather station is recorded within a shaded radiation shelter with louvres to allow air circulation, thus approximating the likely ambient temperature a cow will experience when resting, walking or feeding in the shade of the trees in the river.
Figure 4: Field Materials used during the study

a) Recording sheet  
b) The ASUS field laptop  
c) AWT GPS collars  
d) Yogi Antennae & Transceiver  
e) Binoculars  
f) Suzuki Gypsy 1.3i 4x4 Bakkie

3.6. Data analysis

3.6.1. Habitat selection by cattle in the lower Kuiseb River area

The spatial data downloaded from the GPS collars with the UHF transceiver and field computer was converted into a CSV or Microsoft Excel file and imported into Google Earth 7.3.2.5491. Maps were created to reveal cattle location and movement patterns for specific times from 09 April to 30 June 2018, which were then interpreted as habitats selected and used by cattle. Quantum geo–informatics system (QGIS) and R version 3.3.3 were used to create three shape files for the three ecosystems, to sum up the number of GPS points in the form of counts for each. This revealed
how frequently cattle occupied or was found in a specific habitat during the course of the study. A Chi–squared test in SPSS version 22.0.0.0 (version 22) was used to statistically test the first hypothesis (after a test for normality was done), which was to determine if cattle selected different habitats during dry conditions and after a rainfall event. The distance travelled by cattle before and after rainfall was analyzed using linear mixed models in R.

3.6.2. Cattle foraging behaviour in relation to air temperature

Data acquired through direct observation and data from the GPS collars were captured, stored and sorted in Microsoft Excel 2010 before analyzed using R version 3.3.3 and SPSS 22.0.0.0.

A linear regression test in SPSS was used to look at the relationship between the proportion of time feeding and maximum air temperature, comparing events of feeding at defined maximum temperatures determines how cattle in the lower Kuiseb area behave on extreme hot days. The Linear mixed effects model was used in R to model the temperature differential (collar temperature minus weather station ambient air temperature) as a function of habitat, with a random effect of an individual cow, to examine in which habitat was a cow exposed to more heat stress through air temperature or solar radiation.

These results were used to evaluate the influence of air temperature on the intensity of livestock activity, thus trying to quantify the effect of thermal stress on cattle behavior.
CHAPTER 4

RESULTS

4.1. Habitat selection by cattle in lower Kuiseb River area

The study examined data recorded over 82 days, consisting of 29 441 data entries from 09 April to 30 June 2018. For the dry, pre–rainfall period from 09 April–24 May 2018, a total of 2200 GPS locations were recorded on the gravel plains 4562 GPS locations were from inter–dune habitats and 8041 GPS locations were from Kuiseb Riverine woodland habitat. After the rain event, 1984 GPS locations were recorded from the gravel plain, 9279 GPS locations were from inter–dune areas, and 3375 GPS locations were in Riverine woodland.

Table 1:  Data acquisition performance of each African Wildlife Tracking UHF–GPS enabled collar from 09 April–30 June 2018.

<table>
<thead>
<tr>
<th>GPS collar ID</th>
<th>UHF Tag: 2478</th>
<th>UHF Tag: 2479</th>
<th>UHF Tag: 2481</th>
<th>UHF Tag: 2482</th>
<th>UHF Tag: 2485</th>
<th>UHF Tag: 2486</th>
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</thead>
<tbody>
<tr>
<td>Settlement</td>
<td>Homeb</td>
<td>Homeb</td>
<td>Natab</td>
<td>Natab</td>
<td>Klipneus</td>
<td>Klipneus</td>
</tr>
<tr>
<td>Total GPS readings</td>
<td>6855</td>
<td>7882</td>
<td>2848</td>
<td>5577</td>
<td>3359</td>
<td>2920</td>
</tr>
<tr>
<td>% of collar data acquisition</td>
<td>88.16</td>
<td>77.01</td>
<td>59.93</td>
<td>71.72</td>
<td>40.22</td>
<td>36.87</td>
</tr>
</tbody>
</table>

Collar 2485 (40.22) and 2486 (36.87) recorded the lowest reading during the data collection period and, being inactive some days.

