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Using remote sensing to explore the role of ambient temperature in determining gemsbok (Oryx gazella) usage of a heterogeneous landscape in the central Kalahari

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USING REMOTE SENSING TO EXPLORE THE ROLE OF AMBIENT TEMPERATURE IN DETERMINING GEMSBOK (*ORYX GAZELLA*) USAGE OF A HETEROGENEOUS LANDSCAPE IN THE CENTRAL KALAHARI

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A research report submitted to the Faculty of Science, University of the Witwatersrand, in partial fulfilment of the requirements for the degree of Master of Science

Johannesburg, August 2015

DECLARATION

I declare that this Research Report is my own, unaided work. It is being submitted for the Degree of Master of Science at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination at any other University.



(Signature of candidate)

Signed at Johannesburg on this 31st day of August 2015

ABSTRACT

The central Kalahari is likely to become hotter and drier as a result of climate change in the region. These changes may result in behavioural changes in Gemsbok due to temperature induced stress, in spite of physiological and behavioural adaptations, and are likely to manifest in a preference for particular landscape patch classes. Recent Landsat 8 satellite imagery and classification analysis were used to map landscape patch classes in a heterogeneous landscape in the central Kalahari. The classification map of the research area identified 6 classes of landscape patches used by Gemsbok. Eight collared Gemsbok were tracked by satellite to monitor their movement in their respective home ranges over a period of 9 months. Gemsbok locations were plotted on to the classification map, and location frequency distributions were produced for each landscape patch class. Gemsbok home ranges were calculated using minimum convex polygon geometry, and the available patch class areas within each home range were analysed against the usage patterns of each animal. The analysis showed less preference for shade producing classes and more preference for open classes. Exploration of the role of temperature in landscape patch selection showed that temperature is a weak predictor of patch class, that critical temperature thresholds have not yet been reached, and that Gemsbok preference for pans is more likely related to seasonally available forage and reduced predation risk in a "landscape of fear" (Laundré, Hernández, & Altendorf, 2001).

Keywords: Landsat 8; classification; CKGR; Gemsbok; landscape patches; home range; usage; availability; temperature.

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TABLE OF CONTENTS

Chapter 1 Introduction 8
1.1 General introduction 8
1.2 Statement of the problem 10
1.3 Aim of the project 10
1.4 Research questions and hypotheses 11
Chapter 2 Literature review 12
2.1 Use of GPS based location data in animal ecology 12
2.2 Gemsbok 12
2.3 Central Kalahari 16
2.4 Satellite imagery 19
Chapter 3 Methodology 22
3.1 Research area 22
3.2 Data collection 24
3.3 Image classification 30
3.4 Landscape patch class preference 32
3.5 Preference modelling 34
Chapter 4 Results 36
4.1 Classification Analysis 36
4.2 Patch class preference analysis 41
4.3 Patch class temperature analysis 49
4.4 Home range size estimation 55
4.5 Preference modelling 57
Chapter 5 Discussion and conclusions 63
5.1 Landscape heterogeneity 63
5.2 Gemsbok landscape patch preference 63
5.3 Role of temperature in landscape patch preference 64
5.4 Conclusion 67
References 69
Appendix 77
Appendix A List of software 77
Appendix B Classification accuracy proofing photographs 78
Appendix C Individual Gemsbok analyses 84

LIST OF FIGURES

Figure 2.1 Shade for Gemsbok from woody cover on Sunday Pan, CKGR 13
Figure 2.2 Gemsbok on short grass grazing in CKGR 14
Figure 2.3 Sunday Pan, CKGR 19
Figure 3.1 The research area in Botswana 22
Figure 3.2 The research area in CKGR in more detail 23
Figure 3.3 Research area of interest image, showing release sites 30
Figure 4.1 ISODATA classification image of the research area 36
Figure 4.2 Research area size in hectares for each class 37
Figure 4.3 Gemsbok patch class usage frequency histogram 41
Figure 4.4 Home range patch class usage vs patch class availability 43
Figure 4.5 Preference metrics per landscape patch class 44
Figure 4.6 Comparison of patch class usage, by Day and by Night 45
Figure 4.6.1 Patch class usage by time of day 47
Figure 4.6.2 Comparison of Gemsbok use of Class 1 and Class 6 47
Figure 4.6.3 Comparison of Gemsbok use of Class 4 and Class 5 48
Figure 4.6.4 Predicted Gemsbok activity profiles 49
Figure 4.7 Mean temperature in °C per patch class 50
Figure 4.8 Mean class temperature, by Day and by Night 51
Figure 4.9 Mean monthly temperature in °C by Day and by Night 52
Figure 4.10 Trend in minimum and maximum summer temperatures in the CKGR 53
Figure 4.11 Gemsbok location frequency per class, by month 54
Figure 4.12 Tau Pan in summer 55
Figure 4.13 Home ranges of the 8 tracked Gemsbok in the research area 56
Figure 4.14 Home range size estimates for each Gemsbok 56
Figure 4.15 Class group centroids plotted on Function 1 and Function 2 59

LIST OF TABLES

Table 2.1 Landsat 8 Orbital characteristics 21
Table 2.2 Landsat 8 OLI and TIRS spectral and spatial resolution 21
Table 3.1 Gemsbok tracking data 25
Table 3.2 Landsat 8 image metadata 28
Table 3.3 Pixel values in TOA radiance corrected image 29
Table 4.1 Classification legend and area table 37
Table 4.2 Vegetation class descriptions 38
Table 4.3 Classification error matrix 40
Table 4.4 Available patch class areas in each Gemsbok's home range 42
Table 4.5 Home range Usage and Availability by patch class 43
Table 4.6 Day and night patch class usage vs available patches 45
Table 4.7 Mean class temperature in °C by Day and by Night 51
Table 4.8 Mean monthly temperature in °C, by Day and by Night 52
Table 4.9 Canonical discriminant functions evaluated at Class group centroids 59

Chapter 1 Introduction

1.1 General introduction

Climate change is having an impact on the whole of southern Africa, which has been prioritised as an area for remote sensing research due to anticipated environmental change, particularly in arid and semi-arid areas (Privette & Roy, 2005). Maximum temperatures are rising in South Africa (MacKellar, New, & Jack, 2014), the western part of southern Africa is likely to get drier, and the eastern part is likely to get wetter (Tadross, Jack, & Hewitson, 2005). In addition, particular areas of the western part of southern Africa, such as the central Kalahari, are likely to get hotter (New et al., 2006).

According to the latest 2013 Intergovernmental Panel on Climate Change (IPCC) Assessment Report (AR5), global warming is now indisputable (Stocker et al., 2013). Greenhouse gas concentrations have risen to unprecedented levels, and the primary cause has been traced to anthropogenically sourced increases in CO_2 emissions (Stocker et al., 2013). Global temperatures have risen by 1°C over the past 50 years and are likely to continue to rise by another 2°C by the end of this century. As rising temperature is a key driver of climate change, these temperature increases will have a global impact (Barker, 2007).

The central Kalahari in Botswana has a variable and erratic rainfall that is concentrated from January to March. The impact of global warming and climate change is likely to be negative for the central Kalahari, with hotter and drier conditions predicted by both the IPCC AR5 (Stocker et al., 2013) and others (Mphale, Dash, Adedoyin, & Panda, 2013).

Due to the higher temperatures and reduced rainfall, grazing ungulates such as the Gemsbok (*Oryx gazella*) in the central Kalahari may be subject to stress, through the conflicting needs to move to available forage, the requirement to stay cool and constant predation risk. For Gemsbok, movement from shade provided by trees and woody cover to forage will raise body temperature and add to dehydration. The Arabian Oryx (*Oryx leucoryx*) has adapted to a more harsh environment and even higher temperatures in Saudi Arabia and yet they survive and thrive (Hetem et al., 2010). Many animal species have developed adaptations that permit them to survive in arid environments, and that act as a buffer to the negative influences of climate change. These adaptations include behavioural changes, such as nocturnal foraging, and autonomic adaptations, such as brain cooling (Fuller et al.,

2010). The landscape of the central Kalahari encompasses a vegetation patch structure, comprising interconnected patch classes. Selection of preferred patches represents a response to the patch structure of this environment (Kotliar & Wiens, 1990). In this heterogeneous landscape, micro environments are available that offer Gemsbok shelter from higher temperatures, and that allow cooling strategies to be implemented (Fuller et al., 2010).

Physiological adaptations in Gemsbok include heterothermy, in which excess heat is stored in the body during the day and is then released at night by non-evaporative means when temperatures are lower (Ostrowski & Williams, 2006). The carotid rete is an adaptation consisting of a network of blood vessels which allows the arterial blood pumped to the brain to be cooled by vascular blood that has already been cooled in the nostrils and ears (Maloney, Fuller, Mitchell, & Mitchell, 2002). Gemsbok morphological adaptations include a white underbelly to reflect heat, while behavioural adaptations include standing in shade during the day, lying down on shady cooler sand, maximising body exposure to the available breeze and minimising body exposure to direct sun by parallel orientation to incident sunlight (Hetem et al., 2011; Fuller et al., 2010; Hetem et al., 2010).

The amount of forage available to Gemsbok in the central Kalahari is related to the Mean Annual Precipitation (MAP). As MAP increases, biomass increases in the form of grasses, shrubs and trees (Scholes & Dowty, 2002). If the climate change predictions for the central Kalahari are correct, available forage for Gemsbok in the form of grass and forbs is likely to decline, due to reduced and patchy precipitation (Engelbrecht et al., 2011).

In the research area in the North East corner of the Central Kalahari Game Reserve (CKGR), temperature is rising, and precipitation is erratic and reducing (New et al., 2006; Tadross et al., 2005). Vegetation is therefore under pressure, and herbivores are under stress. As a result of these factors, thermoregulation will be a necessary physiological adaptation for ungulates to cope with increased body temperature (Cain, Krausman, Rosenstock, & Turner, 2006). Gemsbok in particular have developed a range of temporal and spatial behaviours to assist with thermoregulation that will be required to cope with increasing temperatures in this region. Changes to these behaviours may impact patch class selection. This study will examine which patch classes the Gemsbok prefer, which patch classes were available to them, and whether temperature influenced their choice.

1.2 Statement of the problem

Global warming is resulting in climate change in Southern Africa (Stocker et al., 2013). In the central Kalahari, this change is resulting in higher temperatures and reduced rainfall (New et al., 2006). These factors may result in changed behaviour for ungulates like Gemsbok in this region, such as nocturnal foraging (Cain et al., 2006). An understanding of the preference behaviour of a sample of Gemsbok in the research area, under the influence of a specific climate change determinant such as temperature, will provide an indication of how Gemsbok in general may react to the influence of climate change in the central Kalahari.

Vegetation variability at both spatial and temporal scales is a natural characteristic of the Kalahari landscape (Thomas & Twyman, 2004), and is related to the erratic and sporadic nature of the limited rainfall. The variability of landscape patches present Gemsbok in the central Kalahari with a preference choice (Kotliar & Wiens, 1990). The role of temperature and vegetation structure on Gemsbok activity has been studied in the Etosha National Park in Namibia, where temperature was found to be a significant predictor of specific activities (grazing, lying, standing, walking) (Ruckstuhl & Neuhaus, 2009). If ambient temperature is a significant factor in Gemsbok landscape patch selection in the central Kalahari, then the preferred patch class may be related to the vegetation structure and cover in each patch class, the mean temperature variability between classes, and to temperature variability within patch classes from day to night.

1.3 Aim of the project

The aim of the research project is to explore the role of ambient temperature, as measured by collar-mounted black globe thermometers, in determining the use of heterogeneous landscape patches by Gemsbok in the central Kalahari in Botswana.

1.3.1 To identify landscape heterogeneity in the research area

The first objective is to produce a classification map of the research area that shows the predominant classes of landscape patches used by Gemsbok, including pans, short and long grass grazing, shrubland with woody cover and sparse woodlands.

1.3.2 To determine how the available landscape patches are used

The second objective is to plot the locations of collared Gemsbok on to the classification map in order to address the following research questions:

1.3.2.1 What is the frequency distribution of Gemsbok across each landscape patch class?

1.3.2.2 What is the availability of each patch class in the Gemsbok home ranges?

1.3.2.3 How does ambient temperature impact Gemsbok patch class preference?

1.4 Research questions and hypotheses

The central hypothesis is that ambient temperature is a major driver of landscape patch selection by Gemsbok in the CKGR. While the use of particular landscape patches is evidenced by the frequency with which Gemsbok are located in each patch class, preference is a measure of the use of a patch class relative to its availability (Beyer et al., 2010). It is hypothesised that Gemsbok are more frequently located in landscape patches that are cooler. Cooler temperatures are associated with shade, which is related to the structure and amount of vegetation cover. It is expected that higher temperatures will be recorded in pans with less shade from vegetation, and lower temperatures will be recorded in landscape patches comprising denser shrub, trees and woodland. However, the Gemsbok's desire for lower temperatures is balanced by the need to forage and reduce predation risk.

The research questions set out in Section 1.3.2 lead to the following specific hypotheses:

H_1 The frequency with which Gemsbok are located in particular landscape patches is strongly influenced by the vegetation structure and cover of these patches, and show a preference for spending more time in areas that have both grazing and shade available (Research question 1.3.2.1).

H_2 The frequency with which Gemsbok are located in particular landscape patch classes is not simply proportional to the availability of those patch classes within the Gemsbok's home range, but illustrates a deliberate selection of certain landscape patch classes (Research question 1.3.2.2).

H_3 Gemsbok patch selection is driven by ambient temperature, and in the hot conditions prevailing in the Kalahari, Gemsbok are more frequently located in landscape patches that have more vegetation, hence more shade, and hence cooler temperatures (Research question 1.3.2.3).

Chapter 2 Literature review

2.1 Use of GPS based location data in animal ecology

The introduction of Global Positioning System (GPS) based collar mounted tracking devices has had a profound impact on the ability to monitor wildlife in remote areas at fine spatial-temporal scales (Cagnacci, Boitani, Powell, & Boyce, 2010). Besides accurate ground positioning, typically less than 30m (Tomkiewicz, Fuller, Kie, & Bates, 2010), sensor devices can add additional information about the environment, such as temperature, humidity and altitude. The management of the data handling through multiple processing steps and analyses can be a challenge, given the quantity of data available and potential errors inherent in the technology (Urbano et al., 2010).

GPS based location data plays a key role in determining why particular habitats are important to specific animals by providing the necessary data from which to develop an understanding of the habitat-performance relationship for that animal, that takes into account the fitness and well-being of the animal (Gaillard et al., 2010). The benefits of having large amounts of temporal and spatial tracking data available through GPS technology is balanced by a number of problems, ranging from high cost and some equipment failure, to a detached observer approach from “armchair ecologists” who no longer undertake field research (Hebblewhite & Haydon, 2010). Overall, however, the use of GPS based animal tracking has provided the means to undertake a wide range of animal ecology assessments, including habitat use and habitat preference, that are of particular relevance to the current study (Beyer et al., 2010).

2.2 Gemsbok

2.2.1 General

The gemsbok is the iconic antelope of the central Kalahari. Their preferred environment is open grasslands, but they can also be found in open woodlands and dune environments. Female Gemsbok are targeted for collaring as they tend to stay with the herd, in larger home ranges (Knight, 1991), while male Gemsbok tend to be solitary in smaller home ranges (Ruckstuhl & Neuhaus, 2009). Four major hypotheses exist as to why social ungulates tend to separate on sexual grounds, and the most applicable to Gemsbok is the Activity Budget hypothesis (Ruckstuhl & Neuhaus, 2009). The female Gemsbok can be identified by their longer, more slender horns, compared to the slightly shorter, thicker horns of the male Gemsbok (Moller, Cuervo, Soler, & Zamora-Muoz, 1996).

Gemsbok are independent of free-water sources when forage moisture content is ≥ 33%. The Gemsbok is thus the only grass eating grazer that can survive in the arid and waterless regions of the Kalahari (Knight, 1991). This ability stems from physiological and behavioural adaptations that reduce metabolism, resulting in lowered evaporation and dehydration, together with a liking for water-rich melons such as the tsamma melon (*Citrullus lanatus*) (Knight, 1995). Grass accounts for over 80% of the Gemsbok diet throughout the year, and over 90% during the dry season. During the wet season, forbs supplement grass intake and account for 14% of the Gemsbok diet (Knight, 1991).

The combination of the Gemsbok's requirement for shade, and a preference for greener conditions, contribute to the Gemsbok's avoidance of tree savannah as a habitat, and result in a preference for the taller perennial grasslands, where their muzzle anatomy is particularly well suited to longer grass (Knight, 1991).



Figure 2.1 - Shade for Gemsbok from woody cover, NE Sunday Pan, CKGR
Source: Alexis Kanter, May 2012, Position 21° 19' 42.85" S 23° 40' 31.46" E

To assist with thermoregulation, it has been suggested that Gemsbok tend to spend long periods of inactivity in the shade during the heat of the day, and then to engage in nocturnal foraging to prevent heat stress and dehydration (Knight, 1991). It will be part of this study to explore whether rising temperature encourages this anticipated behaviour, or whether other factors, such as predation risk, play a determining role. It has been shown, for example, that the presence of predators, particularly lion (*Panthera leo*), can influence prey in their selection of landscape patches and foraging behaviour (Valeix et al., 2009).



Figure 2.2 - Gemsbok on short grass grazing in CKGR, with woody cover on dunes
Source: Machmut Mofidi, August 2009, Position 21° 10' 48.07" S 23° 39' 47.10" E

2.2.2 Implications of rising temperature for Gemsbok in central Kalahari

The impact of high temperature on Gemsbok needs to be seen against the background that Gemsbok are an established ungulate species in the central Kalahari, and have evolved both physiological and behavioural adaptations that allow them to survive and thrive in the heat and aridity of this part of the Kalahari (Cain et al., 2006; Knight, 1991).

Temperature related studies in the central Kalahari go back over 50 years. Kaminer & Lutz (1960) found the summer diurnal range to be from 5°C to 35°C. Schulze and Torrance in Griffiths (1972) determined summer minima and maxima of 9°C and 40°C respectively. Bothma & Le Riche (1994) found minimum summer (January) temperatures to range from 12°C to 26°C, while maximum summer temperatures ranged from 32°C to 41°C. They found that minimum winter (May) temperatures ranged from -7°C to 16°C and maximum winter temperatures ranged from 16°C to 32°C. Tyson & Crimp (1998) found summer (January) mean daily temperatures ranged from 19°C to 31°C, while winter (July) mean daily temperatures ranged from 6°C to 24°C.

Gemsbok adaptations can cope with current temperature levels in the central Kalahari (Maloney et al., 2002), but the role that temperatures above the norm will play is not clear. It

has been shown that a species of Oryx in Arabia (*O. leucoryx*) can cope with considerably higher temperatures without apparent stress by employing adaptive heterothermy, an adaptation by large ungulates living in arid desert environments that allows heat to be stored in the body during the day, and then to be released at night without evaporation, thereby conserving water (Hetem et al., 2010). That study suggests that Gemsbok could cope with higher temperatures than those currently experienced in the central Kalahari. However, climate change predictions for the central Kalahari do not just involve higher mean temperatures, but also that the frequency and intensity of extreme heatwaves and droughts are likely to increase (New et al., 2006).

If rising temperature in the central Kalahari reaches a critical threshold, then some changes in behaviour may become apparent that show a clear link to temperature (Cunningham, Martin, Hojem, & Hockey, 2013), however if the temperature remains within levels that are tolerable to the Gemsbok, then landscape patch preference may be related to influences other than temperature, such as predation risk (Valeix et al., 2009).

It is likely that a temperature threshold exists for Gemsbok in the central Kalahari (Cunningham et al., 2013), beyond which existing physiological adaptations such as the brain cooling capability of this animal's carotid rete, and behavioural adaptations such as seeking shade, presenting maximum body surface to prevailing wind and standing parallel to incident solar radiation (Hetem et al., 2011), will be insufficient to cope with temperature beyond this critical threshold. Thereafter, new spatial and temporal behaviours are likely to be observed as the Gemsbok continues to adapt to rising temperature in the central Kalahari. This study will endeavour to determine whether the Gemsbok's observed landscape patch class preference is influenced by temperature, and whether there is any indication that a critical temperature threshold has been reached.

In their study of the Arabian oryx, Hetem et al. (2010) observed that these animals continued to use homeothermy rather than heterothermy at collar mounted black globe ambient temperatures as high as 50°C. An important finding in their study of relevance to this Gemsbok study, is that the degree of heterothermy utilised is dependent on the availability of water, either in the form of surface water or in the form of sufficiently high moisture content in available forage (Hetem et al., 2010). An inference from their study is that the critical threshold for Gemsbok in the central Kalahari may be a combination of high temperature combined with increased aridity, rather than a particular threshold temperature alone. It is therefore of concern that both hotter and drier conditions are predicted for this region (Jury, 2013; New et al., 2006; Tadross et al., 2005).

If temperature is rising and rainfall is reducing, then an anticipated consequence is that the quantity and quality of available forage is likely to decline in the central Kalahari. This in turn is likely to cause Gemsbok to forage wider, which will result in an increase in home range size (Thomas, 2010). This anticipated impact on Gemsbok home range size as a result of climate change will be explored during the course of this study.

2.3 Central Kalahari

The central Kalahari has an aridity gradient that runs from north to south (Scholes & Dowty, 2002). The Mean Annual Precipitation (MAP) declines from around 700mm in the north to around 350mm in the south. The research area is located along this gradient and has a MAP of around 400-450mm (Ringrose, Matheson, Wolski, & Huntsman-Mapila, 2003). At MAP levels below 650mm, the growth of vegetation is constrained by MAP, and woody cover does not encroach on grasslands in these arid savannahs (Sankaran et al., 2005). As expected, woody plant biomass increases from south to north along the aridity gradient (Wang, D'Odorico, Ringrose, Coetzee, & Macko, 2007).

Major change factors for climate models are temperature and precipitation (Wilby et al., 2009). Given that both of these factors are expected to change (hotter and drier conditions) (New et al., 2006), the central Kalahari will become more arid as the negative impact of these two change factors take effect. The latent aridity of the Kalahari leaves this region at particular risk from the impact of reduced rainfall predicted as a result of climate change (Engelbrecht et al., 2011).

The heterogeneity or variability of the landscape in the central Kalahari tends to follow the aridity gradient (Scholes & Dowty, 2002), and within a given area comprises patches of trees, shrubs, grasses, Kalahari sand and pans (Ringrose et al., 2003). These landscape patches are not static, but are in a constant cycle of change from active, through degraded to regrowth (Wright, Gurney, & Jones, 2004).

The patch landscape of the central Kalahari is suitable for Gemsbok (Knight, 1991), and through a number of physiological and behavioural adaptations, has enabled Gemsbok to survive and thrive in the hot and dry conditions (Fuller et al., 2010). As the climate in the central Kalahari becomes hotter and drier, higher temperatures and increased aridity will have a negative impact on vegetation in the central Kalahari (Scholes & Dowty, 2002). As a result, the patch landscape may change, as more forage producing patches become

degraded (Wright et al., 2004). This potential change to the patch dynamics of the central Kalahari may result in movement adaptations becoming necessary for Gemsbok in their search for a combination of forage, shade and cover. Thus climate change in the central Kalahari may have an impact on Gemsbok range boundaries (Thomas, 2010).

The hierarchical framework for the study of heterogeneity in terms of scale and patch dynamics set out by Kotliar & Wiens (1990) has been further developed by Wu & Loucks (1995), with particular reference to the relationship between scale and heterogeneity. This concept has application in the Kalahari, where, at a macro scale, the landscape is homogeneous, while at a micro scale the landscape is heterogeneous and patchy.

The topography of the Kalahari is dominated by parallel linear dunes, that are stabilised by vegetation cover (Hürkamp & Völkel, 2011). The vegetation on the dunes consists of perennial grasses such as *Stipagrostis amabilis* and *Eragrostis lehmanniana*, together with woody cover in the form of *Acacia mellifera, Acacia haematoxylon* and *Boscia albitrunca* (Palmer & van Rooyen, 1998).

The Kalahari is influenced by the Inter-Tropical Convergence Zone (ITCZ) and the resultant anti-cyclonic circulation prevalent over central southern Africa (Hürkamp & Völkel, 2011). The strongest and most persistent winds in the central Kalahari are north-easterly in the research area, resulting in parallel linear dunes running roughly NW to SE, with associated troughs between the dunes. The dunes are approximately 15m from troughs to crests, but vary from 2m-30m in relative height (Bullard & Nash, 1998).

Trees, shrubs and grasses of the Kalahari are of critical importance to the Gemsbok. Trees and shrubs provide shade in the increasingly hot climate, while selected shrubs and grasses provide nourishment. Some of these grasses provide sufficient moisture to sustain the Gemsbok in the absence of surface water (Knight, 1991).

2.3.1 Trees of the Kalahari

The distribution of trees in the Kalahari tends to follow the aridity gradient from north to south. From the Mopane woodlands of the north, through the Acacia savannah of the central Kalahari to the Rhigozum grassy shrublands of the arid south, tree species that are able to provide shade for Gemsbok include *Acacia erioloba* (Camel thorn), *Acacia luderitzii* (Kalahari acacia / Bastard umbrella thorn), *Acacia mellifera* (Blackthorn), *Acacia haematoxylon* (Grey

camel thorn), *Boscia albitrunca* (Shepherds tree) and *Terminalia sericea* (Silver cluster leaf / Yellowwood) (Scholes & Dowty, 2002).