**Figure 5:** Overall frequency of time spent by cattle in each habitat in lower Kuiseb River area settlements before and after rainfall ($P < 0.05$).
**Figure 6:** Movement of cattle (collar tags 2478 and 2479) at Homeb in the lower Kuiseb before (09 April–24 May, in Red) and after rainfall (25 May–30 June, in Blue).

**Figure 7:** Cattle movement (collar tags 2481 and 2482) at Natab in the lower Kuiseb before (09 April–24 May, in Red) and after rainfall (25 May–30 June, in Blue).
**Figure 8:** Cattle movement (collar tags 2485 and 2486) at Klipneus in the lower Kuiseb before (09 April–24 May, in Red) and after rainfall (25 May–30 June, in Blue).
Figure 9: Frequency of time spent at each habitat within settlements in the lower Kuiseb River, between 09 April and 30 June 2018 (P < 0.05).
**Figure 10:** Daily movement distance of cattle in the lower Kuiseb River before (09 April–24 May) and after rainfall (25 May–30 June) during 2018 ($P > 0.05$).

### 4.2. Cattle foraging behaviour in relation to air temperature

Using the Linear mixed effects model in R, it revealed that there was no significant relationship ($P \leq 0.05$) between air temperatures and foraging by cattle, spending more than half of their time foraging [09 April–30 June 2018].
Figure 11: Proportion of time spent feeding by 6 cattle in the lower Kuiseb in relation to air temperature.
Figure 12: Temperature difference (Collar temperature–weather station air temperature) as a function of habitat assemblages (P < 0.05).
Figure 13: Accessible Faidherbia albida pods in the Kuiseb River
Figure 14: Cattle in the inter–dunes before rainfall
Figure 15: The inter–dune rangeland after rainfall (note the third cow from the left with a collar)
Figure 16: Cattle seeking shade in the Kuiseb River
5.1. Limitations to the technology

Even though each of the GPS collars was configured to record the location and associated sensor information every 10 minutes and should have resulted in 144 data points per day, or 11,808 data entries per collar, all collars had extended periods during which no information was recorded, but without consistent overlap.

Galster et al., (2001) mentioned that cases that occur were no information was recorded regarded as normal in most biologging studies, hence set recording at 10 minutes interval to acquire more data in a short period, this challenge is mostly due to factors such as cloud cover, vegetative cover, topography and collar itself.

5.2. Cattle habitat selection in Kuiseb River area

This study has shown that cattle in the lower Kuiseb River area tend to select different habitats before and after episodic rainfall events, there was a significant difference (P < 0.05) in habitat selection by cattle before and after a rainfall event. The results in figure 5 indicated that before rainfall, cattle utilise the Kuiseb River habitat (8000 counts) more than the inter–dune (4500 counts) and the gravel plain habitat (2200 counts). But after a rainfall event, cattle utilise the interdune (9600 counts) more than the Kuiseb River (3700 counts) and gravel plain habitat (2000 counts). Figure 16 and figure 15 also depict the change in habitats by cattle before and after rainfall events.
This result is consistent with Owen–Smith et al., (2010) who showed that animals change habitats mainly due to changes in season and availability of forage resources. In Rubanza et al., (2007), stating that cattle can spend many months or more in cases where rainfall is not experienced surviving on pods, despite high levels of secondary chemical compounds in the pods that may affect palatability for cattle. Ortega et al., (1999) in his study stated that browsing behaviour is common in cattle that reside in areas dominated by trees and shrubs instead of grass as forage. The Kuiseb River habitat is dominated by trees such as Vachellia erioloba, Faidherbia albida, Euclea pseudebenus and Salvadora persica. Amongst these trees, the Faidherbia albida and Vachellia erioloba trees are well known as a forage source for livestock, of which the pods have a composition of protein (10% to 16.5%), carbohydrate (50%) and oil (2.7%) (Le Roux et al., 2009).

The inter–dune area supports abundant Stipagrostis ciliata, S. gonatostachys and Centropodia glauca after rainfall, while the gravel plains are dominated by S. ciliata and S. obtusa after rainfall, which are regarded highly palatable and nutritious (Oudtshoorn, 1999). It is for this forage differences in the Kuiseb River area habitats before and after rainfall events that cattle tend to browse during dry periods and grazers when grass cover is available after rain.