2.3.2 Shrubs of the Kalahari

As in the case of the trees of the Kalahari, shrubs also follow the aridity gradient. Commonly occurring shrubs in the central Kalahari that are able to provide some shade for Gemsbok, in the form of woody cover include *Rhigozum trichotomum* (Driedooring), *Acacia hebeclada* (Candle thorn) and *Grewia flava* (Brandewynbos) (Scholes & Dowty, 2002).

2.3.3 Grasses of the Kalahari

As a grazer, grass forms the bulk of the Gemsbok diet (Knight, 1991). Grasses that are available to Gemsbok in the central Kalahari include *Eragrostis pallens* (Gemsbok / elephant grass) - a medium to long grass that is associated with medium to tall shrubs in the Kalahari, while *Stipagrostis amabilis* (Bushman grass / Dunecrest grass) is a shorter grass associated with smaller to medium sized trees such as *Acacia mellifera* (Hüttich, Herold, Strohbach, & Dech, 2011). Other grasses that occur in the central Kalahari include *Aristida meridionalis* (Gemsbok grass / Heigras) and *Eragrostis lehmanniana* (Lehmann love grass) (Makhabu, Marotsi, & Perkins, 2002). The water content of these grasses is particularly important to Gemsbok in the arid Kalahari (Knight, 1991).

2.3.4 Pans

The pans in the research area are of particular interest, as they contain a combination of short grass grazing resources, together with stands of trees and woody cover that provide shade for Gemsbok, as can readily be observed in the satellite image in Figure 2.3 below.

Pans are slight depressions in the surrounding landscape and range in size from a few hundred metres to a few kilometres. Gemsbok located on pans have a good vantage point from which to detect approaching predators across the essentially flat landscape (Vanderpost, Ringrose, Matheson, & Arntzen, 2011).

The pans transform after summer rains, with forbs supplementing short halophytic grasses that can tolerate the saline conditions, as the pans have calcrete and clay soils that are rich in calcium carbonate, while elsewhere the soils are sandy (Makhabu et al., 2002).



Figure 2.3 - Sunday Pan, CKGR
The heterogeneity of vegetation on the pans is illustrated in this image, which clearly shows stands of trees (tree islands), amid short grass and forb grazing, interspersed with patches of shrub vegetation. Source: Google Earth, Digital Globe image, May 2010.

2.4 Satellite imagery

The Landsat 8 satellite was launched on 11 February 2013 by the North American Space Administration (NASA), and is run operationally by the United States Geological Survey (USGS). It is the latest in a series of Landsat Earth Observation Satellites (EOS) and carries new instruments in the form of the Operational Land Imager (OLI) and the Thermal Infrared Sensor (TIRS). The Landsat programme has, over the last 40 years, provided a near continuous record of moderate resolution earth observation imagery, and thereby provides a long-term record of land use, together with natural and anthropogenic change on the earth (USGS, 2013b). The previous Landsat 7 satellite has a successful history of mapping research areas to identify vegetation structure and cover characteristics (Rebelo, Finlayson, & Nagabhatla, 2009). Images from the latest Landsat 8 satellite with enhanced OLI and TIRS instruments (USGS, 2013a) are therefore a good source for mapping the research area in the central Kalahari.

Landsat 4 and Landsat 5 Thematic Mapper (TM) images have been used to explore vegetation structure and cover in the Kalahari (Palmer & van Rooyen, 1998), and Landsat 7 Enhanced Thematic Mapper Plus (ETM+) images were used for both segmentation and classification in the Kalahari (Hüttich et al., 2011). This track record of success in similar studies in the Kalahari make the latest Landsat 8 images produced by the OLI and TIRS instruments the images of choice for the current study.

In a recent classification study in desert conditions using a Landsat 5 image (Rozenstein & Karnieli, 2011), it was found that in a heterogeneous landscape, collecting spectral signatures for supervised classification training sets can be very difficult, particularly where there are complex spectral variations in the landscape patches. In these circumstances, an unsupervised classification was found to produce better classification results than a supervised classification (Rozenstein & Karnieli, 2011). In the heterogeneous research area in the central Kalahari, with significant amounts of bare soil, sparse cover and high reflectance, it would be difficult to develop accurate training sets for supervised classification, and hence the classification analysis in this study was undertaken using unsupervised classification.

The orbital characteristics of Landsat 8 are set out in Table 2.1, and the spectral resolution is set out in Table 2.2 below. Important aspects from these tables that are of relevance to this study are:

- The resolution of the TIRS bands (bands 10 and 11) has been resampled to 30m resolution to be compatible with the remaining bands in Landsat 8 multispectral images. This makes it possible to use all of the Landsat 8 bands for classification purposes (USGS, 2013b), in order to improve the classification.
- The improved radiometric quantization (12 bits) of the Landsat 8 images over the 8 bit quantization of Landsat 7 images, together with improved signal to noise ratios, allows for improved image characterisation of a heterogeneous landscape (USGS, 2013a). This ability to measure slight variations in ground cover has positive implications for classification analysis, particularly considering the highly reflective surfaces in the research area in the CKGR (Roy et al., 2014).

Table 2.1 - Landsat 8 Orbital characteristics

Landsat 8 Orbit	**Characteristics**
Swath width:	185 kilometers
Repeat coverage interval:	16 days (233 orbits)
Altitude:	705 kilometers
Quantization:	12 bits
Orbit:	Polar, sun-synchronous
Inclination:	98.2 degrees
Equatorial crossing:	10:00am +/- 15 min.

Source: North American Space Administration (NASA)
http://landsat.gsfc.nasa.gov/?p=5081

Table 2.2 - Landsat 8 OLI and TIRS spectral and spatial resolution

Bands	**Wavelength**	**Resolution**
	(micrometers)	**(meters)**
Band 1 - Coastal aerosol	0.43 - 0.45	30
Band 2 - Blue	0.45 - 0.51	30
Band 3 - Green	0.53 - 0.59	30
Band 4 - Red	0.64 - 0.67	30
Band 5 - Near Infrared (NIR)	0.85 - 0.88	30
Band 6 - SWIR 1	1.57 - 1.65	30
Band 7 - SWIR 2	2.11 - 2.29	30
Band 8 - Panchromatic	0.50 - 0.68	15
Band 9 - Cirrus	1.36 - 1.38	30
Band 10 - Thermal Infrared (TIRS) 1	10.60 - 11.19	100
Band 11 - Thermal Infrared (TIRS) 2	11.50 - 12.51	100

Source: United States Geological Services (USGS)
http://landsat.usgs.gov/band_designations_landsat_satellites.php

The OLI instrument on Landsat 8 employs push-broom architecture, as opposed to the whisk-broom technology used on the previous Landsat 7 satellite, thus avoiding the need for a scan line corrector that was subject to mechanical failure on Landsat 7 (Knight & Kvaran, 2014). The Coastal aerosol (band 1) and Cirrus (band 9) bands are new bands on the Landsat 8 OLI instrument that add additional capability to Landsat 8, and are included in the image classification in this study. The wavelengths of the NIR (band 5) and Panchromatic band (band 8) have also been shifted slightly relative to Landsat 7, and are somewhat narrower to improve contrast (Knight & Kvaran, 2014). Overall, the post launch on-orbit performance tests have shown that the OLI instrument is stable, providing outstanding results that exceed design specifications and make the Landsat 8 OLI the preferred instrument for earth observation (Markham et al., 2014).

Chapter 3 Methodology

3.1 Research area

The research area is located in the arid central Kalahari, in the NE corner of the CKGR. It measures approximately 115km by 75km, and is located between latitudes 21° 06' S and 21° 48' S and between longitudes 22° 52' E and 24° 02' E, as indicated in Figure 3.1 below.

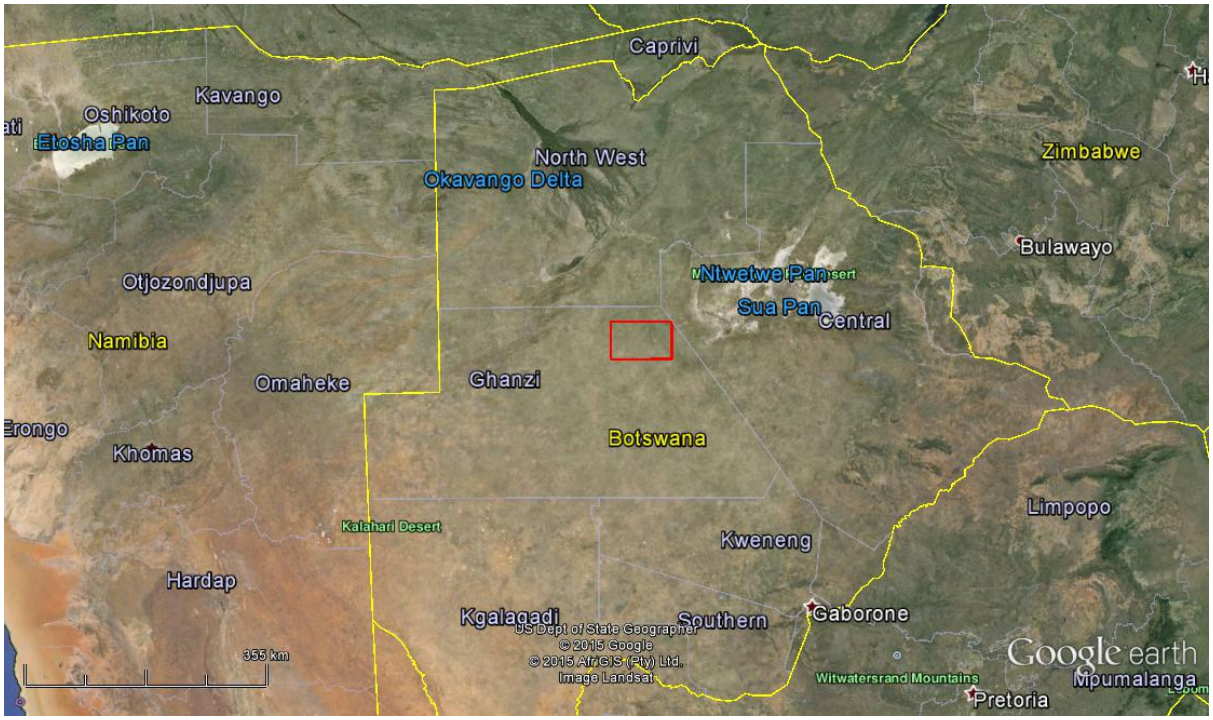

Figure 3.1 – The research area in Botswana, boxed in red, south of the Okavango Delta and west of the Makgadikgadi Pans (Ntwetwe Pan and Sua Pan)
Source: Google Earth, Image date October 2013

The research area is shown in more detail in Figure 3.2 below, clearly illustrating the major features of the area, including Passarge Valley in the North, Deception Valley in the East, Letiahau in the South, together with a number of pans, including Tau Pan, Sunday Pan and Leopard Pan.

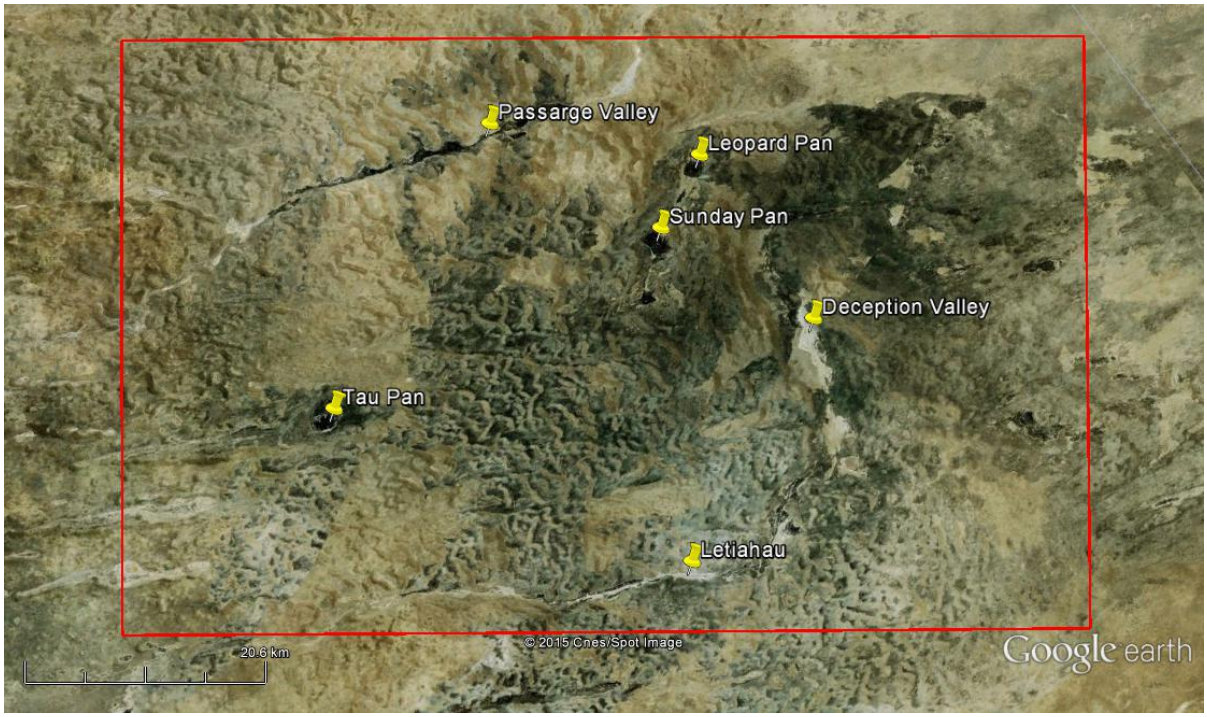

Figure 3.2 – The research area in the CKGR, in more detail, showing key features and pans
Source: Google Earth, Image date August 2009

The elevation profile from West to East shows a gradual slope (mean=0.1% , max=0.2%) decreasing in altitude by approximately 50m from 1003m west of Tau Pan to 952m east of Deception Valley over a distance of approximately 82km. The central Kalahari is an essentially flat landscape, interspersed with immobile sand dunes, fossil rivers and pans (Makhabu et al., 2002). This arid region is rich in biodiversity, and has a number of ungulate species, including Gemsbok (Botswana-Government, 2009).

The vegetation of the central Kalahari is Acacia-Baikiaea savannah (Botswana-Government, 2009). The heterogeneous landscape is characterised by trees, shrubs and grasses (Hüttich et al., 2009), and reflects both the patchiness and patch structure described conceptually by Kotliar & Wiens (1990), and the balanced co-existence between patch classes referred to by Hüttich et al. (2011). From a hierarchical framework perspective, the heterogeneity of this region can be considered both coarse grained and fine grained (Kotliar & Wiens, 1990), contrasting the less vegetated areas in the western region of the research area with the more vegetated areas in the eastern region of the research area (coarse grain), while exhibiting the patch dynamics associated with small, adjacent patches of Kalahari sand, trees, shrubs and grasses that characterise the central Kalahari (fine grain).

3.2 Data collection

3.2.1 Tracking data

During November 2012, a group of researchers collared and released 8 Gemsbok in two distinct regions of the research area. Three animals were released in the SW and the remaining five in the E/NE region of the research area, as shown in Figure 3.3.

The tracking system was provided by African Wildlife Tracking, a South African based company that provides specialised wildlife tracking services. For this study, neck collars were fitted to the Gemsbok that recorded the following data every hour, and transmitted it to a geostationary satellite 36 000km above the equator for subsequent downloading and analysis:

- GPS position in Latitude and Longitude
- Ambient temperature (black globe thermometer)
- Altitude in meters above sea level

The method used to collar the Gemsbok was as follows. A spotter aircraft was used to locate groups of Gemsbok in the research area. A helicopter was then dispatched with a vet and a darting rifle. The vet would dart the selected Gemsbok with an anaesthetic, typically a combination of Thiafentanil (A3080), Medetomidine and Ketamine (Grobler, Bush, Jessup, & Lance, 2001). Once the Gemsbok was down, the vet and helicopter pilot could approach and place plastic pipes over the horns. Gemsbok are aggressive and resist handling when semi-immobilised during collaring operations. Their strength and long sharp horns make them dangerous unless properly anaesthetised (Grobler et al., 2001).

At the same time that the satellite tracking collar was fitted to the Gemsbok, two implants were surgically inserted into the animal to record internal temperature and movement for an ancillary study. Once completed, a suitable antidote was administered by the vet, usually Naltrexone or Atipamizole (Kilgallon, Lamberski, & Larsen, 2010), prior to release. Each animal was then able to roam and forage freely, while the GPS position, temperature and altitude were transmitted hour by hour to the tracking satellite and recorded. Details of the Gemsbok tracking data are summarised in Table 3.1 below.

Table 3.1 – Gemsbok tracking data from November 2012 to July 2013

Gemsbok	Collar ID	Start Date	Herd count	End Date	Observations	Duration (Months)
1	SAT559	11 November 2012	50	31 July 2013	6343	9
2	SAT560	10 November 2012	17	10 July 2013	5921	8.5
3	SAT561	09 November 2012	5	15 June 2013	5273	7.5
4	SAT562	10 November 2012	13	31 July 2013	6357	9
5	SAT563	08 November 2012	6	27 July 2013	6290	9
6	SAT564	08 November 2012	13	10 July 2013	5946	8.5
7	SAT565	11 November 2012	13	20 July 2013	6112	8.5
8	SAT566	09 November 2012	6	22 December 2012	1044	2

The tracking continued for between 2 and 9 months. In most cases, the tracking continued for a period of more than 8 months, as shown in Table 3.1. In November 2013, the location data was downloaded from the tracking satellite. The number of location observations varied from as few as 1044 for SAT566 to 6357 for SAT562. The mean number of location observations per Gemsbok, 5410, was considered more than adequate for this study. Once the data was downloaded, the location data for each Gemsbok was saved as individual Excel spreadsheets for later analysis in ArcGIS.

A number of outliers in the satellite tracking data were identified by inspection where clear errors in the geographic coordinates existed. Typically these errors would involve a 10 degree shift in Latitude or Longitude for between 1 and 4 locations, for 5 of the 8 Gemsbok. These observations were identified and deleted from the analysis.

3.2.2 Temperature data

Ambient temperature was measured for each Gemsbok in the study by 30mm miniature black globe thermometers that have been shown to provide reliable ambient temperatures when fitted to collars on free ranging animals (Hetem & Maloney, 2007). Temperature can be measured by remote sensing, using either the thermal bands (bands 10 and 11) from a Landsat 8 image (USGS, 2013a), or by using the thermal bands from an Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) satellite image (Gillespie, Abrams, & Yamaguchi, 2005). However, remotely sensed temperatures would not take convective cooling available to the Gemsbok into account, and more importantly, remotely sensed temperatures would be image specific, and would provide temperature measurement on the day and the time of that image only, not the hour by hour temperature readings required by this study over a 9 month period. Therefore the use of collar mounted black globe thermometers was required to measure the local ambient temperature applicable to the Gemsbok in this study.

The role of ambient temperature is crucial to this research project. Temperature was logged each hour, together with the animals GPS location. The date and time of each observation was also recorded, in order that analysis could be done on a day-night comparison basis, as well as hourly and monthly analyses. To this end, day was defined in this study as the 12 hours between 06h00 and 18h00, while night was defined as the 12 hours from 18h00 to 06h00. In order to allow comparisons to earlier studies involving ambient temperature in the Kalahari (Tyson & Crimp, 1998; Bothma & Le Riche, 1994; Kaminer & Lutz, 1960) a mid-summer month was defined as December, and a mid-winter month was defined as June.

Given that temperature is a major driver of climate change (Barker, 2007), and climate change for the Kalahari is likely to imply higher temperatures and less rainfall (New et al., 2006), it was important to analyse the ambient temperature data in as much detail as possible, to get an insight into current temperatures in the home ranges of the Gemsbok in this study. The ambient temperatures were therefore analysed on an overall basis by landscape patch class, as well as by day and night and by month, as defined above.

Once ambient temperature had been analysed, and where possible compared to previous studies, then its possible role in determining Gemsbok patch class preference was explored. Specifically, patch class usage frequency was tabulated and correlated against temperature, diurnally and seasonally. A basic tenet of this research is that Gemsbok are able to discriminate between patch classes, and to select a particular patch class based on some preference criterion or criteria (Beyer et al., 2010). If rising temperature in the central Kalahari is increasing temperature induced stress in Gemsbok, then it should be possible to quantify the impact of temperature on Gemsbok patch class preference. Discriminant analysis was employed to examine whether temperature on its own, or in combination with other available variables, could account for apparent preference displayed by the animals in this study. In addition, regression analysis was employed to explore the role of temperature as a predictor of patch class preference, with particular reference to any differences between daytime and night-time preferences, and seasonal preferences.

3.2.3 Shape file data

The Excel spreadsheets for each Gemsbok in turn were loaded into ArcGIS as XY data, using the Latitude / Longitude coordinates in the spreadsheet data to position each location on an ArcGIS map. The Hartebeesthoek94 geographic coordinate system is the official coordinate system for South Africa (Parker, 2011), and is appropriate for use in Southern Africa, including Botswana (Mugnier, 2004). Accordingly, the Hartebeesthoek94 geographic coordinate system was used to map the Gemsbok locations. The set of geographic locations was exported from ArcGIS as a shape file for further analysis in ERDAS. Shape files are a

vector data format for storing points, lines or polygons in Geographic Information System (GIS) applications (ESRI, 1998).

3.2.4 Home range estimates

A home range was defined for each Gemsbok from the location data using minimum convex polygon (MCP) geometry in ArcGIS. MCP's are widely used as a means of estimating home ranges from animal location data (Getz & Wilmers, 2004). The MCP, also known as a convex hull, is the smallest polygon that contains all of the locations, in which no internal angle exceeds 180 degrees (Burgman & Fox, 2003). After outlier removal, all remaining location observations were used to create home range MCP's for each Gemsbok, and were exported from ArcGIS as shape files for further analysis in ERDAS.

3.2.5 Extracting the Landsat 8 image

The research area was mapped using a Landsat 8 multispectral satellite image, suitably subset to the area of interest (AOI) in the central Kalahari. Using appropriate image analysis software (ERDAS), a landscape patch mosaic of the research area was produced by a classification analysis of one of the latest Landsat 8 (April 2013) images.

Data collected by remote sensing instruments carried on board Landsat 8 (OLI and TIRS) are transmitted to receiving stations on the ground via high bandwidth radio transmission. Raw satellite images contain flaws that require correction during pre-processing (Mather & Koch, 2011). A Landsat 8 satellite image was acquired from the USGS containing image data for the central Kalahari in a compressed .tar.gz folder. The image was geometrically corrected, implying that the Landsat 8 image had the scale and projection properties of a map (Mather & Koch, 2011), in this case, the Universal Transverse Mercator (UTM) map projection. The image was additionally corrected to Level 1T, implying that it had been orthorectified by the inclusion of terrain elevation data (USGS, 2013a).

Two Landsat 8 images were available for analysis, dated 15 April and 4 July 2013 respectively. The Landsat 8 image date of 15 April, at the end of the wet season, was chosen to give a fair appraisal of the landscape, avoiding the green-up period of September through December (Archibald & Scholes, 2007), but also avoiding the denuded, parched environment of mid-winter. As the Gemsbok tracking study ran from November 2012 to July 2013, the image date of 15 April 2013 also imaged the research area during the actual course of the Gemsbok tracking study.

The .tar.gz folder was uncompressed to a .tar folder using WinZip to provide access to a series of GEOTIFF (.tif) files corresponding to the 11 bands of a Landsat 8 image. Key

parameters for the Landsat 8 image for 15 April 2013 are summarised in Table 3.2 below. Landsat 8 images comprise 185 km × 180 km scenes defined by the second World-wide Reference System (WRS-2) of path and row coordinates that were also used by the Landsat 4, 5, and 7 satellites (Roy et al., 2014). The path (174) and row (75) numbers refer to that area of Botswana defined by the upper left and lower right Latitude / Longitude coordinates. The World Geodetic System 1984 (WGS84) is a standard co-ordinate system for the earth, and defines a standard spheroid and datum used in GPS systems (Duval et al., 2006). The scene identifier is the particular image to be used for analysis, taken on the date and time specified in the table. Importantly, the zero cloud cover and high image quality indicate that this is a suitable image for classification analysis (USGS, 2013a).

Table 3.2 – Landsat 8 image metadata

Parameters	**Data**
Scene	LC81740752013105LGN01
Path	174
Row	75
Date	15 April 2013
Time	08:27:40
Upper Left LAT LON	S20.68245 E22.24240
Lower Right LAT LON	S22.66000 E24.49188
Sensor	OLI-TIRS
Cloud cover	0.0
Image Quality	9
Map projection	UTM
Datum	WGS84
Ellipsoid	WGS84
UTM Zone	34

3.2.6 Top of Atmosphere (TOA) radiance conversion

In many change detection and tracking studies, atmospheric correction is necessary in order to remove the impact of cloud cover and air pollution (Paolini, Grings, Sobrino, Jiménez Muñoz, & Karszenbaum, 2006; Song, Woodcock, & Seto, 2001). One way to do this is to measure radiance and reflectance at TOA (Schroeder, Cohen, Song, Canty, & Yang, 2006). Although this study involved neither change detection nor a tracking study, an attempt was made to apply a TOA radiance conversion prior to classification analysis, so that this classification could be used as a base-line reference for any future change detection study.

The USGS provides procedures for converting L1 Digital Numbers (DN's) comprising pixel reflectance values in an image to TOA radiance in watts/m^2 (USGS, 2013c). The Landsat 8 image bands were layer-stacked, in order, into one 11 band image and an ERDAS model was built to carry out the TOA radiance conversion on all 11 Landsat 8 TIFF bands, in accordance with values provided in the image metadata (USGS, 2013c).

The conversion changed the pixel values in the TOA radiance image to a much smaller range than in the original, unconverted image produced directly from the individual input TIFF files. In particular, when the range of values for the converted TOA radiance image defined by the extremities of the DN distribution histogram was used, then the range reduced to 38 discrete pixel values. After histogram equalisation stretching, the image had a wider range of values, but not nearly as many discrete values as the original raw image, as summarised in Table 3.3 below:

Table 3.3 – Pixel values in TOA radiance corrected image

TOA Radiance	**Min**	**Max**	**Range**
Range from metadata	0	147	147
Range from histogram	57	95	38
Stretched TOA Radiance			
Range from metadata	40	255	215
Range from histogram	82	255	173
Raw layerstacked 11 band image			
Range from metadata	8970	16477	7507
Range from histogram	9436	12467	3031

A key aspect of this research is to identify what Kotliar & Wiens, (1990) refer to as "coarse-grained and fine-grained" heterogeneous patches. It was clear from Table 3.3 that the reduced range of pixel values in the converted TOA radiance image would reduce the ability to identify small (fine-grained) landscape patches (Vicenteserrano, Perezcabello, & Lasanta, 2008). The TOA Radiance conversion therefore would not produce an image that was more useful for classification of heterogeneous patches than the unconverted image. As TOA Reflectance is a second step after the radiance conversion (USGS, 2013c), the reflectance conversion would also not add to the ability to detect and classify landscape patches.

According to Song et al., (2001), atmospheric correction is not required for a single date image. As this study is based on the classification of a single date, high quality Landsat 8 image (image quality=9), with zero cloud cover (see Landsat 8 parameters in Table 3.3), in an area of essentially unpolluted atmosphere, it was decided that the raw (Level 1T processed) image was the best image to use for classification analysis, and the TOA radiance conversion would not be applied.

By including band 8, the panchromatic band, in the final layer-stacked image, the image was pan-sharpened. Pan-sharpening is the process whereby a high resolution panchromatic image is combined with lower resolution colour images, to produce a high resolution colour image in a process known as image fusion (Mather & Koch, 2011). This has important implications for this study, as a 30m resolution would have left small landscape patches

undetected in the classification map, while Gemsbok would have been able to perceive these patches of shade or forage. After pan-sharpening, with an image resolution of 15m, this problem of scale was reduced.

Even though bands 10 and 11 are thermal bands, their inclusion would add subtle differentiation between clusters extracted in the classification analysis. For example, long grass is cooler than short grass, and the inclusion of thermal characteristics in the layer-stacked image, would assist the classification process in distinguishing between short and long grass patches. The final AOI image, that encompassed all of the Gemsbok locations, is shown in Figure 3.3 below.

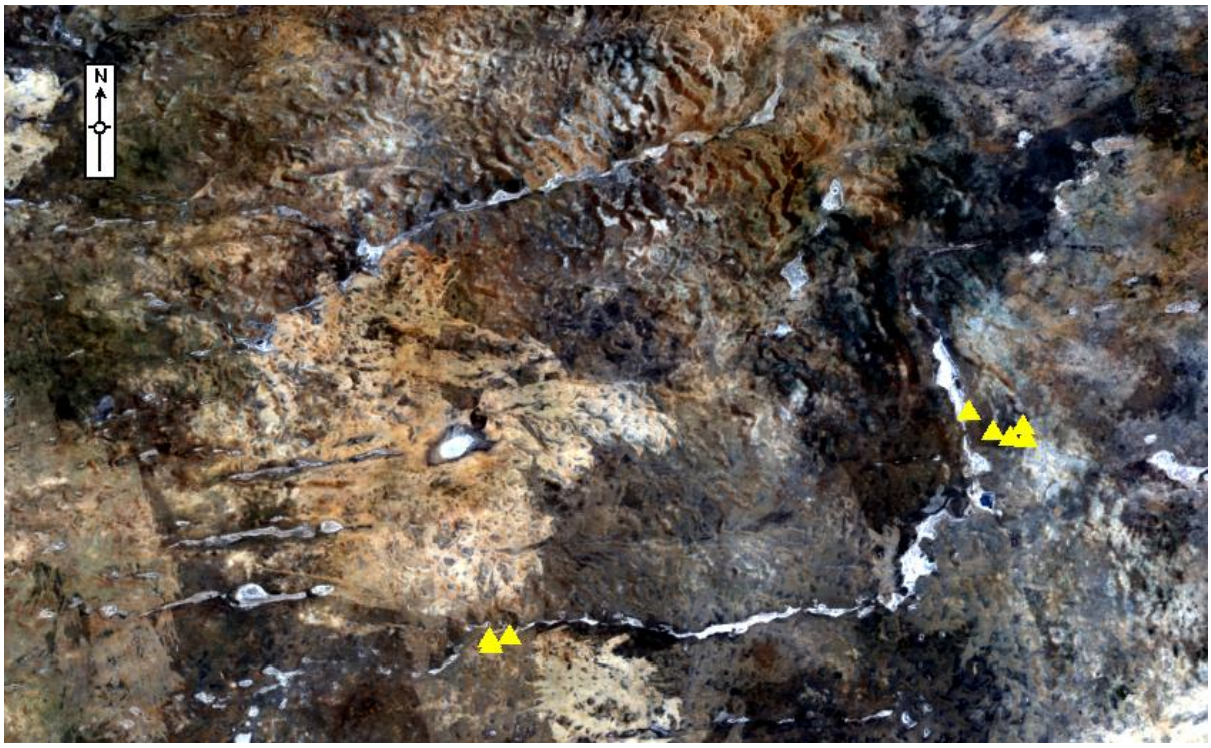

Figure 3.3 - Research area of interest in CKGR (11 band Landsat 8 image), showing the 3 Gemsbok release sites in the SW and the 5 release sites in the E.

3.3 Image classification

The Landsat 8 image of the research area was subject to classification analysis to identify landscape patch classes. Broadly, there are two classification options (Tso & Mather, 2009). In a supervised classification, training sets are made available to the classification software as examples of particular land use or landscape patch classes. Classification software then uses algorithms such as the Maximum Likelihood (ML) classifier to classify pixels with the same spectral signature. In an unsupervised classification, algorithms such as the Iterative Self Organising Data Analysis Technique (ISODATA) and K-Means algorithm cluster pixels

into classes that are spectrally distinct. These classes then need to be labelled by an analyst with knowledge of the area and the landscape (Mather & Koch, 2011).

In this study, an unsupervised classification analysis of the AOI of the Landsat 8 image was undertaken in ERDAS using the ISODATA algorithm. In this method, a pixel to be classified is initially assigned to the nearest cluster of pixels, and cluster means and standard deviations are calculated. Thereafter, the number of clusters produced by the algorithm varies as clusters are merged and split iteratively. If the distance between 2 clusters is less than a specified threshold, then the 2 clusters are merged. If the variance between pixel values within a cluster exceeds a specified threshold, then the cluster is split into two. Pixels are iteratively re-assigned to new clusters, small clusters are eliminated and cluster statistics are recalculated, until the iterations cease when specified convergence criteria are met (Mather & Koch, 2011; Tso & Mather, 2009).

An initial 36 cluster analysis of the AOI image was subsequently reduced to 6 clusters, by manually grouping adjacent clusters as outlined by Mather & Koch (2011). Personal knowledge of the central Kalahari, together with aerial photographs and high resolution Google Earth images greatly facilitated the task of grouping and describing the clusters. The resultant 6 clusters correspond to 6 identifiable vegetation structure and cover classes in the ISODATA classification image, that were colour coded to distinguish between adjacent classes, as shown in Table 4.1.

The ISODATA classification output was verified against a 6 cluster K-Means classification, and was found to produce the same classification classes and areas. In the K-Means algorithm, individual pixels are also allocated to an initial cluster, based on the Euclidean distance from the pixel point to the nearest cluster centre. Clusters are not split and merged, as in the case of the ISODATA algorithm, but new cluster means and the distance between each pixel point and the cluster means are recalculated iteratively until specific convergence criteria are met (Mather & Koch, 2011).

A classification accuracy assessment was undertaken to verify that the classification was adequate as the basis of further analysis (Stehman & Czaplewski, 2003). The results of the classification accuracy assessment are presented in Section 4.2 together with the appropriate assessment metrics, including the Kappa coefficient and the users and producers accuracy (Ismail & Jusoff, 2008).

Attribute tables contain information about raster images and vector layers. For raster images that have been produced as the output of a classification analysis, the attribute table will typically contain the class variable and data pertaining to that class, such as the area of that

class in the image. For a vector layer, such as an animal location shape file, the attribute table may contain data pertaining to each location observation, such as date, geographic coordinates in Latitude and Longitude, temperature and other data variables (ESRI, 1998).

A key aspect of the research methodology was to overlay the Gemsbok location shape files on to the classified image; to extract the landscape patch class from the underlying classification image attribute table, and to append the correct classification class to each location observation in the location shape file attribute table. This was achieved using the Zonal Attributes functionality in ERDAS.

When overlaying a vector layer on to a raster image, care needs to be taken to ensure that the coordinate systems are compatible (DeMers, 2005). In addition, the effective 15m resolution of the classification image needs to be compatible with the minimum distance between points of the GPS coordinates in the location shape file attribute table (Goodchild, 2010). In order to improve the ability of the Zonal Attributes functionality to append a unique class to each of the locations in the shape file attribute table, the raster image resolution was resampled by a factor of 0.1 to produce an effective classification image resolution of 1,5m prior to the extraction of the zonal statistics. This process was done to ensure as many as possible one-to-one relationships between every GPS point and the underlying class. The image classification was done, as described previously, at the native 15m pan-sharpened image resolution.

The question of scale is of considerable importance to this study. The Landsat 8 image under analysis has 15m resolution, as a result of pan-sharpening by including band 8, the panchromatic band. The classification analysis can therefore produce patch classes that are also at 15m resolution. It is therefore possible to “miss” small patches that could provide shade or forage to a Gemsbok, and that are in all likelihood discernible to the animal, but are too small to map. This disparity in mapping resolution and Gemsbok perception resolution is a fundamental limitation to the class preference analysis.

3.4 Landscape patch class preference

The question of how to assess landscape patch class preference under the dual considerations of usage and availability has been the subject of study and debate in ecology literature (Beyer et al., 2010; Aarts, MacKenzie, McConnell, Fedak, & Matthiopoulos, 2008). In its simplest form, usage of a particular patch class (frequency of location in that class) can be seen as an initial measure of preference, but true selection of a preferred class is dependent on knowing not just the use of a patch class, but also the availability of that class

to the animal (Beyer et al., 2010). Accessibility to available patch classes in a home range is a further complication that is difficult to quantify, but is an important aspect of the consideration of availability (Aarts et al., 2008).

In this study, once the landscape patch class had been appended to each location observation for each Gemsbok, a frequency analysis of locations per class would determine the distribution of Gemsbok across each landscape patch class, thereby directly addressing research question 1.3.2.1.

For individual collared animals, a frequency analysis or histogram distribution plot would provide an indication of the apparent preference for particular landscape patches. However, without knowing what patch classes were available to the animal from which it could choose, the apparent preference could be misleading. It was therefore necessary to determine what landscape patch classes were available to the Gemsbok in each animal's home range.

Using the Geometry functionality in ERDAS, each individual animal's home range, as determined in Section 4.5 and shown in Table 4.4, was used to subset the research area classification image to produce a home range classification image that contains only those patch classes that were actually available to each individual animal. This subset image also has an attribute table that was used to obtain the area and percentage area of each patch class that was available for use in that individual animal's home range. A more meaningful analysis was then possible whereby apparent patch class preference could be assessed against the backdrop of the patch class availability.

In order to produce an analysis of the availability of patch classes for all the collared Gemsbok combined, it was necessary to sum the area of each patch class for each animal across all patches of the same class within each home range. This meant summing the areas of each class in each home range image attribute table, and then comparing the actual location frequency within a particular class for all the Gemsbok against the total area of the patch classes available to each of the Gemsbok to derive a measure of preference, in the form of a location usage frequency count per available hectare (Beyer et al., 2010). It was also necessary to test statistically whether the patch class usage was independent of the patch class availability, thereby addressing research question 1.3.2.2.

This approach is dependent on the assumption that MCP's are an acceptable means of determining home range estimates (Getz & Wilmers, 2004; Burgman & Fox, 2003), and that frequency of location in a particular patch class is a simplistic proxy for patch class preference (Beyer et al., 2010). More complex methods of assessing preference are available (Wells et al., 2014), but are beyond the scope of this research report.

A useful by-product of this analysis is that the physical area of each Gemsbok's home range can be determined from the convex hull shape files, and as a result, the mean home range area in hectares could be calculated. Although a small sample of only 8 animals, the mean home range area provided a useful estimate of Gemsbok home range size in the CKGR.

In summary, it is the intention of this study to examine Gemsbok landscape patch usage in the CKGR against the background of availability of heterogeneous landscape patches in individual animals' home ranges. In this regard, heterogeneous landscape patch usage is based on location frequency, whereas availability is based on the physical areas of each patch class.

3.5 Preference modelling

This study has over 40 000 observations of GPS recorded Gemsbok locations, together with the matching patch class from the classified image. Other variables recorded for each observation, include the ambient temperature and altitude, the date and time, from which the appropriate month and day-night indicator were extracted. These data formed the basis for patch class frequency analyses, patch class availability areas, and mean temperature analysis by day and night, by hour and by month.

In order to explore and model the role of temperature as a predictor of patch class preference, and thereby address research question 1.3.2.3, a different set of analyses was required and these are motivated as follows:

1. Patch class would be correlated with temperature and other variables to determine whether any other variables were more closely associated with patch class than temperature. Spearman's rho is the appropriate non-parametric correlation coefficient to determine the strength of relationship between Class and interval scale variables (Myers & Well, 2003).
2. Discriminant analysis would determine whether temperature on its own, or in combination with other variables, could separate the patch classes on one or more axes. Discriminant analysis is a multivariate statistical procedure designed to identify a linear combination of independent variables that together maximally separate defined groups, in this case, landscape patch classes (Hair, Black, Babin, & Anderson, 2006).
3. Under the assumption that patch class was more than just a categorical variable, and that it had pseudo ordinal scale properties by virtue of the implied vegetation gradient from Class 1 (most vegetation) to Class 6 (least vegetation), a linear regression would examine the degree to which temperature could predict patch class over the range of temperatures recorded per location. Linear regression will determine the contribution of

one or more independent variables (temperature) in predicting a dependent variable (class) of at least ordinal scale (Freedman, 2009).

4. In order to refine the regression, multinomial logistic regression would be used to determine whether temperature would influence the likelihood of moving from the pans (Class 6 as base) to other patch classes. Multinomial logistic regression predicts the log probability of an independent variable (temperature) influencing the multi-category dependent variable (class) (Hilbe, 2009).

Chapter 4 Results

The results of the analysis of the data collected are presented by landscape patch class. The first result relates to the classification of the Landsat 8 image and is followed by a classification accuracy assessment. Analyses of usage, availability and preference overall is followed by more detailed analysis of usage by day and by night, by hour and by month. Temperature data are then analysed and home range estimates for the Gemsbok are presented. Analyses of individual Gemsbok's usage of available patches and each Gemsbok's locations in its own home range are shown in Appendix C for completeness. Finally, the role of temperature in patch class selection is then explored in a series of statistical analyses to model Gemsbok patch class preference.

4.1 Classification Analysis

The ISODATA classification image in Figure 4.1 below clearly illustrates the heterogeneous nature of the patch landscape in the research area in the CKGR, and the 6 predominant classes of landscape patches utilised by Gemsbok, are shown in legend Table 4.1. This classified image readily identifies the major features of the research area, including Passarge Valley, Deception Valley, Letiahau and Tau Pan.

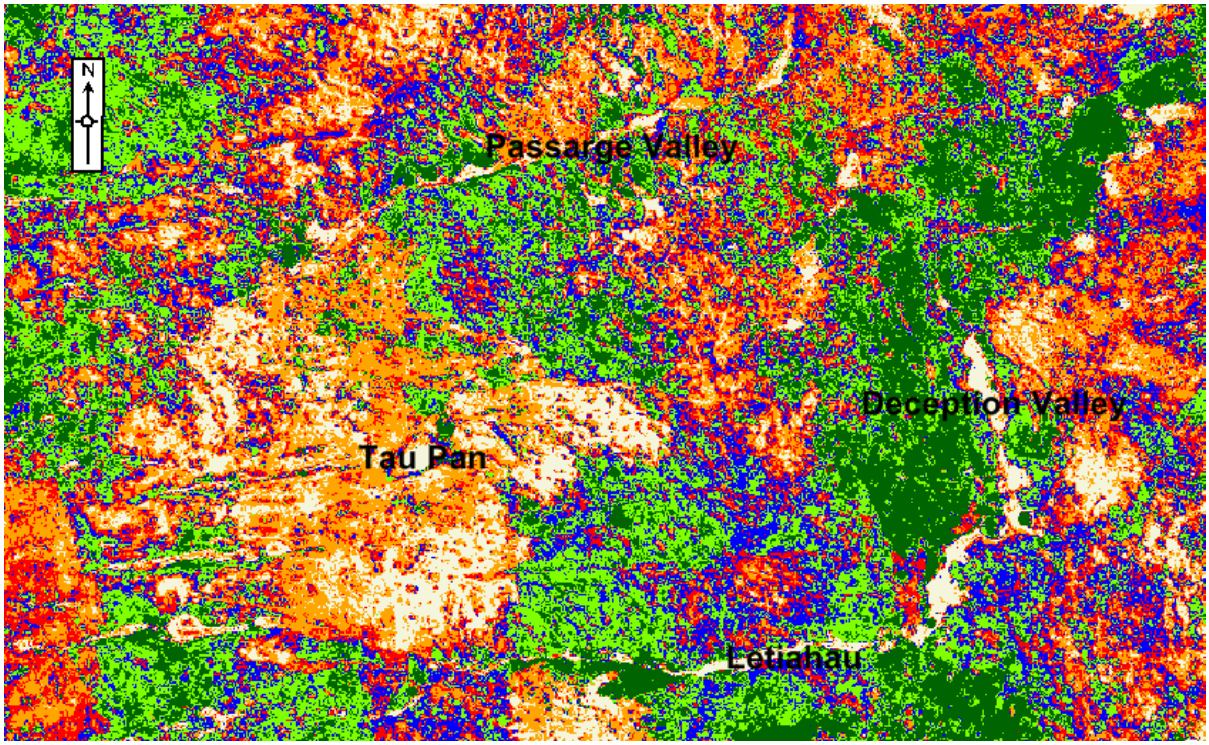

Figure 4.1 – The ISODATA classification image of the research area, illustrating the heterogeneity of the research area, and showing some of the key pans and valleys.

The classification map indicated that the western / south-western region of the research area had less vegetation cover and comprised more of patch classes 5 and 6, while the eastern / north-eastern region had more vegetation cover, comprising more of patch classes 1 and 2.

The size of the research area (855 593 hectares / 8 555 km^2), the area of each classification class, and the percentage area of each class, was calculated in ERDAS and added to the attribute table of the classification image. The legend of the classified image and the respective class areas are set out in Table 4.1 below:

Table 4.1 – Classification legend and area table

Class	Legend	Description	Area (hectares)
1	Class 1	Tall shrubs, with more woody cover, and some trees in sparse woodland	117865
2	Class 2	Taller shrubland with woody cover	183054
3	Class 3	Longer grass with medium shrubs and some woody cover	168102
4	Class 4	Shorter grass with small to medium shrubs	159706
5	Class 5	Sparse cover, Kalahari sand with some small shrubs	146154
6	Class 6	Pan, bare clay soil with some sparse cover	80712

The relative size and percentage area of each patch class in the research area is shown graphically in Figure 4.2:

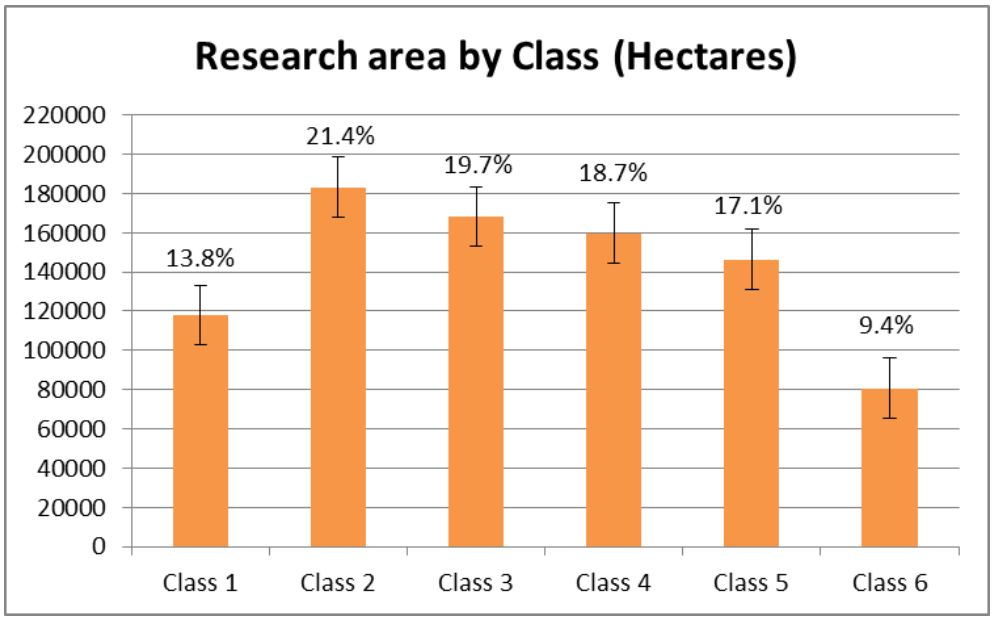

Figure 4.2 - Research area size in hectares for each class, with percentage size of each class and Std. error bars

The degree of vegetation cover is the major differentiator of patch classes in this study, and it is appropriate to define the vegetation cover per class in more detail. Essentially, the vegetation gradient can be described in 3 broad categories:

- Woody cover with trees and tall shrubs
- Grasslands with medium shrubs and grasses
- Pans and sparsely covered areas with some small shrubs

The classification analysis enabled each of these categories to be subdivided into two distinct classes, resulting in the 6 classes used in this study. Each class is described in Table 4.2 below in terms of the dominant species of vegetation cover, and the vegetation gradient is illustrated with photographs taken by the author in August 2013. The land cover classification and class descriptions are based on the Land Cover Classification System (LCCS) (Di Gregorio & Jansen, 2005), recent work in the central Kalahari by Mishra (2014) and studies by Fairbanks et al. (2000) and Thompson (1996).

Table 4.2 – Vegetation class descriptions

Class 1 Tall shrubs, with more woody cover, and some trees in sparse woodland	**Trees:** *Acacia erioloba,* *Acacia haematoxylon* **Shrubs:** Mostly absent **Grasses:** *Schmidtia kalahariensis*	
Class 2 Taller shrubland, with woody cover	**Trees:** *Acacia luederitzii* **Shrubs:** *Rhigozum trichotomum* **Grasses:** Mixed	

Class 3 Longer grasses, medium shrubs, with some woody cover	**Trees:** *Boscia albitrunca,* *Acacia mellifera* **Shrubs:** *Grewia flava* **Grasses:** *Eragrostis pallens*	
Class 4 Shorter grasses, small to medium shrubs	**Trees:** *Terminalia sericea* **Shrubs:** *Rhigozum trichotomum* **Grasses:** *Aristida meridionalis,* *Stipagrostis amabilis*	
Class 5 Sparse cover, Kalahari sand with some small shrubs (Photo Source: Niti Mishra, May 2010)	**Trees:** Few trees **Shrubs:** Few shrubs **Grasses:** Some halophytic grasses (Genus *Sporobolus*)	
Class 6 Pans, bare clay soil, sparse cover	**Trees:** Occasional tree islands **Shrubs:** No shrubs **Grasses:** Essentially no grass	

4.1.1 Classification accuracy assessment

The assessment of classification accuracy is a necessary part of classification analysis in order to determine the overall accuracy of the classification and some key supporting statistics (Mustapha, Lim, & MatJafri, 2012). Stehman (1996) recommends that between 25 and 75 sampling units be chosen for classification assessment. The sampling units can

range from individual pixels to 3x3 pixel blocks, to GPS points, to polygons on a map (Stehman & Czaplewski, 1998). In this study, 45 GPS points were selected, randomly distributed across all 6 patch classes, for classification accuracy assessment.

An agreement table (Table B1, Appendix B) was produced listing the classified Class of each selected point as determined by the classification analysis, together with the actual Class as determined by inspection of GPS ground referenced photographs (Appendix B) or by high resolution images on Google Earth (Luedeling & Buerkert, 2008). From the agreement table, a classification error matrix was produced in Table 4.3 below.

The error or confusion matrix is the generally accepted way to assess the accuracy of a classification, and is typically created so that columns represent referenced data, from which the producer accuracy is calculated, while the rows represent classified data, from which the user accuracy is determined (van der Wiele, Khorram, & Yuan, 2012; Stehman & Czaplewski, 1998). The user accuracy represents errors of commission, analogous to a Type 1 error, when a pixel that was allocated to a particular class, should in fact have been allocated to a different class. The producer accuracy refers to the proportion of ground truth points that were correctly classified, and indicates errors of omission, analogous to a Type 2 error, when GPS points are allocated to the incorrect class. The overall accuracy is simply the percentage of pixels correctly classified (Mustapha et al., 2012).