There was also a significant difference in time spent at each habitat within settlements (P < 0.05) from 09 April 2018 to 30 June 2018; figure 6,7,8 and 9 revealed that cattle at each settlement utilise habitats unproportionally. At Homeb settlement, cattle utilise the Kuiseb river habitat (7900 counts) more than the interdune (7000 counts) and hardly utilise the gravel plain habitat (250 counts). At Natab settlement, cattle utilise the interdune habitat (4400 counts) more than the gravel plain (2000 counts) and the Kuiseb river habitat (1900 counts). Meanwhile at Klipneus settlement, cattle utilise the interdune habitat (2700 counts) more than the Kuiseb river (2100 counts) and the gravel plain habitat (2000 counts). A similar trend regarding uneven utilisation of land was stated.
in Bailey et al., (1996), saying that it is caused by land that has vegetation which is not uniform across, this heterogeneity then forces cattle opt for habitats with higher forage densities, areas that are more accessible and patches that are closer to water sources. Homeb settlement for instance is comprised of several inselbergs which are on the gravel plain habitat that prevent cattle access; hence cattle are forced to utilise more of the Kuiseb river and the inter–dune habitat.

There was no significant difference (P>0.05), in distance travelled before and after rainfall at each of the settlements (Figure 12). However, another outcome from the results is that the cattle travel great distances, up to more than 15 km per day. This result was consistent with Zuo & Miller–Goodman (2004), who stated that cattle tend to move long distances in cases where water is a scares resource. Hall (2002) on the other hand stated that cattle tend to move longer distances if they are under free–ranging conditions, as they have no restrictions. Cattle in the Kuiseb River area are free ranging, moving freely between habitats, each settlement has a waterpoint where cattle have access to water, however it is uncertain if the quantity given by farmers is enough. Therefore the distance travelled by cattle in the Kuiseb River area could be more influenced by free–ranging conditions than of lack of water.

5.2. Foraging behaviour in relation to air temperature

This study indicated that temperature does not influence foraging behaviour, figure 13 shows that there is no significant relationship between average maximum temperature and feeding of cattle in the Kuiseb River area (P > 0.05). Cattle in the lower Kuiseb River area dedicate 65% of their time feeding, and 35% on other beneficial activities. These cattle tend to actively feed at maximum average temperature range of 24°C–39°C ambient temperature. The results obtained are in contradiction with Blackshaw & Blackshaw (1994) and Vermunt & Tranter (2011) who stated that
feeding is normal at temperatures of 15°C–25°C, and that feed intake declines as temperature rises (above 35 °C it can fall by 10–35%). Bond et al., (1967) however stated that shade is one of the factors that are important in heat regulation, that shade structure can reduce heat load by as much as 30% in cattle, especially in hot–arid climates. Although the Kuiseb River habitat is mainly utilised for forage purposes (figure16),this habitat also has trees that can act as shade, providing shade for cattle during hot and dry days while they browse (figure 16). This is consistent with Frank et al., (2012), who stated that woodlands (especially those in desert environments) are heavily used habitats for cattle away from water, and provides critical forage and shade resources. This is also evident in figure 14,although there was no significant difference (P<0.05) between collar temperature and ambient temperature, the cattle that were present in the Kuiseb River habitat experiencing less radiation heat (7.7 °C) as compared to when they are in the open interdune (8.9 °C) and gravel plain (9.1°C) habitat. Comparing habitats according to the amount of radiant heat experienced by the collars active on cattle reveals the amount of heat experienced by these cattle.
CHAPTER 6

CONCLUSIONS AND RECOMMENDATIONS

6.1. Conclusion

(a) This study revealed that cattle in lower Kuiseb River area tend to select different habitats before and after rain events. They remain in the Kuiseb River habitat during dry periods browsing on pods of *Faidherbia albida* and *Vachellia erioloba* trees, but after episodic rain events that trigger *Stipagrostis ciliate, Stipagrostis gonatostachys, Stipagrostis obtusa* and *Centropodia glauca* grass production in the inter–dune and gravel plain habitats, cattle tend to graze in the dunes away from the Kuiseb River habitat. Cattle in lower Kuiseb River area also spent time in each habitat differently in each settlement, cattle in Homeb settlement for instance utilised the Kuiseb river habitat more often as compared to cattle that are in other settlements of study interest, this is influenced by heterogeneity and lack of access in some areas within habitats. Another outcome from this study is that these cattle travel great distances up to more than 15 km per day, which is influenced by free–ranging conditions that grant no animal restrictions.