Table 4.3 – Classification error matrix

Classification data		Ground referenced data						Total	Users Accuracy
		1	2	3	4	5	6		
Patch Class	Class 1	7	1	0	1	0	0	9	78%
	Class 2	0	2	2	1	0	0	5	40%
	Class 3	0	1	4	1	0	0	6	67%
	Class 4	0	0	1	6	0	0	7	86%
	Class 5	0	1	2	2	5	0	10	50%
	Class 6	0	0	1	0	0	7	8	88%
Total		7	5	10	11	5	7	45	
Producers Accuracy		100%	40%	40%	55%	100%	100%		

Overall Classification Accuracy 69%

A number of statistics can be calculated from the error matrix, including the Kappa coefficient of agreement, and the overall classification accuracy. The Kappa statistic is widely accepted as the measure of agreement between classification data and ground reference data for classification accuracy assessments (Foody, 2009; Stehman, 1996). The strong point of Kappa is that it takes all the elements of the error matrix into account, not just

the primary diagonal, as is the case with the overall classification accuracy (Mustapha et al., 2012). Kappa statistics in the range 0.4 to 0.7 are considered good for classification analysis (Ismail & Jusoff, 2008).

Based on the calculated Kappa statistic of 0.628 (n=45; T=9.658; p<0.05), and the overall classification accuracy of 69%, the classification analysis in this study was deemed acceptable for further analysis of Gemsbok usage of heterogeneous landscape patch classes in the research area. Confirmation of how well the classification was able to detect and identify pockets of vegetation is illustrated by Figures B4 and B4.1 in Appendix B, showing an aerial photograph of a tree island on a pan, and the corresponding area of the classified image, in which the trees are clearly detected and classified correctly.

4.2 Patch class preference analysis

4.2.1 Patch class usage and availability

Attribute tables for each Gemsbok's location observations, with the patch class, were analysed to prepare a frequency distribution of the observed location classes. The patch class usage by all Gemsbok is illustrated in Figure 4.3 below. The chart represents, in percentage terms, the number of times the position of the animal, as recorded by satellite GPS, was located in a particular landscape patch class. Overall, while 5.7% of the locations could not be allocated to a patch class by the ERDAS Zonal Attributes function, 94.3% of the location observations were uniquely related to a landscape patch class, which was deemed acceptable for this research project.

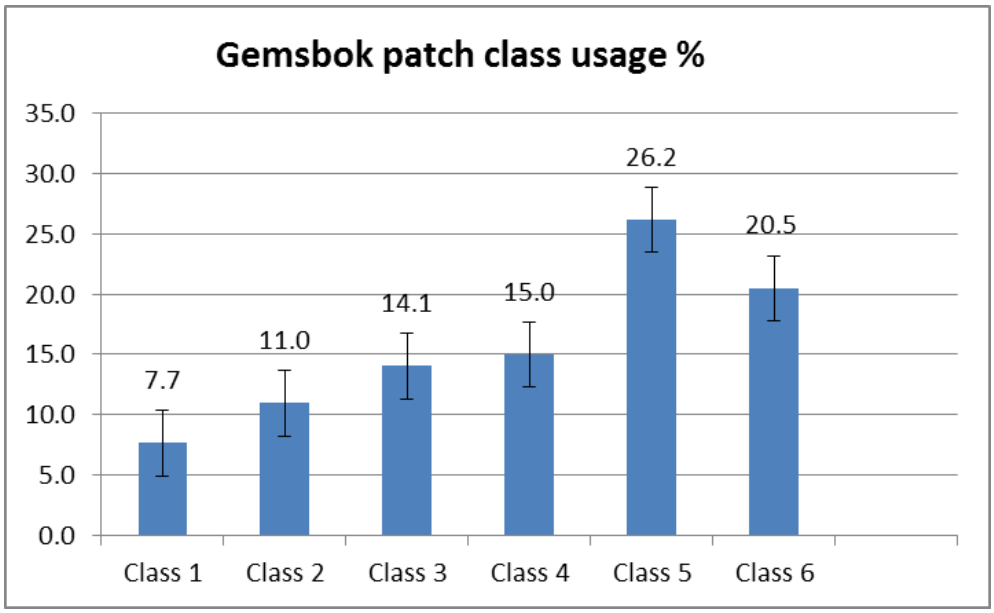

Figure 4.3 - Gemsbok patch class usage percentage, with Std. error bars

In order to test whether the observed class frequency distribution indicated a preference for those patch classes with more vegetation structure and cover for shade, and more forage for grazing (Classes 1-3), as opposed to those open patch classes with less structure and cover for shade and less forage for grazing (Classes 4-6), a non-parametric one-sample Binomial test was carried out to test the null hypothesis that there is no difference between the proportions of these two dichotomous groups. The null hypothesis was rejected ($n=40829$; $p<0.05$), indicating the preference for the open patch classes illustrated in Figure 4.3. Hypothesis H_1, associated with research question 1.3.2.1, was therefore disproved.

The available areas per class were calculated from the attribute tables of each animal's home range, when subset from the research area classification image. The results are shown in Table 4.4 below:

Table 4.4 – Available patch class areas in each Gemsbok's home range

			Available Areas and Home Ranges (Hectares)				
Gemsbok ID	**Class 1**	**Class 2**	**Class 3**	**Class 4**	**Class 5**	**Class 6**	**Home Range**
SAT559	5495	11369	10198	7950	12598	11067	**58676**
	9.4%	19.4%	17.4%	13.5%	21.5%	18.9%	100.0%
SAT560	4503	3250	2031	1617	2030	1836	**15267**
	29.5%	21.3%	13.3%	10.6%	13.3%	12.0%	100.0%
SAT561	8473	5471	5475	5960	6074	3203	**34656**
	24.4%	15.8%	15.8%	17.2%	17.5%	9.2%	100.0%
SAT562	4822	10742	9948	16213	30354	16539	**88616**
	5.4%	12.1%	11.2%	18.3%	34.3%	18.7%	100.0%
SAT563	2660	6021	10787	8419	6603	4280	**38770**
	6.9%	15.5%	27.8%	21.7%	17.0%	11.0%	100.0%
SAT564	21871	19172	20643	24266	22103	7408	**115463**
	18.9%	16.6%	17.9%	21.0%	19.1%	6.4%	100.0%
SAT565	8487	19019	14784	11411	17739	12759	**84198**
	10.1%	22.6%	17.6%	13.6%	21.1%	15.2%	100.0%
SAT566	3018	6267	10784	12697	11124	4234	**48125**
	6.3%	13.0%	22.4%	26.4%	23.1%	8.8%	100.0%
Total	59330	81312	84652	88533	108628	61326	**483781**
Class %	**12.3%**	**16.8%**	**17.5%**	**18.3%**	**22.5%**	**12.7%**	100.0%

Gemsbok home range patch class usage and patch class availability are illustrated in Table 4.5 and Figure 4.4 below:

Table 4.5 – Home range Usage and Availability by patch class

	Class 1	Class 2	Class 3	Class 4	Class 5	Class 6
Usage %	7.7	11.0	14.1	15.0	26.2	20.5
Available %	12.3	16.8	17.5	18.3	22.5	12.7

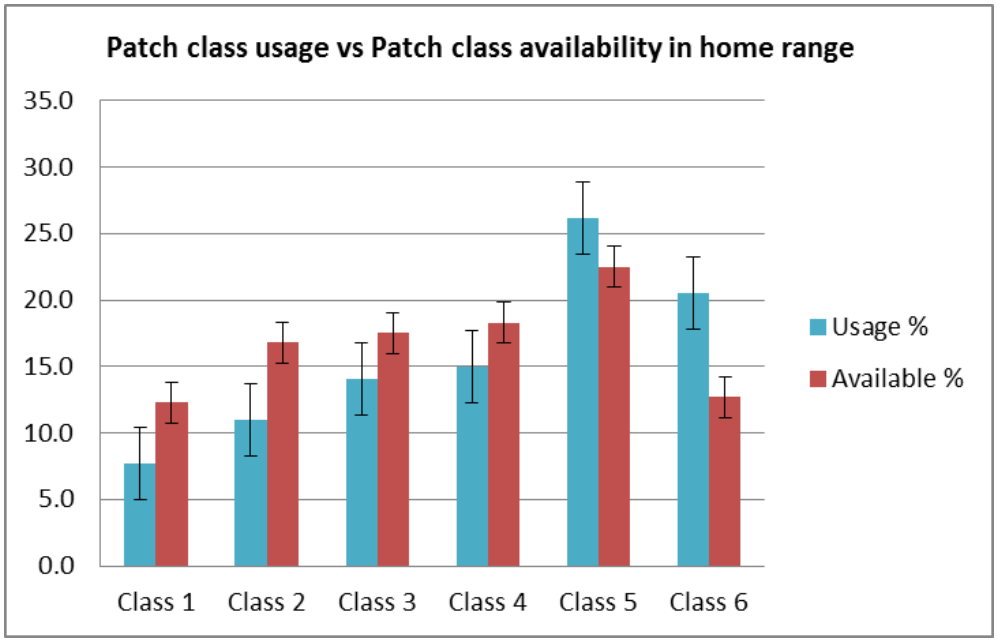

Figure 4.4 – Home range patch class usage and patch class availability, with Std. error bars

From Figure 4.4 above, it is clear that the collared Gemsbok made comparatively less use of patch classes containing more vegetation, structure and cover (Class 1 to Class 4) than of patch classes containing less vegetation (Class 5 and Class 6). The Gemsbok were therefore most frequently located in open patch classes, ranging from bare Kalahari sand to patches with sparse cover and some shrubs. These conditions typically exist on the pans and the areas surrounding the pans (Mishra, 2014).

In order to test whether the patch class usage was in proportion to the patch class availability as summarised in Table 4.5 above, a non-parametric one-sample Chi Squared test was carried out to test the null hypotheses that the distribution of Class occurs with probabilities of the availability of that Class (as calculated in Table 4.4 above). The null hypothesis was rejected ($n=40829$; $\chi^2=4620.1$; $df=5$; $p<0.05$), indicating that the class frequency distribution was not in proportion to the available area of each class, thereby suggesting selective class usage. Selective class usage occurs when actual class usage is significantly different to the availability of that class (Beyer et al., 2010). There is therefore evidence of selective class usage (Class 5 and Class 6 preferred). Hypothesis H_2, associated with research question 1.3.2.2, is therefore accepted.

As discussed in Section 3.4, there is no single definition of what constitutes preference in terms of landscape patch selection (Beyer et al., 2010; Uuemaa, Antrop, & Marja, 2009). The chosen preference metric is location frequency count per available hectare (Beyer et al., 2010). The resultant class preference metrics are illustrated in Figure 4.5 below, and confirm that Class 6 (pans and valleys) is the preferred landscape patch class. Further analysis was undertaken to explore the reasons for this preference.

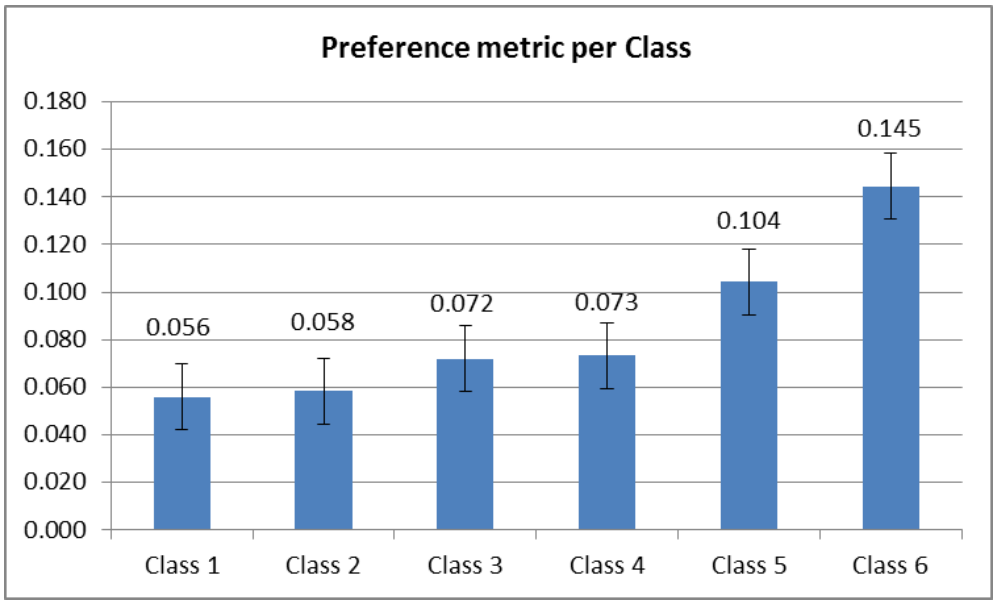

Figure 4.5 - Preference metrics per landscape patch class, with Std. error bars.
The metric is the location frequency per available hectare of that class.

4.2.2 Day-Night preference analysis

One of the anticipated adaptations for Gemsbok under conditions of temperature induced stress is for foraging patterns to change from day to night, and for nocturnal foraging to increase (Fuller et al., 2010; Knight, 1991). The analysis of class preference for the Gemsbok in this study by day and by night does not support this view. The commonly held belief that Gemsbok will seek shade during the heat of the day, and forage in grassland patches at night (Knight, 1991) is not supported by the analysis of class preference by day and by night in Table 4.6 and Figure 4.6 below.

Table 4.6 – Day and night patch class usage vs available patches

	Class 1	Class 2	Class 3	Class 4	Class 5	Class 6
Day Usage%	6.4	10.4	14.7	17.3	28	18.8
Night Usage %	9.0	11.6	13.4	12.6	24.3	22.2
Available %	12.3	16.8	17.5	18.3	22.5	12.7

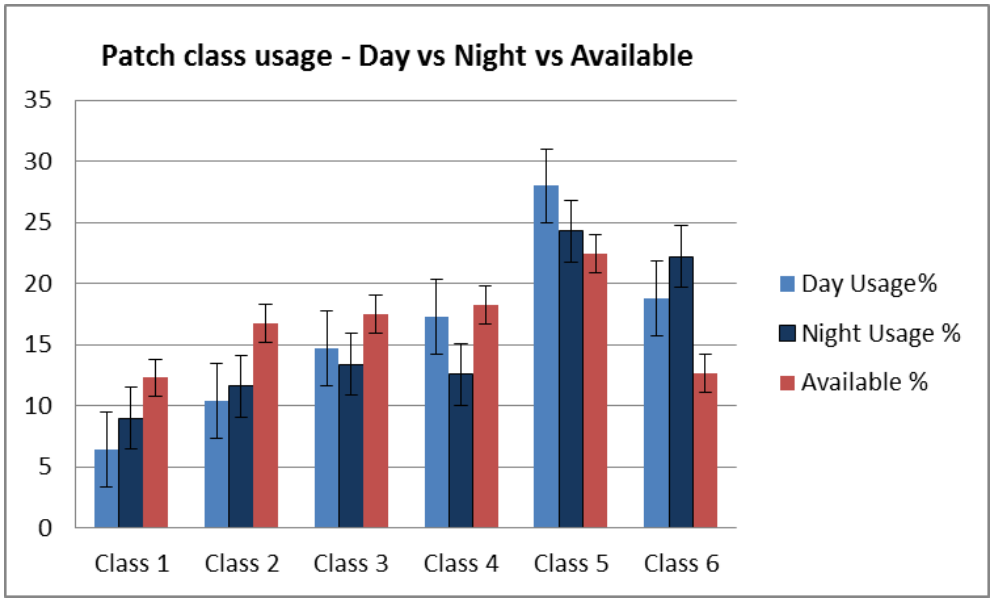

Figure 4.6 - Comparison of patch class usage, by Day and Night, showing availability of each patch class, with Std. error bars

While there are significant differences between patch class preference from day to night (n=40829; χ^2=396.1; df=5; p<0.05), the usage of patches with more structure and cover (Class 1 and Class 2) remains well below what was available. Furthermore, Class 1 and Class 2 are used less during the day than at night, contrary to what was expected if Gemsbok sought shade during the day. Usage of patch classes by day was significantly different to the availability of that patch class (n=20817; χ^2=2244.6; df=5; p<0.05) and also by night (n=20012; χ^2=2778.7; df=5; p<0.05).

The grasslands in the study area are represented by Class 3 (longer grass) and Class 4 (shorter grass). While Gemsbok prefer to forage on grass (Knight, 1991), usage of these patch classes was greater during the day than at night. These results therefore do not support the nocturnal foraging behaviour suggested by Knight (1991), and instead suggest that when Gemsbok need to forage on grass, they prefer to do so during the day when the predation risk is lower, in spite of the higher daytime temperature.

Patch classes with the least vegetation cover, (Class 5 and Class 6), remain the most highly used, by day and by night, with Class 6 (pans and valleys) being particularly frequently used by Gemsbok at night, relative to the availability of this patch class. Possible reasons for this patch class preference at night may be related to protection from predators.

Overall, the more vegetated classes (Class 1 to Class 4) are less preferred relative to the availability of these classes, both by day and by night. Similarly, the least vegetated classes (Class 5 and Class 6) are more preferred relative to their availability, both by day and by night, as illustrated in Table 4.6 and Figure 4.6 above. This result suggests that patch preference for Gemsbok is not based on shade and shelter during the day, and nocturnal foraging during the night. Rather, it would appear that patch preference is based more on defensive behaviour towards predators, with Gemsbok preferring open areas with less vegetation, where predators can be seen, and seeking cover in the more vegetated areas at night as a strategy to avoid nocturnal predators. This interpretation is in line with the findings of Valeix et al. (2009), who established that African herbivores prefer open spaces as a defensive strategy against predators, particularly lion.

To further explore the use of the available landscape patch classes, an hourly analysis of the frequency with which Gemsbok were located in particular patch classes during the day and night was undertaken, and is illustrated in Figure 4.6.1 below. The hourly use of this heterogeneous patch landscape is dominated by Class 5 (sparse cover, Kalahari sand with some small shrubs). In her recent PhD Thesis on ungulate movement patterns in the Kruger National Park (KNP), Goodall (2014) identified key time periods for specific activities of the Sable antelope (*Hippotragus niger*). Using these times as a reference to likely periods of Gemsbok activity, the use of Class 6 (pans) from 18h00 to 05h00 corresponds with the travel (18h00 to 20h00) and rest (20h00 to 05h00) periods identified for Sable (Goodall, 2014).

During the day from 07h00 and 17h00, Gemsbok were frequently located in patch classes suitable for foraging (Classes 3, 4 and 5), straddling the morning and evening foraging periods of Sable from 07h00 to 09h00, and again from 17h00 to 19h00 (Goodall, 2014). This extended foraging period for Gemsbok includes the morning movement period identified for Sable (Goodall, 2014), and suggests that Gemsbok need more time to forage wider in the arid environment in the Kalahari, with less nutritious forage than is available to Sable in the KNP. The small differences in timing of particular activities by Gemsbok in the Kalahari, when compared to Sable in the KNP, is to be expected given the reduced forage availability and increased thermal stress experienced by Gemsbok in the Kalahari. The timing of these activities by Gemsbok may be further adapted during periods of extreme heat.

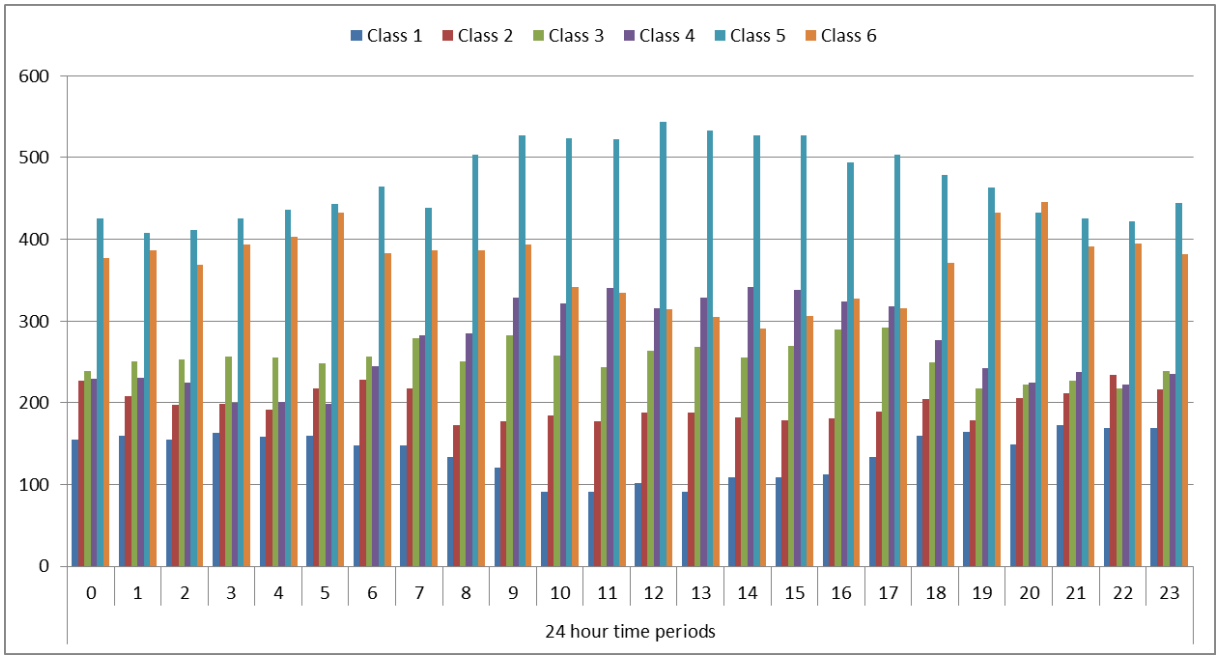

Figure 4.6.1 – Patch class usage by time of day, showing the frequency of Gemsbok use of heterogeneous patches from midnight to midnight. The use of Class 5 (sparse cover, Kalahari sand with some small shrubs) dominates the usage profile throughout the 24 hours.

The comparison between two pairs of patch classes is worth noting. Firstly, the comparison between Class 1 (shade) and Class 6 (pans) is illustrated in Figure 4.6.2 below.

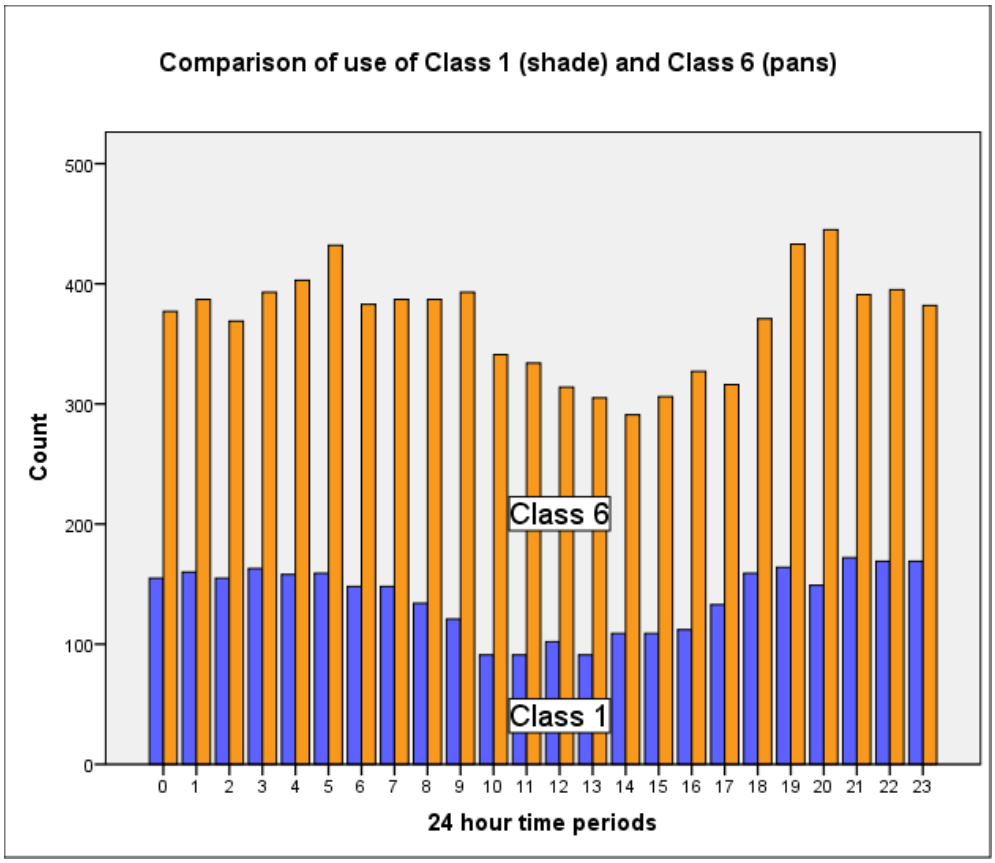

Figure 4.6.2 – Comparison of Gemsbok use of Class 1 (shade) and Class 6 (pans) over 24 hour periods, showing peak usage during night hours.

While Class 6 is used more frequently than Class 1 throughout the 24 hour time period, Gemsbok use of both these classes follows broadly the same profile. Both are used less during the day than at night, understandably so in the case of Class 6, but Gemsbok use of the most vegetated patch class (Class 1) is enlightening, in that this patch class is used least between 10h00 to 14h00 during the heat of the day, when it would have been expected that Gemsbok would move to shade (Class 1). Figure 4.6.2 clearly shows that this is not the case, and that Class 1 is instead used most between 21h00 and 05h00 during the period of highest predation risk at night. This analysis suggests that Gemsbok in this study did not seek shade during the day to meet thermoregulation needs, but used vegetation structure and cover as shelter to reduce predation risk at night.

The second noteworthy comparison is between Class 4 (short grass) and Class 5 (sparse cover), both of which provide foraging opportunities for Gemsbok (Lehmann et al., 2013). As illustrated in Figure 4.6.3 below, the use of both these patch classes peak during the daylight hours and reduces considerably at night, indicating that while some nocturnal foraging does take place, most foraging occurs during daylight hours for these collared Gemsbok. This analysis does not support the view of Knight (1991) that Gemsbok engage in nocturnal foraging as an adaptation in response to thermal stress.

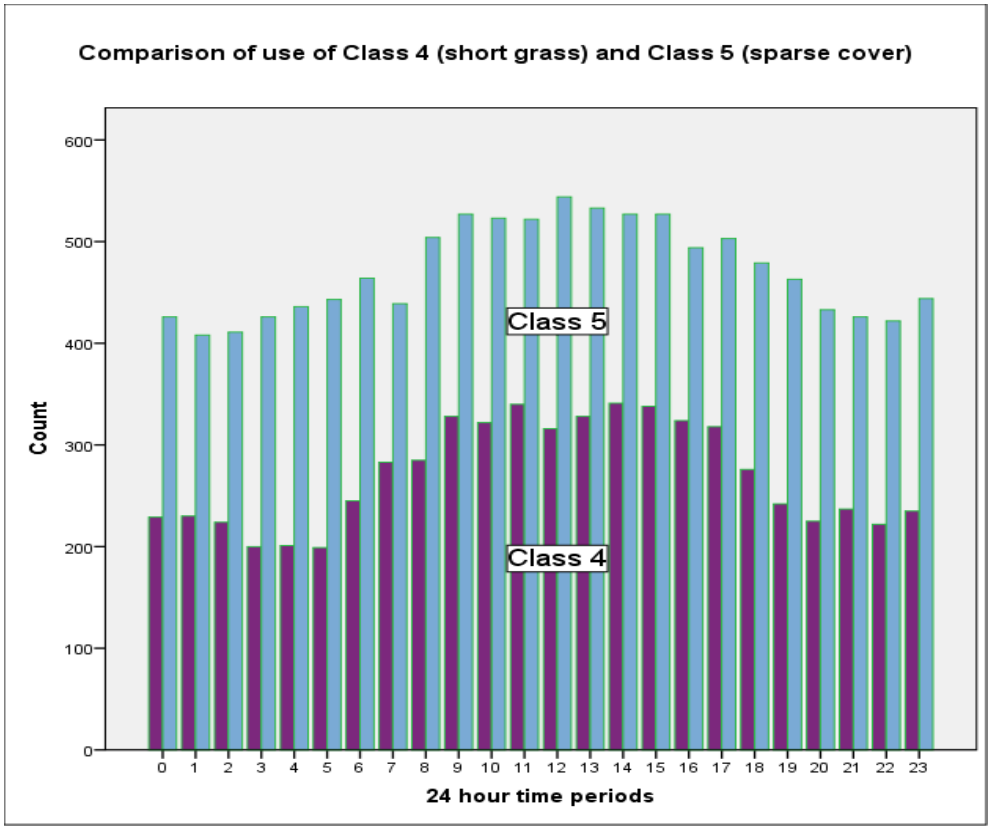

Figure 4.6.3 – Comparison of Gemsbok use of Class 4 (short grass grazing) and Class 5 (sparse cover) over 24 hour periods, showing peak usage during daytime hours, with reduced nocturnal use.

Applying the time periods for Sable activities (Goodall, 2014) to predict likely Gemsbok activities in the same time periods, the resultant likely Gemsbok class usage profiles for particular activities are illustrated in Figure 4.6.4 below. The usage profiles for predicted foraging and moving activities are essentially identical to the overall class usage profiles illustrated in Figures 4.3 and 4.4, while the predicted resting activity takes place mainly in Class 5 and Class 6.

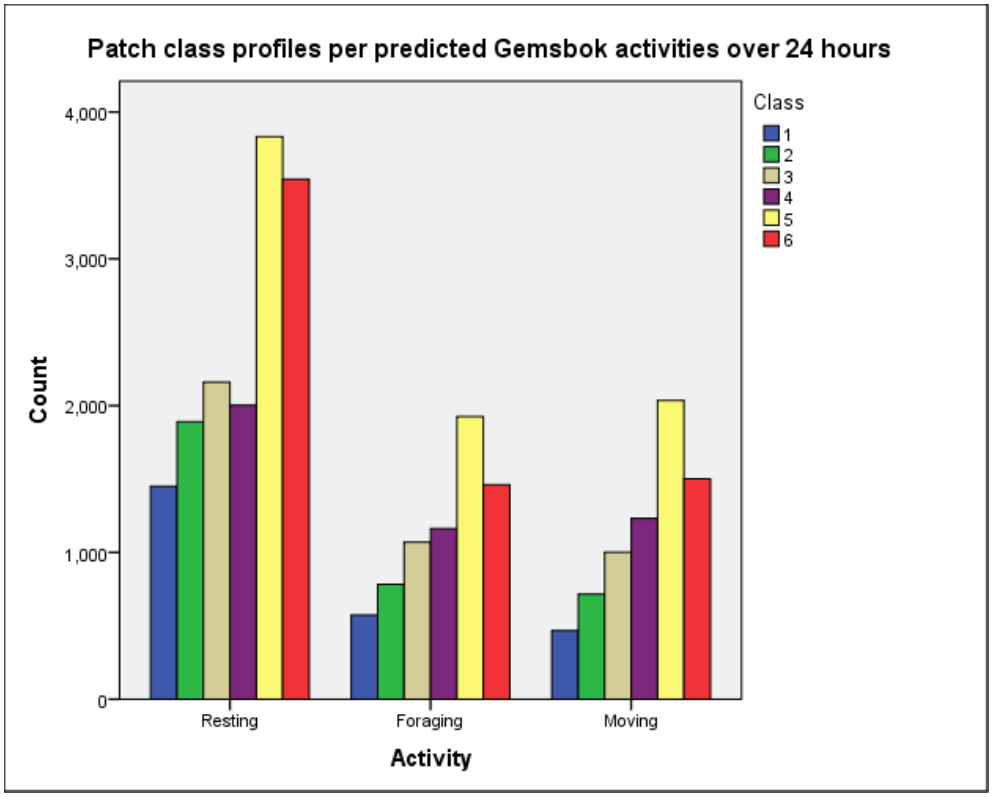

Figure 4.6.4 – Predicted Gemsbok activity profiles based on activity periods for similar sized Sable ungulates in the KNP (Goodall, 2014)

Ruckstuhl & Neuhaus (2009) indicate that temperature and available vegetation are both significant drivers of Gemsbok activity. In the following section, the focus will now shift to an analysis of the role of temperature in patch class selection.

4.3 Patch class temperature analysis

The aim of the following detailed analysis of the collar collected temperature data is to explore the role of ambient temperature in determining the use of heterogeneous landscape patches by Gemsbok, thereby addressing research question 1.3.2.3. The overall mean temperature by class is illustrated in Figure 4.7 below.

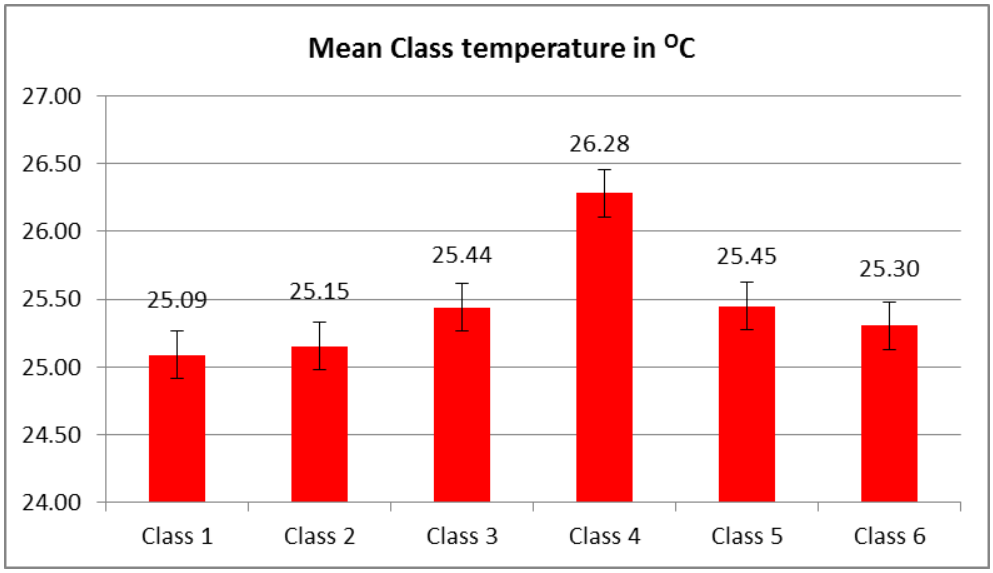

Figure 4.7 - Mean temperature in °C per patch class, with Std. error bars

From Figure 4.7 above, Class 4 (shorter grasses, small to medium shrubs) had the highest mean temperature (26.28°C; n=6488; std. dev.=8.42) and Class 1 (open shrubland, more woody cover, sparse woodland) had the lowest mean temperature (25.09°C; n=3321; std. dev.=7.97). An analysis of variance (ANOVA) showed that there was a significant difference in temperature between patch classes (n=40829; F=16.364; df=5; $p<0.05$). A post hoc Dunnett's T3 test showed that the only significant difference lay between Class 4 (shorter grasses, small to medium shrubs) and all other patch classes (n=40829; min. diff.=0.83°C; std. error=0.13; $p<0.05$). The remaining patch classes were insignificantly different in terms of temperature. This may be interpreted to suggest that Gemsbok are able to compensate for temperature in all patch classes except Class 4, which with its short grass and only small to medium shrubs, does not offer sufficient vegetation structure and cover to provide shade during the day, while noctural foraging would attract a higher predation risk. Class 6 (pans) offers no structure and cover, but temperature may be accomodated by using this open patch class during the cooler periods of early morning and late afternoon (see peak usage of Class 6 at 05h00 and 19h00 and 20h00 in Figure 4.6.2 above).

If the Gemsbok in this study were under thermal stress, then the patch class with the highest mean temperature (Class 4) could be expected to be the patch class with the lowest usage. This supposition is not borne out by the analysis. From Figure 4.3 it is clear that Class 1 to Class 3 all have lower overall usage that Class 4, while Figure 4.6 confirms that these classes, all with lower mean temperatures than Class 4, do not have higher usage than Class 4 by day, when temperature is highest. This analysis did not provide support for the research hypothesis that temperature is a key determinant of landscape patch selection.

In order to explore further the role of temperature in determining landscape patch class preference, detailed analysis of diurnal and seasonal temperature was undertaken.

4.3.1 Diurnal temperature analysis

The mean daytime temperature for all patch classes was 29.5°C (n=20817, std. dev.=7.8). The mean night time temperature was 21.3°C (n=20012, std. dev.=6.2). The difference in mean temperature from day to night of 8.2°C is significant (t=117.49; df=40827; p<0.05). The mean temperatures per patch class, by day and by night, are shown in Table 4.7 below, and illustrated in Figure 4.8.

The difference in temperature between patch classes during the day was small, providing little incentive for Gemsbok to select an alternative patch class on temperature grounds. At night, when thermal stress was reduced, the small differences in night-time temperature again did not warrant a move from one patch class to another.

A possible exception is Class 6 (pans and valleys) where Gemsbok located in this class recorded marginally the coolest mean temperature by day, and marginally the highest mean temperature at night, as indicated in Table 4.7. This may contribute to the comparatively high usage of patch Class 6, relative to the availability of this class, and the resultant high preference metric for Class 6, illustrated in Figure 4.5.

Table 4.7 – Mean class temperature in °C, by Day and by Night

	Class 1	Class 2	Class 3	Class 4	Class 5	Class 6
Day	29.37	29.34	29.71	30.04	29.57	28.95
Night	22.01	21.35	20.68	21.08	20.62	22.19
Diff.	7.36	7.99	9.03	8.96	8.95	6.77

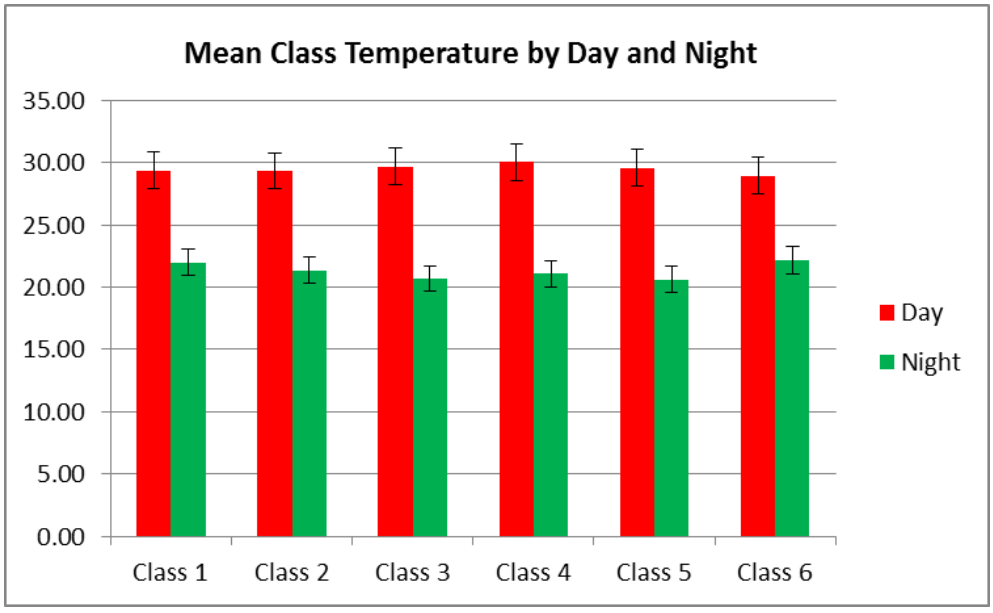

Figure 4.8 - Mean class temperature, by Day and by Night, with Std. error bars

4.3.2 Monthly temperature analysis

The mean monthly temperatures, by day and by night, are recorded in Table 4.8 below, together with the mean daily difference in temperature for each month of this study. Figure 4.9 illustrates the difference between day and night time temperatures by month. The mean temperatures are near constant from November 2012 through to March 2013. From April 2013 to July 2013, the mean temperatures decrease, while the difference in temperature from day to night increases. These temperature data are consistent with established seasonal temperature data for the central Kalahari (Tyson & Crimp, 1998).

Table 4.8 – Mean monthly temperature in °C, by Day and by Night

Month	November	December	January	February	March	April	May	June	July
Day	32.48	31.91	31.94	33.28	31.87	28.21	25.43	24.01	23.78
Night	24.68	24.43	24.68	25.73	24.83	19.92	15.10	13.57	13.44
Diff.	7.80	7.48	7.26	7.55	7.03	8.29	10.34	10.45	10.33

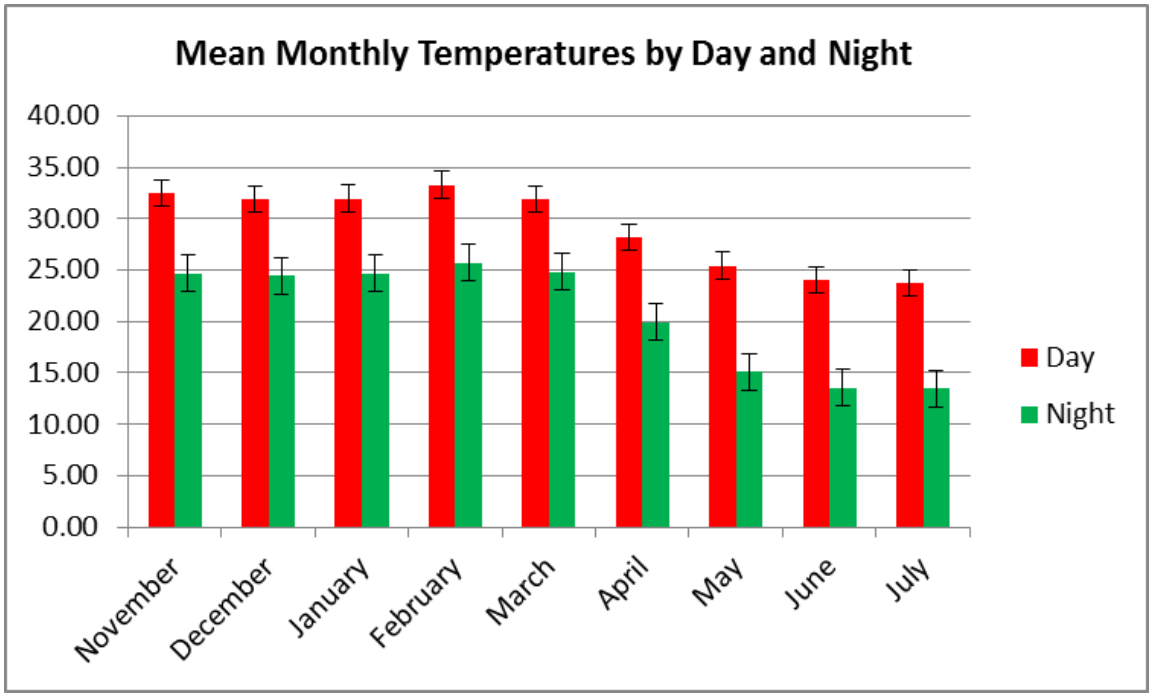

Figure 4.9 - Mean monthly temperature in °C, by Day and by Night, with Std. error bars

4.3.3 Temperature trend in the central Kalahari

The monthly ambient temperature data obtained from this Gemsbok study in 2012/2013 are shown in Table 4.8 above, and indicate a summer (December) mean daily temperature range of 24.4°C to 31.9°C, and a winter (June) mean daily temperature range of 13.5°C to 24.0°C. In December 2012, the temperature ranged from 16.3°C to 47.1°C (n=5566; mean=28.17; std. dev.=6.41), while in June 2013, the temperature ranged from a minimum of 1.1°C to a maximum of 38.7°C (n=4456; mean=18.97; std. dev.=8.48).

Figure 4.10 below illustrates the rise in summer temperatures derived from the literature review and the collar temperature record from this current Gemsbok research study. This analysis and the higher 2013 minimum and maximum summer temperatures confirms the predictions of rising temperature in the central Kalahari (New et al., 2006).

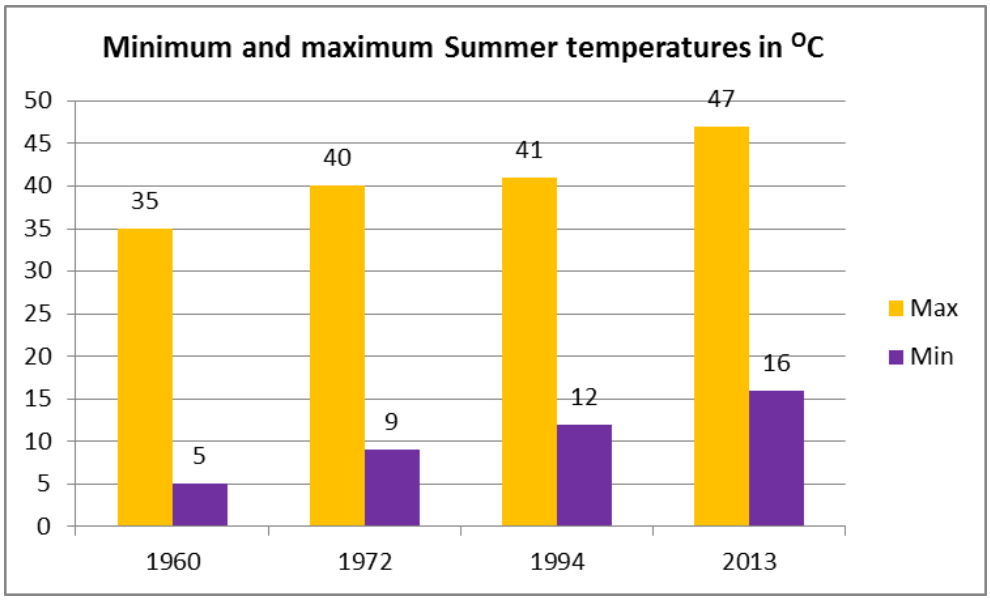

Figure 4.10 - Illustration of the trend in minimum and maximum summer temperatures in the Central Kalahari in °C, as reported in the literature from 1960 to 1994, and the current study

4.3.4 Monthly preference analysis

The analysis of Gemsbok preference for particular landscape patch classes has been undertaken overall in Section 4.2.1, and by day and night in Section 4.2.2. Patch class temperatures have been analysed by day and night, and by month in Sections 4.3.1 and 4.3.2 above. Significant differences in patch class preference have been found, but the reasons for the observed preference have not been fully explained by the analyses thus far. Accordingly, the Gemsbok location data were also analysed by month, in order to explore the monthly and seasonal role in patch class preference. The resultant monthly patch class frequencies are illustrated in Figure 4.11 below.

The high usage of Class 6 (pans and valleys) in December, January and February requires explanation. These months coincide with the peak summer rainfall in the central Kalahari (Tyson & Crimp, 1998). During this time, the pans are transformed from dry, bare clay soil with minimal ground cover, to areas covered in short grasses and forbs, as depicted in the photograph of Tau Pan after summer rains in Figure 4.12 below. This transformation during the peak summer rainfall period provides nutritious foraging for Gemsbok while located on

the pan (Lehmann et al., 2013), where there is also relative security from predators. The water retention characteristics of the clay soil and the high mineral content, only add to the attractiveness of the pans as a preferred location for Gemsbok in summer (Mishra, 2014).

As the summer rains diminish in March and April, and then cease in May, June and July (Tyson & Crimp, 1998), available forage on the pans reduces, and Gemsbok are required to forage off-pan. The vegetation gradient around the pans is such that the closest available forage, and the next available patch class, is Class 5 (sparse cover, Kalahari sand with some small shrubs) (Mishra, 2014). This vegetation is suitable for Gemsbok in dry periods, and allows them to exhibit the dietary plasticity reported by Lehmann et al. (2013), consuming a variety of forage available in Class 5. Temperature related stress reduces in autumn and winter as mean temperatures decrease, and Class 5 patches are typically close to the relative security of the pans. As a result, from March to July, Class 5 was the preferred landscape patch class for use by the Gemsbok in this study.

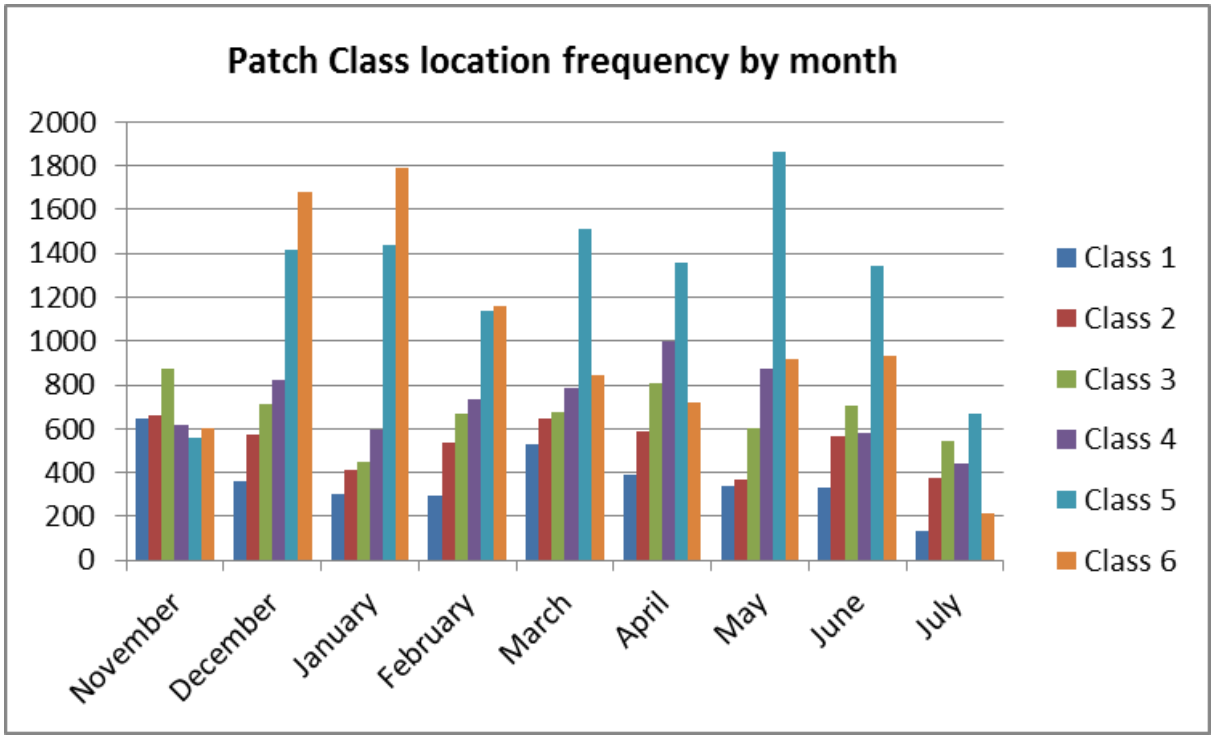

Figure 4.11 - Frequency with which Gemsbok were located in each class, by month, during the 9 months of this study



Figure 4.12 - Tau Pan in summer, showing grass and forbs for forage, and trees for shade by day and shelter at night.
Source: Botswana Wildlife Photography, January 2007

The role of temperature and other available variables in Gemsbok patch class preference will be modelled in detail using multivariate statistical analysis in Section 4.5.