(b) This study has revealed that ambient temperature does not affect the foraging behaviour of cattle in the lower Kuiseb River area, actively feeding at maximum average temperature range of 24°C–39°C. These results obtained are in contradiction with most literature, as they expect cattle to reduce feed intake as ambient temperature rises. The Kuiseb river however provides shade, a factor that is important in heat regulation as it reduces heat load in cattle, especially in hot–arid climates such as of the lower Kuiseb River area. This study also compared differences between collar temperature and ambient temperature, revealing that cattle present in the Kuiseb River
habitat experiencing less radiation heat as compared to when they are in the open interdune and gravel plain habitat, which supports the importance of shade in heat reduction for cattle.

6.2. Recommendations

(a) Since cattle tend to select different habitats during sporadic rainfall events, I recommend that a study be done to determine the quality, quantity and duration of available forage in these habitats.

(b) This study revealed that temperature does not influence cattle foraging behaviour in the lower Kuiseb River, however this may not be completely accurate, I recommend a long–term direct observation of foraging behaviour be done and compared with Gobabeb weather station data to compare results.

(c) It is known that cattle forage on the *Faerdherbia albida* and *Vachellia erioloba* before rainfall and *Stipagrostis* species amongst others after rainfall in the Kuiseb River surrounding, but nothing is known about rate of feed intake during these seasons. I recommend a study be done on the rate of foraging before and after rainfall events, this will reveal forage preference and quality.
REFERENCES


https://ir.library.oregonstate.edu/concern/graduate_thesis_or_dissertations/x059cb603


APPENDICES

Chi–Square Tests (for figure 7)

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Appendix 1: Results of habitat selection by cattle before and after rainfall in lower Kuiseb River area settlements.

Chi–Square Tests (for figure 11)

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Appendix 2: Results of habitat selection by cattle at each settlement from 09 April to 24 May 2018 in the lower Kuiseb River area settlements.

Linear Mixed effects model (For figure 12)

|                      | Estimate | Std. Error | Df    | t value | Pr(>|t|)    | P value |
|----------------------|----------|------------|-------|---------|-------------|---------|
| (Intercept)          | 7754.922 | 391.310    | 7.461 | 19.818  | 1.01e–07    | 0.70    |
| After Rainfall       | –149.614 | 389.273    | 309.004 | –0.384 | 0.701       | 0.70    |

Appendix 3: Results of daily movement distance of the cattle in the lower Kuiseb River
SPSS ANOVA\textsuperscript{a} (Results for figure 13)

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<th>Model</th>
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<th>Df</th>
<th>Mean Square</th>
<th>F</th>
<th>Sig.</th>
</tr>
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<td>Residual</td>
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<td>322</td>
<td>.014</td>
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<td></td>
<td>Total</td>
<td>4.476</td>
<td>323</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Appendix 4: The proportion of time spent feeding in relation to ambient temperature

Linear Mixed effects model (for figure 14)

|                | Estimate  | Std. Error | Df       | t value | Pr(>|t|) | P value |
|----------------|-----------|------------|----------|---------|---------|---------|
| (Intercept)    | 7.730e+00 | 6.831e-01  | 5.036e+00| 11.32   | 9e-05   | 0.001   |
| Habitat gravel | 1.449e+00 | 1.222e-01  | 1.463e+04| 11.86   | <2e-16  | 0.001   |
| Habitat interdune| 1.172e+00 | 8.361e-02  | 1.463e+04| 14.02   | <2e-16  | 0.001   |

Appendix 5: Temperature difference between collar and ambient statistical results
Appendix 6: The proportion of daily time cattle spent in the River as a function of date and site.
Appendix 7: Daily travel distance as a function of season and home site for cattle.
Appendix 8: The proportion of time spent by cows in each habitat before and after rainfall
Appendix 9: Proportion of time spent in each habitat per settlement before and after rainfall