4.4 Home range size estimation

The home ranges for the collared Gemsbok are shown in Figure 4.13 below. Three Gemsbok were released and tracked in the SW region of the research area (SAT559, SAT562, SAT565), while the remaining 5 animals were released and tracked in the E-NE region. Detailed analysis of the usage and availability of each Gemsbok's home range are shown in Appendix C.

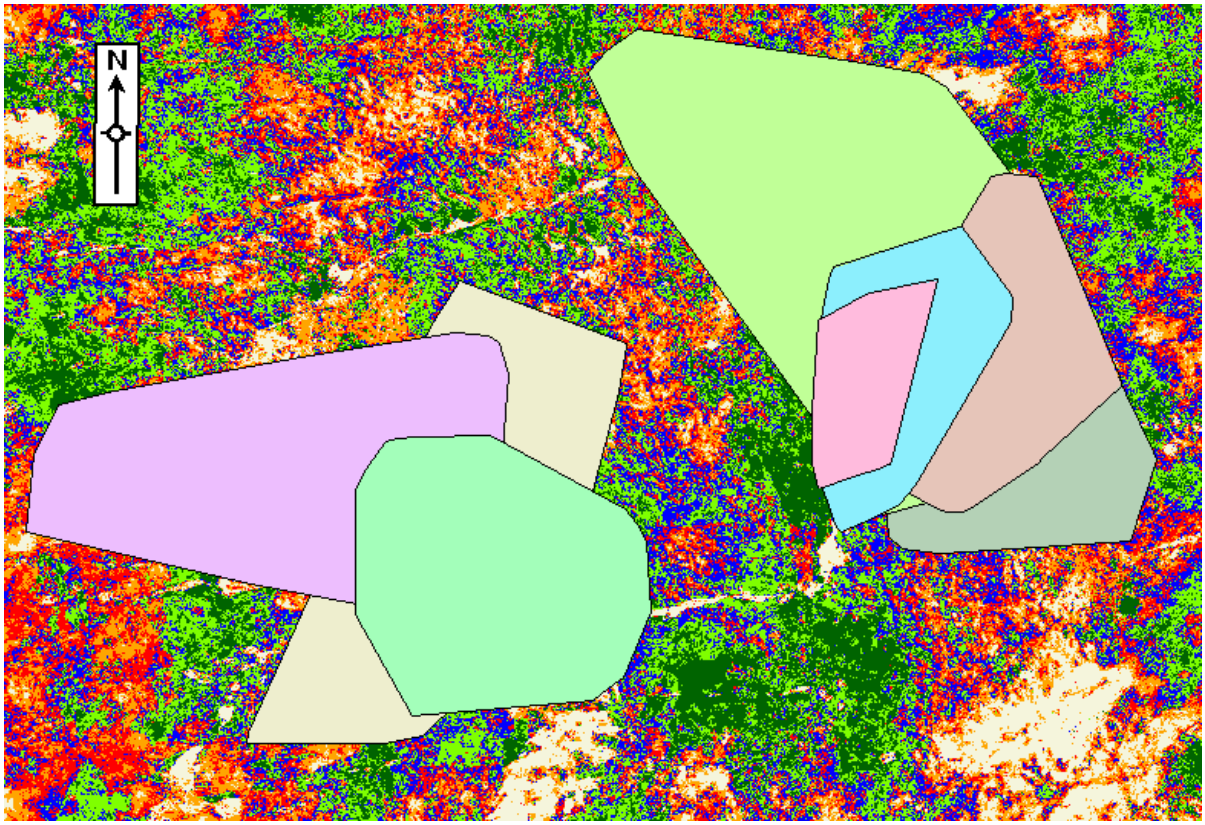

Figure 4.13 - Home ranges of the 8 tracked Gemsbok in the research area

The variance in the size of the home ranges is considerable, as is clearly illustrated in Figure 4.14 below. The home ranges vary from 15 267 hectares to 115 463 hectares, with a mean home range size of 60 472 hectares (604 km^2) each for these 8 Gemsbok. This estimate is considerably less than the home range size reported by Skinner & Chimimba (2005) of 143 000 hectares (1 430 km^2) for female Gemsbok, and even less than the 110 000 to 130 000 hectares (1 100 to 1 300km^2) estimated by Knight (1991).

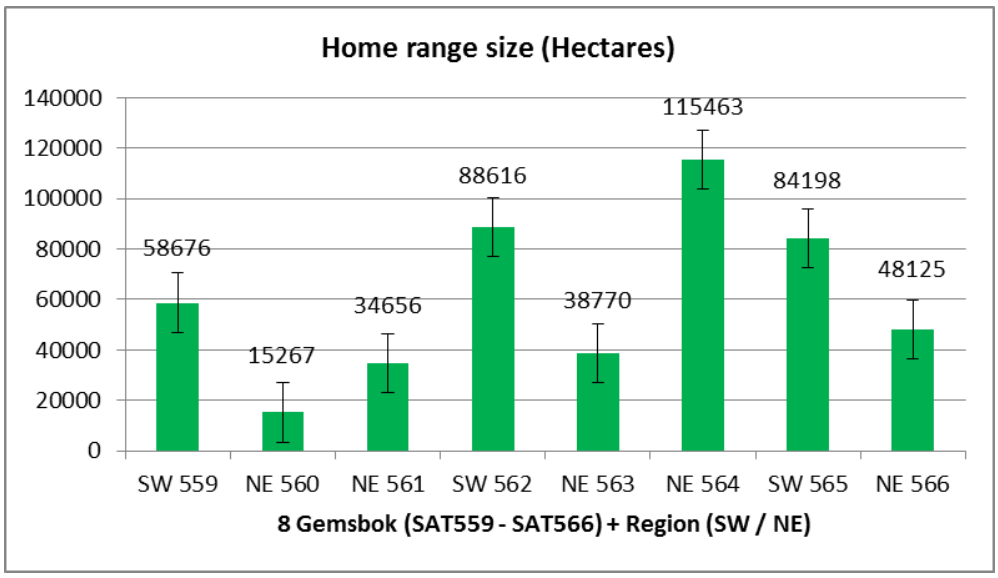

Figure 4.14 - Home range size estimates for each Gemsbok, with Std. error bars

The apparent reduction in home range for these Gemsbok is consistent with the diurnal and monthly usage patterns described in Section 4.2.2 and Section 4.3.4 above, and with the findings of Thomas (2010), that for most species, range boundaries change in response to climate change. The high usage of Class 6 (pans and valleys) during the summer rainfall period and the high usage of Class 5 (sparse cover, Kalahari sand with some small shrubs) during much of the remaining period of the study suggest a foraging pattern of using pans and adjacent patch classes during the day, and returning to the relative security of the pans at night. Furthermore, in an environment of increasing ambient temperature, a reduced home range with more time spent at rest, would be an effective thermoregulation strategy, since the brain cooling of Gemsbok through the carotid rete is effective when the animal is at rest, but not while the animal is active (Maloney et al., 2002). The likely rest periods for Gemsbok, deduced from observed rest periods for Sable (Goodall, 2014) and shown in Figure 4.6.4, confirms the high use of Class 5 and Class 6 during the resting activity.

4.5 Preference modelling

Thus far, the usage of the heterogeneous landscape in the central Kalahari by the collared Gemsbok has been reported as the frequency with which each animal was located in a particular patch class, by day and by night, by hour and by month. Availability of the patch classes was reported by the area of each patch class within each Gemsbok's home range. Similarly, the analysis of the ambient temperature record over the 9 month observation period of the study has been reported in terms of mean temperatures per patch class, by day and by night, and by month. This has led to useful insight into patch class preference, as set out in Section 4.3, and to an understanding of diurnal and monthly temperature variability in this patch landscape, but has not yet fully explored the role that temperature has played in the observed patch class preference.

The methodology approach set out in Section 3.5, in which temperature and the other available variables (altitude, day-night indicator and month) were to be analysed, yielded the following results:

4.5.1 Non-parametric correlation analysis

Overall, landscape patch class was not significantly correlated with temperature (Spearman's rho=0.002; n=40829; p=0.741), but was correlated to altitude (Spearman's rho=0.084; n=40829; $p<0.05$). By day, patch class was negatively correlated with temperature (Spearman's rho=-0.030; n=20817; $p<0.05$), while at night, the correlation was

positive (Spearman's rho=0.027; n=20012; p<0.05), implying that temperature influenced the preference for different patch classes during the day and at night. Altitude, on the other hand, was positively correlated with Class both by day (Spearman's rho=0.116; n=20817; p<0.05), and by night (Spearman's rho=0.051; n=20012; p<0.05), and would need to be considered as a possible discriminating variable between patch classes.

Using December data as a proxy for mid summer temperatures, patch class was negatively correlated with both temperature (Spearman's rho=-0.054; n=5566; p<0.05), and altitude (Spearman's rho=-0.049; n=5566; p<0.05). Conversely, using June data as a proxy for mid winter temperatures, patch class was positively correlated with both temperature (Spearman's rho=0.060; n=4456; p<0.05), and altitude (Spearman's rho=0.351; n=4456; p<0.05). On its own, the variable month was significantly negatively correlated with patch class (Spearman's rho=-0.079; n=40829; p<0.05), implying that different patch classes were preferred by Gemsbok during different months of the year (Class 6 preferred December through February, and Class 5 preferred March through July, as indicated in Figure 4.11).

This analysis suggests that temperature is not the only influence in patch class preference, and that in order to explain the Gemsbok's apparent discrimination between available patch classes, other variables would have to be considered and included in the analyses.

4.5.2 Discriminant Analysis

As outlined in Section 4.5.1, preliminary non-parametric correlation analysis between patch class and other available variables collected in this study revealed no significant correlation between class and temperature, but a weak correlation between class and the GPS altitude variable collected for each Gemsbok. Consequently, although temperature is the variable under study, altitude was added to temperature as an independent variable in the analysis to improve the predictive capability of the discriminant model.

The disciminant analysis identified two weak discriminant functions (canonical correlations 0.072 and 0.043) that accounted for the separation between the landscape patch classes. The Wilks' Lambda test showed that though weak, the two discriminant functions were significant (Wilks' Lambda=0.993; χ^2=284.1; df=10; p<0.05 and Wilks' Lambda=0.998; χ^2=74.6; df=4; p<0.05). Function 1 accounted for 73.7% of the variance that could be attributed to a model comprising these two discriminant functions. Altitude loaded positively on to Function 1 (0.971) while temperature loaded negatively (-0.227). Function 2 accounted for the balance of the variance (26.3%) on which both temperature (0.974) and altitude

(0.238) loaded positively. The loading of each variable on to a discriminating axis represents the correlation between the variable and the discriminant function. The magnitude of the correlation is indicative of the relative importance of each varaible on that function (Hair et al., 2006). A spatial representation of how the discriminant analysis was able to maximally separate the patch classes is depicted in Figure 4.15 below, where the discriminant functions have been evaluated at the group centroids (class means).

Table 4.9 – Canonical discriminant functions evaluated at Class group centroids

	Class 1	Class 2	Class 3	Class 4	Class 5	Class 6
Function 1	-0.066	0.021	-0.095	-0.079	0.092	0.02
Function 2	-0.065	-0.037	-0.028	0.081	0.017	-0.018

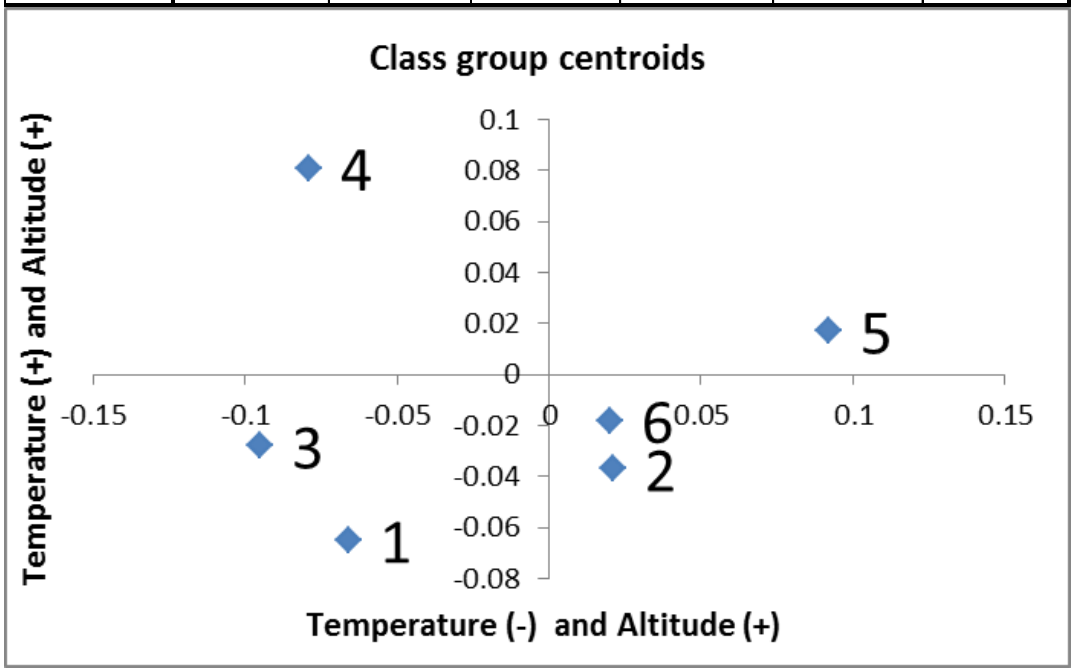

Figure 4.15 - Landscape patch class group centroids plotted on Function 1 (horizontal axis) and Function 2 (vertical axis). Most of the separation between classes is along the horizontal axis.

The class group centroid plot can be interpreted as a spatial representation of the differences between the classes on mean altitude on the horizontal axis, from Class 5 (highest) to Class 3 (lowest) and the differences between the classes on mean temperature on the vertical axis, from Class 4 (warmest) to Class 1 (coolest), as measured by the GPS altitude and collar mounted black globe thermometers on the Gemsbok.

The discriminant model can be used to predict class membership, based solely on the temperature and altitude variables. Using the model to retrospectively predict the patch class, only 19,3% of the locations were correctly classified. This low prediction accuracy confirms the weakness of a discriminant model comprising only temperature and altitude as

discriminating variables. Other factors are therefore likely to account for patch class preference.

4.5.3 Regression analysis

In order to further explore the role of temperature specifically in determining Gemsbok usage of landscape patch classes, the research data was subjected to linear regression analysis. A weak regression model exists (n=40829; R^2=0.002; F=34.99; p<0.05) in which temperature is not a significant contributor to the explained variance in the model (temperature: B=0.001; t=1.356; p=0.175). The null hypothesis that temperature is not a significant predictor of patch class preference can therefore not be rejected. It can therefore be concluded that, overall, temperature does not play a significant role in landscape patch class preference for the Gemsbok in this study. Hypothesis H_3, associated with research question 1.3.2.3, is therefore disproved.

In Section 4.3.1, it has already been determined that there is a significant difference between patch class usage by day and by night. In Figure 4.7, it has also been shown that there is a significant difference between patch class temperatures. Although temperature has been shown to be an insignificant predictor of patch class preference overall, separate analyses were undertaken to determine whether temperature played more of a role either during the day or at night.

The results of the daytime analysis confirm that a weak regression model exists, (n=20817; R^2=0.011; F=110.69; p<0.05), and that temperature is a weak predictor of patch class preference by day (temperature: B=-0.003; t=-2.341; p=0.019). but is not a significant predictor at night (n=20012; R^2=0.001; F=8.21; p<0.05) (temperature: B=0.003; t=1.643; p=0.100). This analysis suggests that when temperatures are high during the day, a temperature threshold is reached when patch class preference decisions are influenced by the temperature (Cunningham et al., 2013). At night, when temperatures are below this critical threshold, patch class preference decisions are influenced by factors other than temperature. The most likely influences are forage availability and predation risk.

The analysis was further extended to determine whether temperature was an influence in patch class preference in winter and summer. Using June as a proxy for winter, and December as a proxy for summer, regression analysis showed that temperature was a significant predictor of patch class preference in winter (n=4455; R^2=0.096; F=237.2; p<0.05)

(temperature: B=0.009; t=3.554; p<0.05), where temperature accounted for 9.6% of the variance in the model. In summer, temperature was a much weaker, but still significant predictor of patch class, accounting for less than 1% of the explained variance (n=5565; R^2=0.003; F=8.90; p<0.05) (temperature: B=-0.012; t=-3.585; p<0.05).

Reasons for the stronger role for temperature as a predictor of patch class selection in winter may relate to the larger daily temperature differences from day to night in winter, and different Gemsbok thermoregulation behaviour in winter as opposed to summer, but the probable explanation of the particular patch class usage profiles for December and June is more likely to be related to rainfall and available forage, as discussed in Section 4.3.4, than to temperature as a preference driver.

4.5.4 Multinomial logistic regression

It became clear that the Gemsbok in this study show a preference for the more open, less vegetated patch classes (Class 5 and Class 6), with a particular preference for Class 6 (pans and valleys) relative to the availability of this class. The degree to which temperature can influence the likelihood of Gemsbok moving from Class 6 to other patch classes was explored using multinomial logistic regression, together with the role of the day-night variable.

As in the case of linear regression, multinomial logistic regression is used to predict the patch class based on independent variables, in this case temperature and the day-night indicator. The advantage of the multinomial logistic regression is that by using Class 6 as a base, it will indicate the log likelihood that a Gemsbok will move from Class 6 to another patch class (Starkweather & Moske, 2011; Kwak & Clayton-Matthews, 2002).

The Likelihood Ratio tests in the multinomial logistic regression indicate that the coefficient of at least one of the predictor variables in the regression is not zero, and that inclusion of the independent variables temperature and the day-night indicator improves the prediction of patch class (χ^2=442.8; df=10; p<0.05) (Shtatland, Kleinman, & Cain, 2002). While multinomial logistic regression does not have an equivalent to R^2 in linear regression, the pseudo R^2 statistic (Nagelkerke=0.027) provides some support to the hypothesis that temperature and the day-night indicator play a role in contributing to patch class selection (Nagelkerke, 1991).

The analysis of the multinomial logistic regression coefficients and Wald χ^2 statistic indicated that when a Gemsbok moved from Class 6, it was most likely to move to Class 5 (B=-0.010; Wald χ^2=24.9; df=1; p<0.05). Gemsbok were less likely to move from Class 6 to other patch classes under the influence of temperature. However, while the individual Likelihood Ratio tests indicate that temperature is a predictor of patch class (χ^2=45.5; df=5; p<0.05), the role of the day-night indicator was more important than temperature (χ^2=360.7; df=5; p<0.05). Thus, the role of temperature in the likelihood to move from Class 6 to another class was secondary to the role played by whether it was day or night. From a location in Class 6, at night, the influence of night turning to day is most likely to influence the Gemsbok to move to Class 5 (χ^2=145.0; df=1; p<0.05) or to Class 4 (χ^2=161.7; df=1; p<0.05). This analysis supports the scenario outlined earlier in Section 4.4 of a Gemsbok home range centred on the pans (Class 6) at night for security, and initial movement to adjacent patch classes (Class 5 and Class 4) for daytime foraging.

4.5.5 Summary of the preference modelling

The non-parametric correlation analysis indicated correlations between patch class and temperature, but stronger correlations between class and altitude. As a result, altitude was included in the discriminant analysis, where it was shown that these two variables together contribute to the extraction of two functions that were able to distinguish between patch classes. Linear regression showed that temperature, on its own, was not a significant predictor of patch class. However, separate analyses showed that by day, temperature was a significant predictor of patch class, but not by night. By analysing December and June data, it was shown that temperature was a significant predictor of patch class preference in both months, but that other factors, such as seasonal rainfall and available forage (Tyson & Crimp, 1998), were likely to be stronger influences than temperature in explaining the high usage of Class 6 in December and Class 5 in June.

Finally, the multinomial logistic regression showed that temperature was a significant influence in the decision to move from patch Class 6 to some, but not all, of the other patch classes, and the most likely move would be to a Class 5 location. Whether it was day or night played a bigger role in the Gemsbok preference decision than temperature, and when day followed night, it was most likely that Gemsbok would move to Class 5 or Class 4. This analysis is consistent with the scenario outlined earlier, where Gemsbok are centred on the pans at night, and move away from the security of the pan during the day to forage nearby, by following the vegetation gradient from the pan through sparse cover to short grass grazing.

Chapter 5 Discussion and conclusions

While specific aims and objectives were formulated for this study and have been set out in Section 1.3, it is hoped that this research report will make a contribution to the field of mega herbivore ecology, in particular in improving our understanding of Gemsbok usage of heterogeneous landscape patches in the central Kalahari.

5.1 Landscape heterogeneity

The classification of the research area into 6 patch classes in this study is broadly similar to the 5 vegetation classes described by Mishra (2014), that he refers to as woodlands, open shrubland, very open shrubland, grasslands and pans. Mishra's description of pans corresponds to Class 6 (Pan, bare clay soil with some sparse cover), but his other classes correspond loosely to Class 1 to Class 5 in this study. The classification in this study was able to differentiate the grasslands into two patch classes, longer grass (Class 3) and shorter grass (Class 4). The inclusion of the TIRS bands in the classified image may have facilitated the differentiation based on different thermal characteristics of long grass and short grass.

A shortcoming of the classification in this study is that no indication is given of the height of the trees and shrubs that could potentially provide shade to Gemsbok in the more vegetated areas (Class 1 and Class 2). In his more comprehensive PhD thesis, Mishra (2014) provides mean heights of the vegetation structure of the classes that he identified. Drawing on his thesis, it is likely that patch Class 1 to Class 4 in this study would provide vegetation of an adequate height to provide shade to Gemsbok (Mishra, 2014). It is also clear from his thesis that these shady areas also provide foraging potential, in the form of a herbaceous layer beneath the shade canopy (Mishra, 2014). The stands of trees, or tree islands, situated on pans in the research area therefore provide shade and some forage to Gemsbok during the day, and some security at night, thereby adding to the attractiveness of pans as the preferred location for Gemsbok in this study.

5.2 Gemsbok landscape patch preference

In his comprehensive examination of Gemsbok ecology, Knight (1991) found that Gemsbok were particularly adapted to long grass grazing, and engaged in nocturnal foraging, while sheltering in shade during the day. This would suggest that Gemsbok would frequently be located in long grass patches, that they would spend more time in these patches at night, and more time during the day in patches providing more cover and potential shade. The results of this study do not support these anticipated behaviours. The use of grasslands

(Class 3 and Class 4) was significantly less than the less vegetated patches (Class 5 and Class 6), and when Gemsbok were located in grasslands patches, it was more frequently during the day than at night. The usage of the most vegetated patches (Class 1 and Class 2), was less during the day than anticipated from Knight's thesis, and was greater at night, suggesting that trees and taller shrubs may have more value in providing security at night than shade during the day.

It is suspected that foraging at night in grasslands away from the relative security of the pans attracted increased predation risk, and thermoregulation constraints mitigated against some of the grassland patches, where Class 4 had the highest mean temperature. Using a preference metric of location frequency per hectare suggested by Beyer et al. (2010), Class 6 (pans and valleys) was the preferred patch class in the research area. This preference for Class 6 was most apparent during the summer rainfall months when the pans provided more than adequate forage, shade during the day and shelter at night. During the autumn and early winter months, when limited rainfall reduced forage on the pans, Gemsbok preferred the typically adjacent Class 5, where, through their dietary plasticity (Lehmann et al., 2013), Gemsbok were able to find adequate nourishment.

Fear of predation can have a significant impact on how prey animals use their landscape (Valeix et al., 2009). This concept, a "landscape of fear" (Laundré et al., 2001), may help to explain both the temporal and spatial use of patch classes in the central Kalahari (Hernández & Laundré, 2005). The Gemsbok preference for more open landscapes (Class 5 and Class 6), their preference for using structure and cover (Class 1 and Class 2) more at night for shelter, rather than for shade during the day, and their reduced use of grasslands (Class 3 and Class 4) at night, are all consistent with a landscape usage pattern of foraging during the day on nearby vegetation patches, then sheltering under the cover of trees and tall shrubs available on the larger pans at night for protection from predators. Overall, the preferred landscape patch usage found in this study is therefore consistent with a "landscape of fear" (Laundré et al., 2010).

5.3 Role of temperature in landscape patch preference

The aim of this research report was to explore the role of temperature in determining Gemsbok use of heterogeneous landscape patches in the research area. Despite extensive analysis of the available data, temperature has not been shown to be a key determinant of Gemsbok patch class preference. Temperature did play a significant role during the day, and in winter, but there was little evidence that it was a major driver of Gemsbok behaviour in

terms of patch class selection in the research area. This suggests that temperature has not reached the critical level at which thermoregulation stress dominates Gemsbok behaviour, and that patch class preference may be based more on forage availability and predator avoidance.

The peak summer temperature in the central Kalahari has been recorded in isolated studies over the past 50 years (Bothma & Riche, 1994; Griffiths, 1972; Kaminer & Lutz, 1960). Analysis of peak summer (December 2012) temperature in this study confirms a rising temperature trend, with higher maximum and higher minimum temperatures observed, in line with current climate change predictions (Jury, 2013; Stocker et al., 2013).

Ungulates in arid environments have thermoregulation mechanisms to cope with high temperatures (Cain et al., 2006). Gemsbok employ a number of physiological and behavioural adaptations to enable them to cope with hot and dry environments (Hetem et al., 2011; Fuller et al., 2010). For Gemsbok, current variations in ambient temperature can be accommodated by adaptive heterothermy and brain cooling (Maloney et al., 2002; Mitchell et al., 2002), together with behavioural adaptations (Hetem et al., 2011) that allow the Gemsbok to cope with the rising temperatures observed in the research area in this study.

The fact that Gemsbok thrive in the Kalahari is testament to the success of these adaptations (Knight, 1991). When critical temperature thresholds are exceeded, changes to the physiology and fitness of other species in the Kalahari have been reported (Cunningham et al., 2013). It may be that the frequency and intensity of extreme temperature and drought may be the trigger for changes in Gemsbok behaviour, rather than a gradual increase in mean temperature. Behavioural changes in Gemsbok use of the heterogeneous patch dynamic of the central Kalahari are unlikely to be linear in response to gradual temperature increase, and may impact individuals or whole populations in a quantum change in behavioural adaptation when the critical temperature threshold is exceeded (Cunningham et al., 2013).

Preference decisions by animals are a complex set of interactions, particularly in a heterogeneous landscape (Beyer et al., 2010). It is unlikely that patch class selection would be based on a single variable, such as temperature. Other variables, such as altitude, played a bigger role in discriminating between patch classes, and the day-night indicator played a bigger role in determining to which class the Gemsbok was most likely to move when it left the security of the pan (Class 6). The propensity for these Gemsbok to use pans extensively in the summer months was more likely due to seasonal rainfall and resultant abundant

forage than to temperature. Equally, the tendency for Gemsbok to move a little further from the pans to Class 5 (sparse cover, Kalahari sand with some small shrubs) during the autumn months leading up to winter (June) is more likely to be related to reduced rainfall and reduced forage availability than to temperature.

Other studies have found that temperature does significantly affect Gemsbok activity budgets and foraging behaviour (Ruckstuhl & Neuhaus, 2009). In their study, daily maximum temperatures, as provided by the Etosha Park Administration, were used as a predictor variable. In this research, however, ambient temperature was recorded hourly as measured by collar mounted black globe thermometers. The limitation of this method of establishing the ambient temperature is that it is difficult to separate cause from effect. For example, when temperature is high, it is likely that Gemsbok seek cooler shade. Once in the shade, temperature-class correlations will indicate incorrectly that Gemsbok are located in shade when temperatures are lower. In short, the animals have already reacted to the high temperature, and have compensated for it by moving to lower temperature shade. If accurate hour by hour temperature metrics were available for the home ranges, it would be possible to get a much better understanding of how Gemsbok patch class selection is related to the true ambient temperature, and how effective their thermoregulation and behavioural adaptations are, by comparing collar temperature in a patch class to true ambient temperature elsewhere. These temperature measurements would have to be provided by ground stations and not by satellite based thermal sensors, as orbiting satellites would not be able to provide the required frequency of measurements, nor would image based temperatures be subject to the convective cooling available to animals on the ground.

Although the estimation of the size of the Gemsbok home ranges in the CKGR was not a specific aim of this research project, the results obtained are important, and relate to temperature. The home range for each Gemsbok was calculated using minimum convex polygon geometry in order to assess the availability of patch classes within each home range. The mean home range size of 604 km^2 found in this study is significantly smaller than previous estimates of 1 430 km^2 (Skinner & Chimimba, 2005) and 1 100 km^2 to 1 300 km^2 (Knight, 1991) for female Gemsbok. A reduced home range size would be consistent with a home range centred on pans and surrounding areas, and forage selection decisions based on forage availability, predation risk and thermoregulation constraints associated with the hotter and drier conditions being experienced in the CKGR (New et al., 2006; Tadross et al., 2005).

In Section 2.2.2, it was anticipated that Gemsbok home range sizes might increase as a result of a decline in forage quality and quantity, due to higher temperatures and reduced

rainfall. The fact that the findings of this study indicate that Gemsbok home range sizes are decreasing, suggest that rising temperature and reduced rainfall have not yet reached critical thresholds that impact available forage to the extent that necessitate larger home ranges for these animals. Rather, this study indicates that current temperatures can be tolerated by the Gemsbok, and reduced home ranges centred on the pans have advantages for the Gemsbok in thermoregulation and predation risk reduction.

5.4 Conclusion

This research has suggested that critical temperature thresholds that might alter Gemsbok behaviour in terms of landscape patch class selection have not as yet been reached in the central Kalahari. As a result, Gemsbok are not as frequently located in shade during the day as expected, nor do they appear to engage in nocturnal foraging on grasslands to the extent anticipated by Knight (1991).

This research further suggests that fear of predation is a significant factor in Gemsbok behaviour (Valeix et al., 2009) and resultant patch class preference (Hernández & Laundré, 2005). While not yet critical, the research has also suggested that rising thermoregulation stress, in combination with predation risk, has had an impact on reducing Gemsbok home range size. This reduction is conditional on the availability of adequate forage close to the refuge of the pans. Further research in these areas is warranted, and some possible projects are suggested below, but additional data will be required:

- Predator density counts or estimates for the research area, particularly for lion
- True ambient temperature measurements from ground stations located in each animals home range
- Access to rainfall and fire records for the research area, to correlate with assessment of available forage
- A biomass change detection study to assess whether significant changes in the available biomass have occurred alongside rising temperatures and reduced rainfall in the research area
- A larger study of more Gemsbok, that allows for some casualties, that will enable a full 12 month survival analysis and tracking study to provide new estimates of Gemsbok home range size in response to the impact of climate change on the central Kalahari
- Diel displacement (24 hour), diurnal displacement (12 hour) and nocturnal displacement (12 hour) analysis of Gemsbok movement patterns in the central Kalahari, as outlined by Rahimi & Owen-Smith (2007).

In conclusion, it is hoped that this research study has made contributions to the field of mega herbivore ecology in the following areas:

1. Confirmation of rising summer maximum and minimum temperatures in the CKGR
2. Indication that temperature is not fundamental to Gemsbok landscape patch selection
3. Identification of diurnal and monthly differences in Gemsbok patch class usage
4. Indication that Gemsbok spend less time in shade during the day than expected
5. Indication that Gemsbok engage less in nocturnal foraging in grasslands than expected
6. New estimates of reduced Gemsbok home range size
7. Use of a preference index to demonstrate Gemsbok preference for pans
8. Recognition that Gemsbok preference for pans may be based on a “landscape of fear” (Laundré et al., 2001).

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Appendix

APPENDIX A

Appendix A List of software

A1 ArcGIS 10.2
http://www.esri.com/software/arcgis

A2 ERDAS 2014
http://www.hexagongeospatial.com/products/remote-sensing/erdas-imagine

A3 Mendeley Desktop 1.13.3
http://www.mendeley.com

A4 Microsoft Excel 2010
http://office.microsoft.com

A5 SPSS Release 22
http://www-01.ibm.com/software/analytics/spss

A6 WinZip 17.5
http://www.winzip.com

Appendix B Classification accuracy proofing photographs

During November 2012, B.F.N. Erasmus took a number of photographs from a helicopter over the research area. The GPS ground position of each photograph was recorded, together with the photograph number and date.

Some of these photographs are shown in this appendix to illustrate examples of each of the 6 landscape patch classes identified in the classification analysis. In addition, 15 photographs were used for classification accuracy assessment. Each photograph was examined and visually assessed as a patch class in the range 1 to 6, corresponding to an ordinal vegetation scale from 1 (more vegetation) to 6 (less vegetation). The photograph's GPS position was transferred to the ERDAS classification image and plotted. The class number for that GPS position was extracted to determine the classified landscape patch class number. The classified patch class and the ground referenced actual class were recorded in the agreement table below, together with the GPS coordinates of each assessment point for subsequent analysis.

In Table B1 below, the classified classes that did not match the assessed class at that point are colour-coded red, while those that did match are colour-coded green. The points that were assessed by ground referenced photographs are highlighted.

Overall, 45 assessment points were examined, using 15 ground referenced photographs provided by B.F.N. Erasmus, one by M. Mofidi and one by A. Kanter. The balance of the assessment points were drawn from the classification image, and the classification accuracy was assessed by high resolution Google Earth images. While subjective, this assessment method is widely used (Luedeling & Buerkert, 2008).

Table B1 – Classification accuracy agreement table

GPS Point	Classified Class	Actual Class	Latitude	Longitude
1	1	1	21° 28' 56.12" S	23° 47' 47.30" E
2	3	2	21° 57' 51.00" S	23° 51' 15.83" E
3	4	4	21° 26' 08.76" S	23° 35' 03.59" E
4	4	4	21° 36' 21.18" S	23° 10' 14.27" E
5	5	5	21° 32' 14.56" S	23° 20' 06.32" E
6	6	6	21° 35' 30.62"S	23° 11' 53.37" E
7	1	1	21° 30' 47.52" S	23° 32' 48.91" E
8	1	4	21° 28' 17.88" S	23° 49' 58.97" E
9	3	3	21° 31' 35.66" S	23° 37' 46.05" E
10	4	3	21° 36' 16.43" S	23° 25' 35.13" E
11	5	2	21° 20' 16.53" S	23° 40' 21.19" E
12	6	6	21° 28' 31.71" S	23° 24' 3.35 " E
13	1	1	21° 30' 30.13" S	23° 45' 30.35" E
14	2	4	21° 26' 55.96" S	23° 49' 23.47" E
15	3	3	21° 29' 49.33" S	24° 01' 33.13" E
16	4	4	21° 36' 15.52" S	23° 23' 11.57" E
17	5	5	21° 14' 07.07" S	23° 35' 51.21" E
18	6	6	21° 24' 55.00" S	23° 47' 56.30" E
19	1	1	21° 36' 52.32" S	23° 34' 01.15" E
20	2	2	21° 26' 55.96" S	23° 49' 23.47" E
21	3	4	21° 26' 43.39" S	24° 00' 25.18" E
22	4	4	21° 33' 26.15" S	23° 45' 08.11" E
23	5	4	21° 22' 34.49" S	23° 53' 24.44" E
24	6	6	21° 33' 23.82" S	23° 46' 45.75" E
25	1	1	21° 18' 22.46" S	23° 43' 13.82" E
26	2	3	21° 14' 33.28" S	23° 11' 02.01" E
27	3	3	21° 30' 47.49" S	23° 29' 55.95" E
28	4	4	21° 32' 42.30" S	23° 05'50.74" E
29	5	5	21° 15' 40.22" S	23° 29' 23.84" E
30	6	6	21°16 '56.72" S	23° 42' 08.71" E
31	1	1	21° 14' 38.98" S	23° 52' 56.95" E
32	2	2	21° 20' 41.13" S	23° 24' 31.70" E
33	6	3	21° 10' 48.07" S	23° 39' 47.10" E
34	4	4	21° 30' 14.42" S	23° 31' 14.10" E
35	5	5	21° 29' 19.08" S	23° 22' 23.62" E
36	6	6	21° 14' 58.41" S	23° 33' 49.25" E
37	1	2	21° 19' 42.85" S	23° 40' 31.46" E
38	3	3	21° 30' 01.07" S	23° 32' 17.74" E
39	5	4	21° 27' 43.54" S	23° 29' 43.16" E
40	2	3	21° 33' 30.86" S	23° 12' 25.22" E
41	5	5	21° 32' 25.39" S	23° 15' 36.90" E
42	1	1	21° 22' 29.01" S	23° 45' 16.93" E
43	6	6	21° 19' 38.21" S	23° 52' 22.52" E
44	5	3	21° 25' 16.16" S	23° 37' 53.85" E
45	5	3	21° 25' 52.07" S	23° 35' 58.82" E



Figure B1 Example of Class 1: Open shrubland, with more woody cover, and some trees in sparse woodland

Photo 20121109_4695.jpg, Position 21° 28’ 56.12” S 23° 47’ 47.30” E
Source: B.F.N. Erasmus, November 2012



Figure B2 Example of Class 2: Shrubland with woody cover

Photo 20121109_4703.jpg, Position 21° 27’ 51.00” S 23° 51’ 15.83” E
Source: B.F.N. Erasmus, November 2012



Figure B3 Example of Class 3: Longer grass with shrubs and some woody cover

Photo 20121109_4513.jpg, Position 21° 25' 52.07" S 23° 35' 58.82" E
Source: B.F.N. Erasmus, November 2012



Figure B3 Example of Class 4: Shorter grass with shrubs

Photo 20121109_4515.jpg, Position 21° 26' 08.76" S 23° 35' 03.59" E
Source: B.F.N. Erasmus, November 2012



Figure B4 Example of Class 4: Shorter grass with shrubs, viewed across a pan

Photo 20121109_4589.jpg, Position 21° 36’ 21.18” S 23° 10’ 14.27” E
Source: B.F.N. Erasmus, November 2012

The tree island on the pan in the middle of photograph 4589 in Figure B4 above is clearly identifiable in the classification image, Figure B4.1 below:

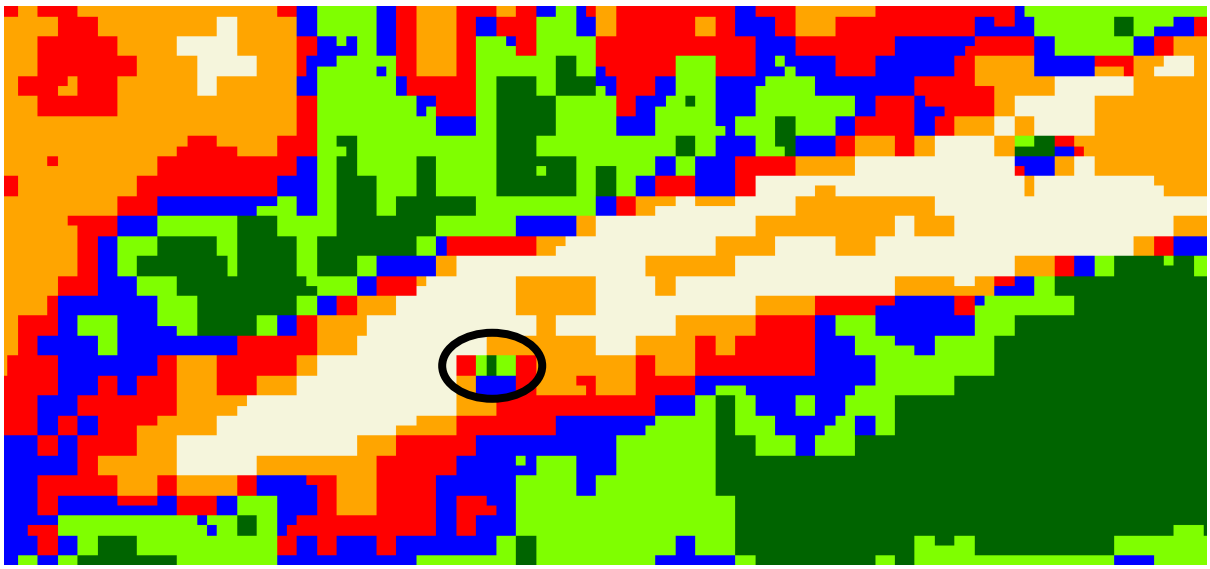

Figure B4.1 Heterogeneous landscape patch classes corresponding to the photograph in Figure B4 above. The detailed accuracy of the classification is supported by the photograph and ground truth points using Google Earth GPS coordinates.



Figure B5 Example of Class 5: Sparse cover, Kalahari sand with some small shrubs

Photo 20121109_4622.jpg, Position 21° 32’ 14.56” S 23° 20’ 06.32” E
Source: B.F.N. Erasmus, November 2012



Figure B6 Example of Class 6: Bare pan soil with some sparse cover, and tree islands in the distance on the pan

Photo 20121109_4597.jpg, Position 21° 35’ 30.62” S 23° 11’ 53.37” E
Source: B.F.N. Erasmus, November 2012

Appendix C Individual Gemsbok analyses

The following analyses for each Gemsbok in turn illustrate the different ways in which these collared Gemsbok react to biotic and abiotic influences in their usage of the heterogeneous patch landscape within their home ranges. The analyses confirmed that the collared Gemsbok did not all exhibit the same class preferences.

C1 SAT559

SAT559 was collared and released on 11 November 2012 and continued to be tracked until end July 2013, resulting in 6343 location observations. 97.3% of all location observations for SAT559 were allocated to a classification class in ERDAS. This animal formed part of a herd of 50 Gemsbok tracked in the SW region of the research area.

The locations of Gemsbok SAT559 over the period of the study, together with its estimated home range, are shown in Figure C1.1 below:

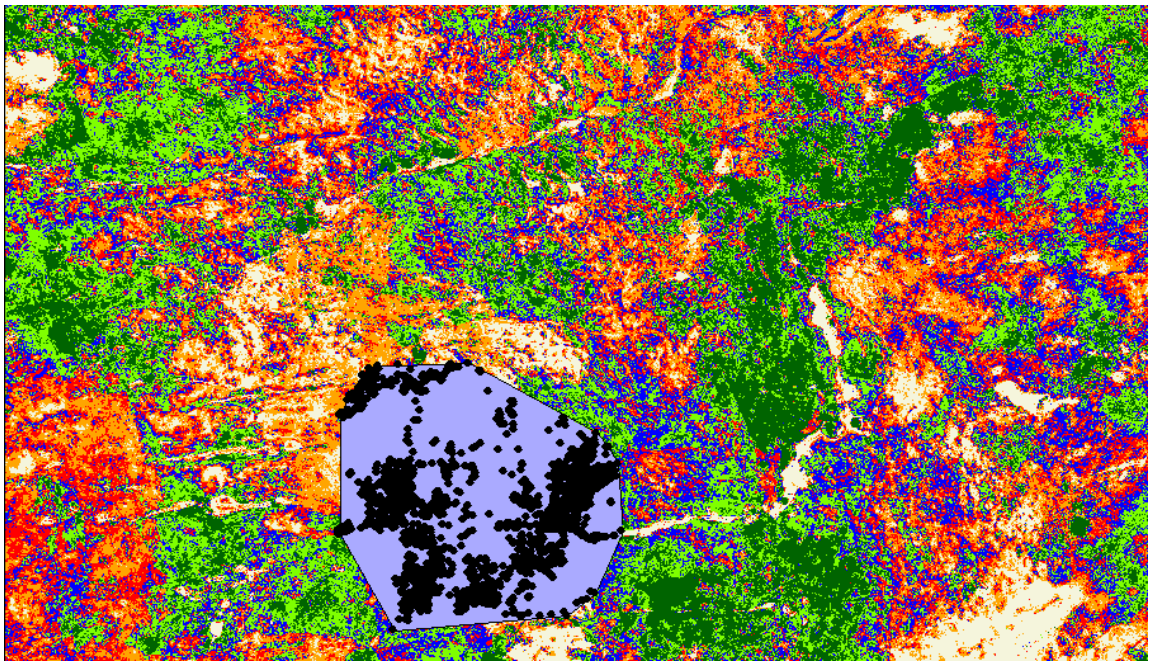

Figure C1.1 – SAT559 locations and home range

C1.1 Usage and availability – SAT559

The usage of patch classes by Gemsbok SAT559, and the availability of landscape patch classes to this animal, is shown in Table C1.1 and Figure C1.2 below:

Table C1.1 – SAT559 Usage and Availability

	Class 1	Class 2	Class 3	Class 4	Class 5	Class 6
Usage %	4.9	15.2	16.1	13.6	19.4	28.2
Available %	9.4	19.4	17.4	13.6	21.5	18.9

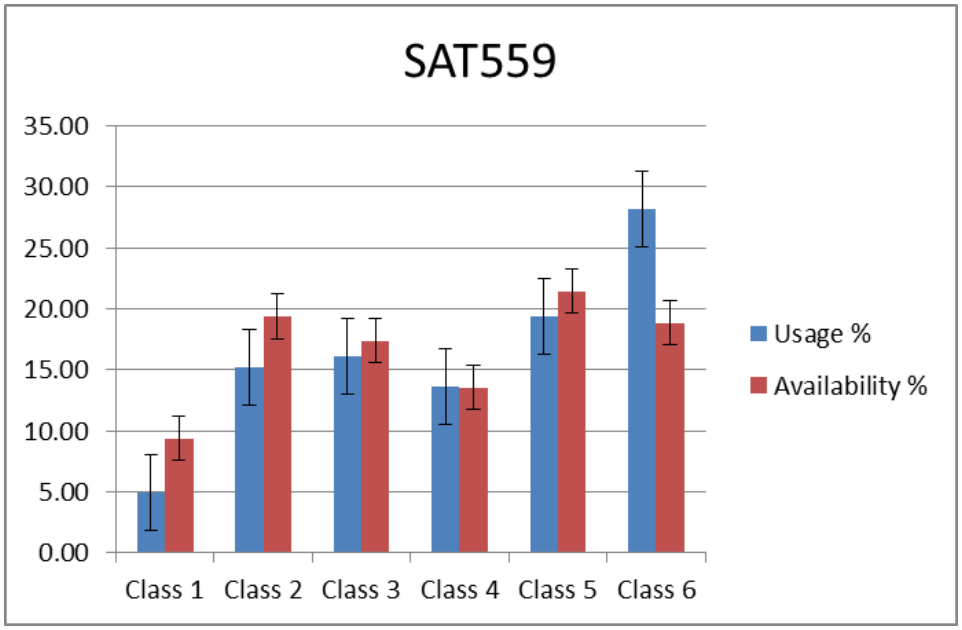

Figure C1.2 - SAT559 Usage and Availability, with Std. error bars

Gemsbok SAT559 Summary

- Class usage dominated by Class 6 (pans and valleys)
- Less use of patch classes with more structure and cover (Class 1 and Class 2)
- This Gemsbok used less of Classes 1 to 3 and Class 5 than might be expected from the availability of these classes, and significantly more of Class 6

C2 SAT560

SAT560 was collared and released on 10 November 2012 and continued to be tracked until mid July 2013, resulting in 5921 location observations. 94.1% of all location observations for SAT560 were allocated to a classification class in ERDAS. This animal formed part of a herd of 17 Gemsbok tracked in the NE region of the research area.

The locations of Gemsbok SAT560 over the period of the study, together with its estimated home range, are shown in Figure C2.1 below:

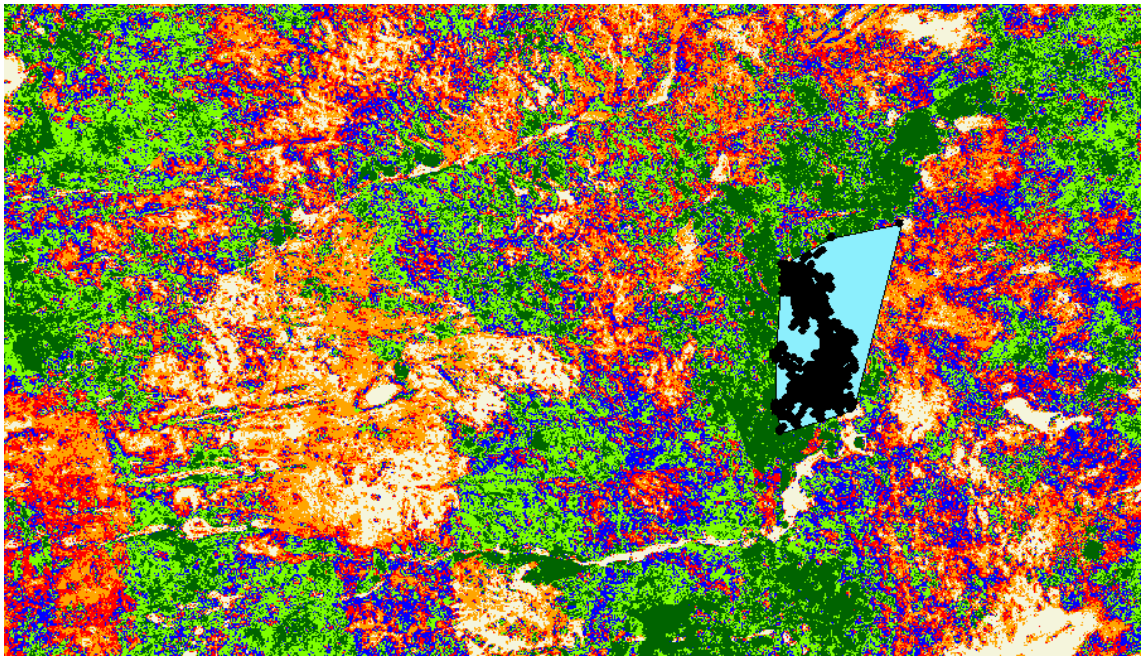

Figure C2.1 – SAT560 locations and home range

C2.1 Usage and availability – SAT560

The usage of patch classes by Gemsbok SAT560, and the availability of landscape patch classes to this animal, is shown in Table C2.1 and Figure C2.2 below. This animal was most frequently located in the more vegetated patch classes (Class 1 – Class 3), utilising the availability, but still making disproportionately high usage of the pans (Class 6).

Table C2.1 – Usage and Availability SAT560

Class	**Class 1**	**Class 2**	**Class 3**	**Class 4**	**Class 5**	**Class 6**
Usage %	25.6	18.8	14.1	6.5	7.2	22.0
Availability %	29.5	21.3	13.3	10.6	13.3	12.0

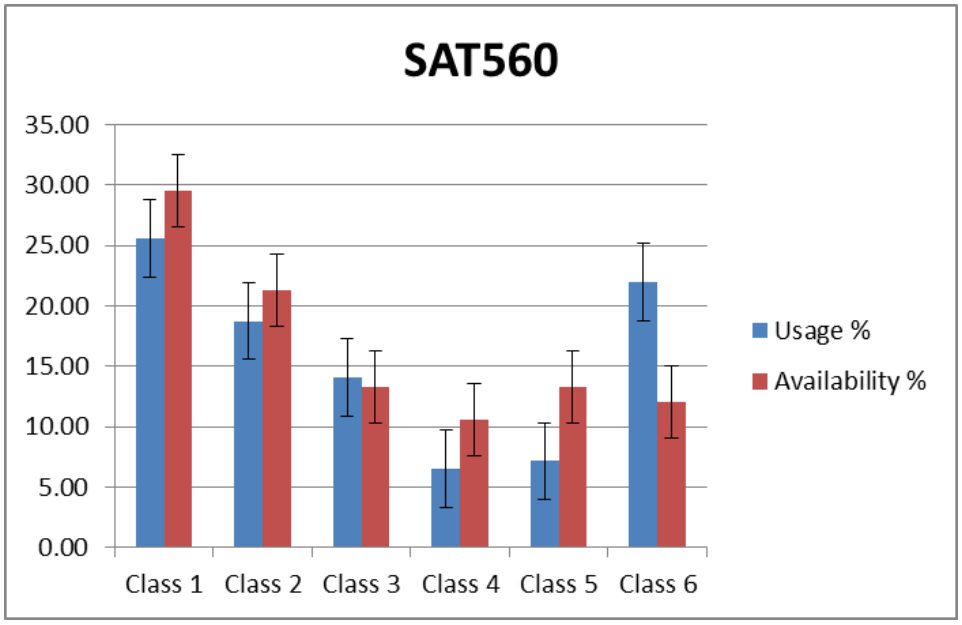

Figure C2.2 - SAT560 Usage and Availability, with Std. error bars

Gemsbok SAT560 Summary

- Home range availability predominantly Class 1 and Class 2, with high use of these classes that have more structure and cover
- Disproportionately high use of Class 6 (pans and valleys)

C3 SAT561

SAT561 was collared and released on 9 November 2012 and continued to be tracked until mid June 2013, resulting in 5273 location observations. 96.9% of all location observations for SAT561 were allocated to a classification class in ERDAS. This animal formed part of a herd of 5 Gemsbok tracked in the NE region of the research area.

The locations of Gemsbok SAT561 over the period of the study, together with its estimated home range, are shown in Figure C3.1 below:

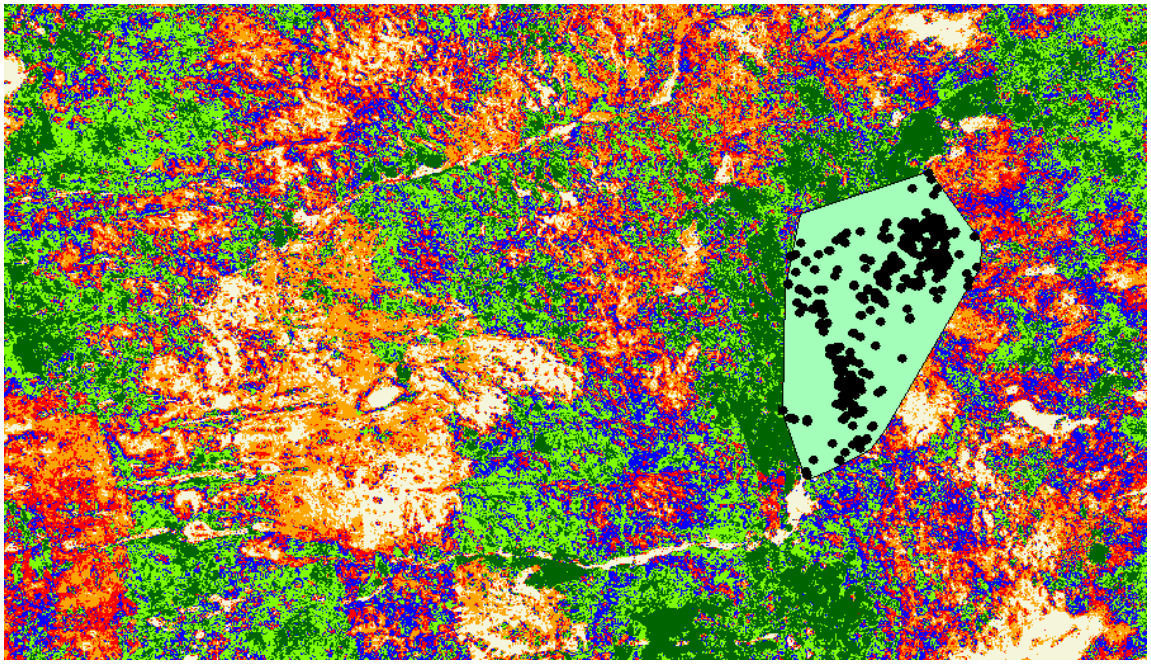

Figure C3.1 – SAT561 locations and home range

C3.1 Usage and availability – SAT561

The usage of patch classes by Gemsbok SAT561, and the availability of landscape patch classes to this animal, is shown in Table C3.1 and Figure C3.2 below. The landscape patch class usage by this animal can be summarised as disproportionately high usage of Class 5 and Class 6 (less vegetation cover) and disproportionately low usage of Class 1 and Class 2

(more vegetation structure and cover), relative to the availability of these patch classes in its home range.

Table C3.1 – Usage and Availability SAT561

Class	Class 1	Class 2	Class 3	Class 4	Class 5	Class 6
Usage %	8.9	10.8	9.0	17.0	27.8	23.4
Availability %	24.5	15.8	15.8	17.2	17.5	9.2

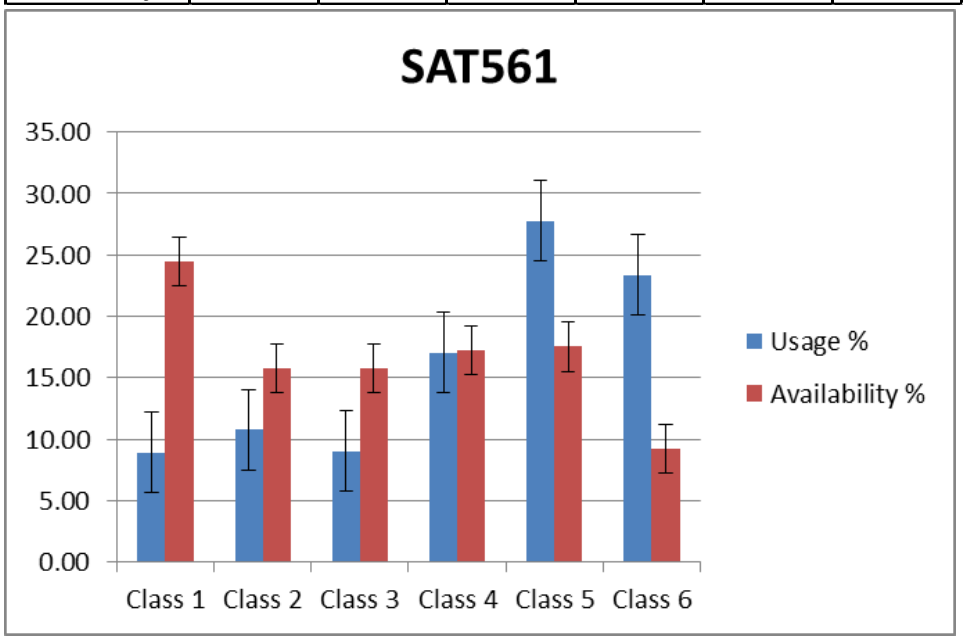

Figure C3.2 – SAT561 Usage and Availability, with Std. error bars

Gemsbok SAT561 Summary

- Most frequently located in Class 5, even though Class 1 is most available
- Over 50% of the time found in open areas (Class 5 and Class 6)
- Under 20% of the time found in patches with structure and cover (Class 1 and Class 2)

C4 SAT562

SAT562 was collared and released on 10 November 2012 and continued to be tracked until end July 2013, resulting in 6357 location observations. 91.8% of all location observations for SAT562 were allocated to a classification class in ERDAS. This animal formed part of a herd of 13 Gemsbok tracked in the SW region of the research area.

The locations of Gemsbok SAT562 over the period of the study, together with its estimated home range, are shown in Figure C4.1 below:

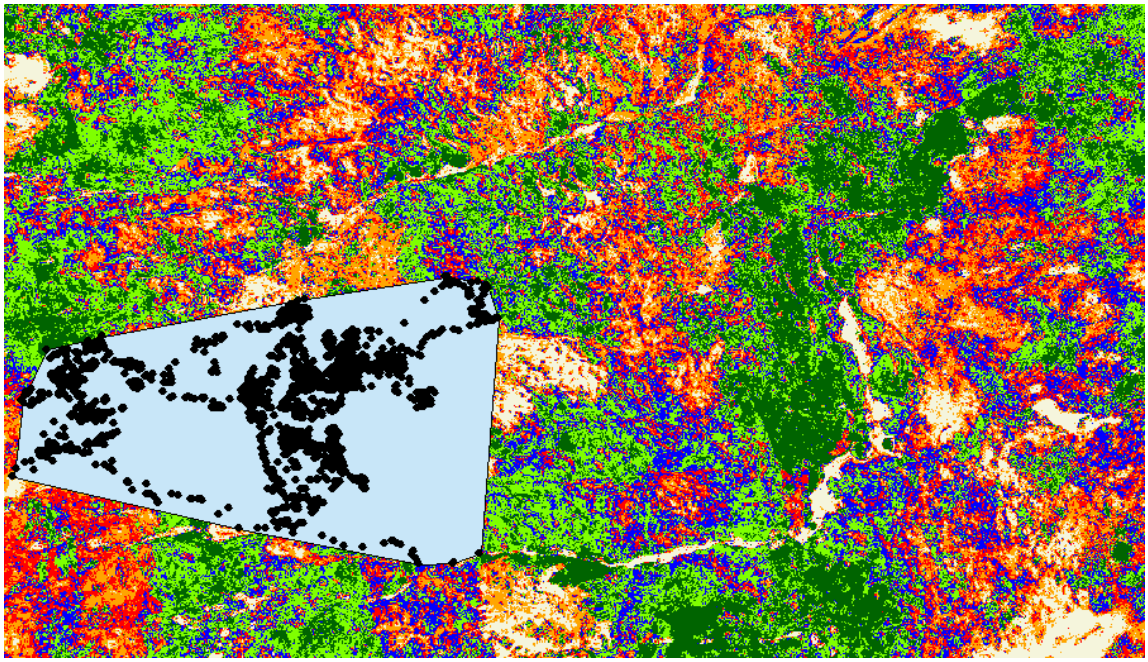

Figure C4.1 – SAT562 locations and home range

C4.1 Usage and Availability – SAT562

The usage of patch classes by Gemsbok SAT562, and the availability of landscape patch classes to this animal, is shown in Table C4.1 and Figure C4.2 below. This animal was predominantly located in Class 5 (sparse cover with some shrubs).

Table C4.1 – Usage and Availability SAT562

Class	**Class 1**	**Class 2**	**Class 3**	**Class 4**	**Class 5**	**Class 6**
Usage %	2.2	6.0	6.5	12.7	48.2	16.1
Availability %	5.4	12.1	11.2	18.3	34.3	18.7

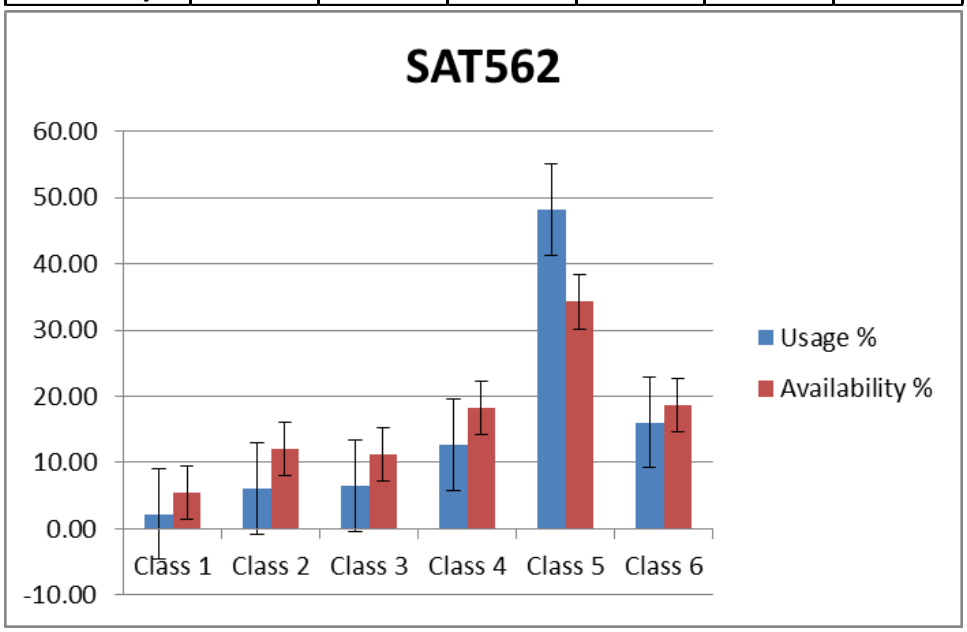

Figure C4.2 – SAT562 Usage and Availability, with Std. error bars

Gemsbok SAT562 Summary

- Class 5 (sparse cover, some shrubs) most available, and most used
- Low use of Class 1 (shade and cover)
- Limited use of other vegetated classes (Class 2, 3 and 4)
- Most use of open areas (Class 5 and Class 6)

C5 SAT563

SAT563 was collared and released on 8 November 2012 and continued to be tracked until end July 2013, resulting in 6290 location observations. 95.4% of all location observations for SAT563 were allocated to a classification class in ERDAS. This animal formed part of a herd of 6 Gemsbok tracked in the E region of the research area.

The locations of Gemsbok SAT563 over the period of the study, together with its estimated home range, are shown in Figure C5.1 below:

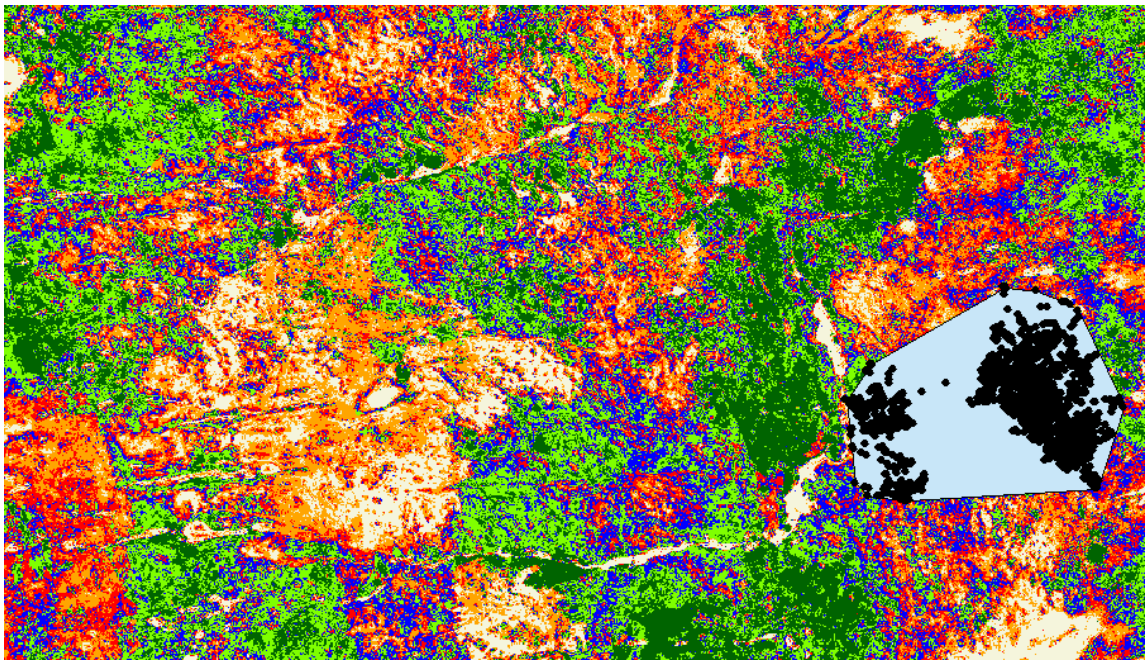

Figure C5.1 – SAT563 locations and home range

C5.1 Usage and Availability – SAT563

The usage of patch classes by Gemsbok SAT563, and the availability of landscape patch classes to this animal, is shown in Table C5.1 and Figure C5.2 below. This Gemsbok showed a preference for grassland patch classes (Class 3 and Class 4).

Table C5.1 – Usage and Availability SAT563

Class	Class 1	Class 2	Class 3	Class 4	Class 5	Class 6
Usage %	4.3	7.4	28.0	20.9	13.8	21.1
Availability %	6.9	15.5	27.8	21.7	17.0	11.0

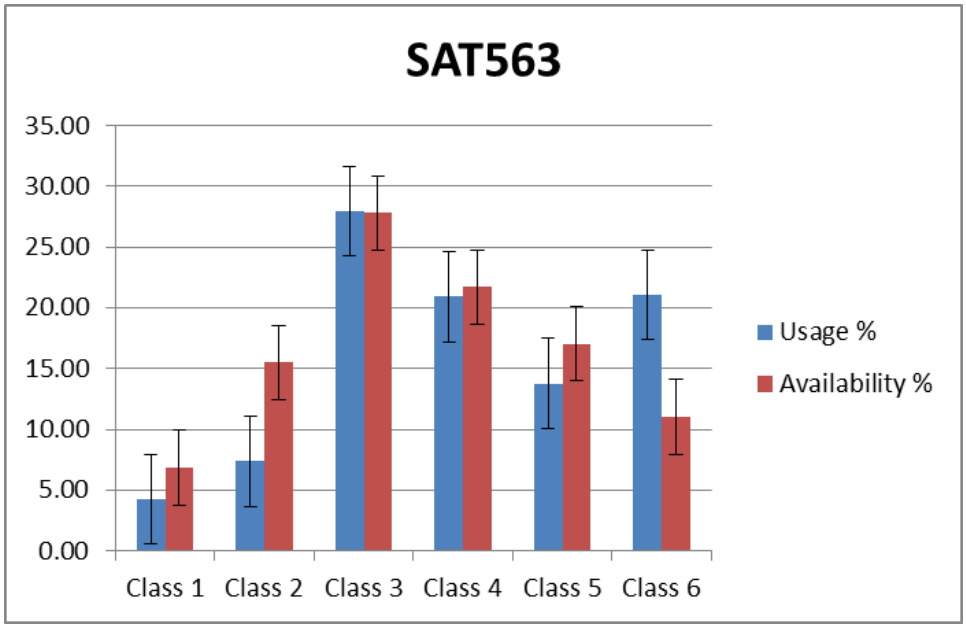

Figure C5.2 – SAT563 Usage and Availability, with Std. error bars

Gemsbok SAT563 Summary

- Class 3 (longer grass with shrubs and some woody cover) most available, and most used in its home range
- Disproportionately high use of Class 6 (pans and valleys)

C6 SAT564

SAT564 was collared and released on 8 November 2012 and continued to be tracked until mid July 2013, resulting in 5946 location observations. 94.0% of all location observations for SAT564 were allocated to a classification class in ERDAS. This animal formed part of a herd of 13 Gemsbok tracked in the NE region of the research area.

The locations of Gemsbok SAT564 over the period of the study, together with its estimated home range, are shown in Figure C6.1 below:

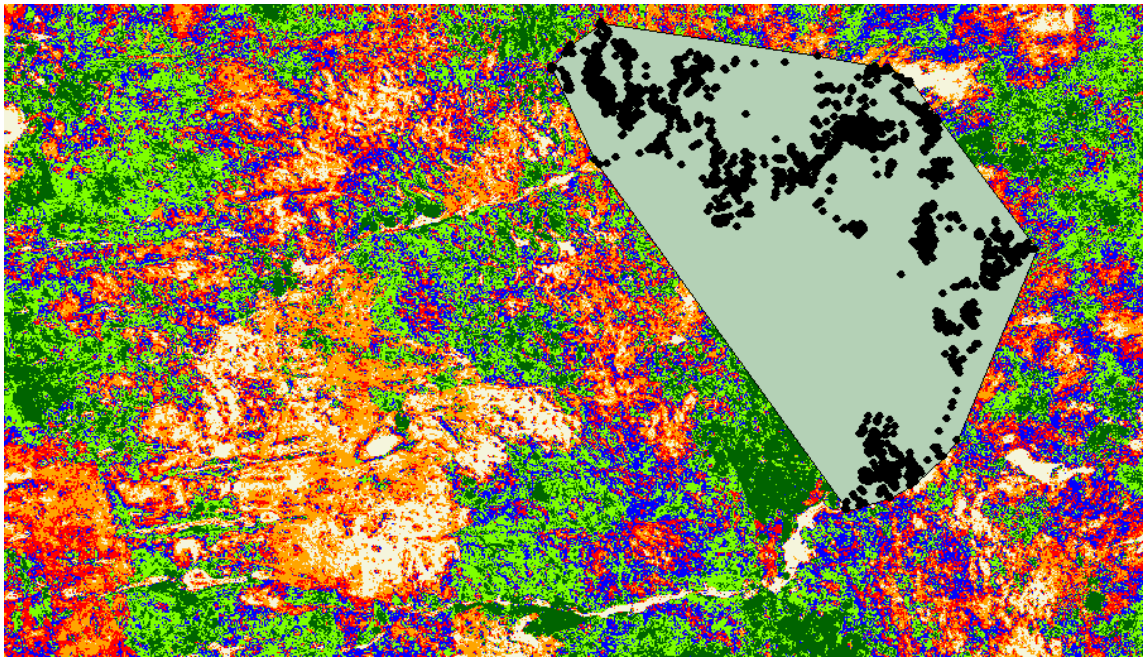

Figure C6.1 – SAT564 locations and home range

C6.1 Usage and Availability – SAT564

The usage of patch classes by Gemsbok SAT564, and the availability of landscape patch classes to this animal, is shown in Table C6.1 and Figure C6.2 below. This animal displayed predominantly high usage of Class 5, and disproportionately high usage of Class 6 relative to the availability of these patch classes in its home range.

Table C6.1 – Usage and Availability SAT564

Class	**Class 1**	**Class 2**	**Class 3**	**Class 4**	**Class 5**	**Class 6**
Usage %	3.8	5.7	12.4	22.3	34.7	15.1
Availability %	18.9	16.6	17.9	21.0	19.1	6.4

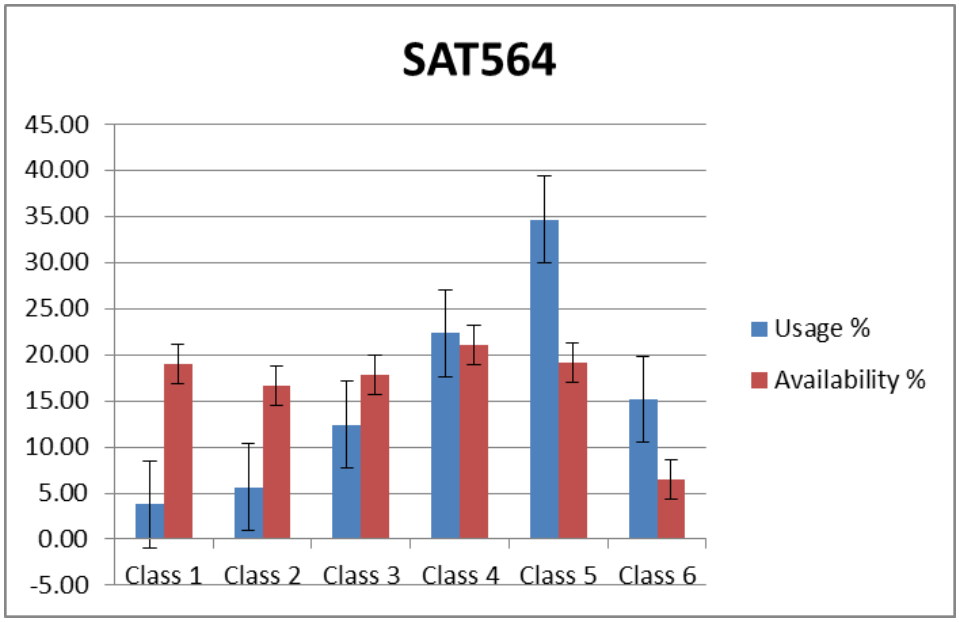

Figure C6.2 – SAT564 Usage and Availability, with Std. error bars

Gemsbok SAT564 Summary

- Predominant use of Class 5 (shrubland with woody cover)
- Disproportionately high use of Class 6 (pans and valleys)

C7 SAT565

SAT565 was collared and released on 11 November 2012 and continued to be tracked until mid July 2013, resulting in 6112 location observations. 90.6% of all location observations for SAT565 were allocated to a classification class in ERDAS. This animal formed part of a herd of 13 Gemsbok tracked in the SW region of the research area.

The locations of Gemsbok SAT565 over the period of the study, together with its estimated home range, are shown in Figure C7.1 below:

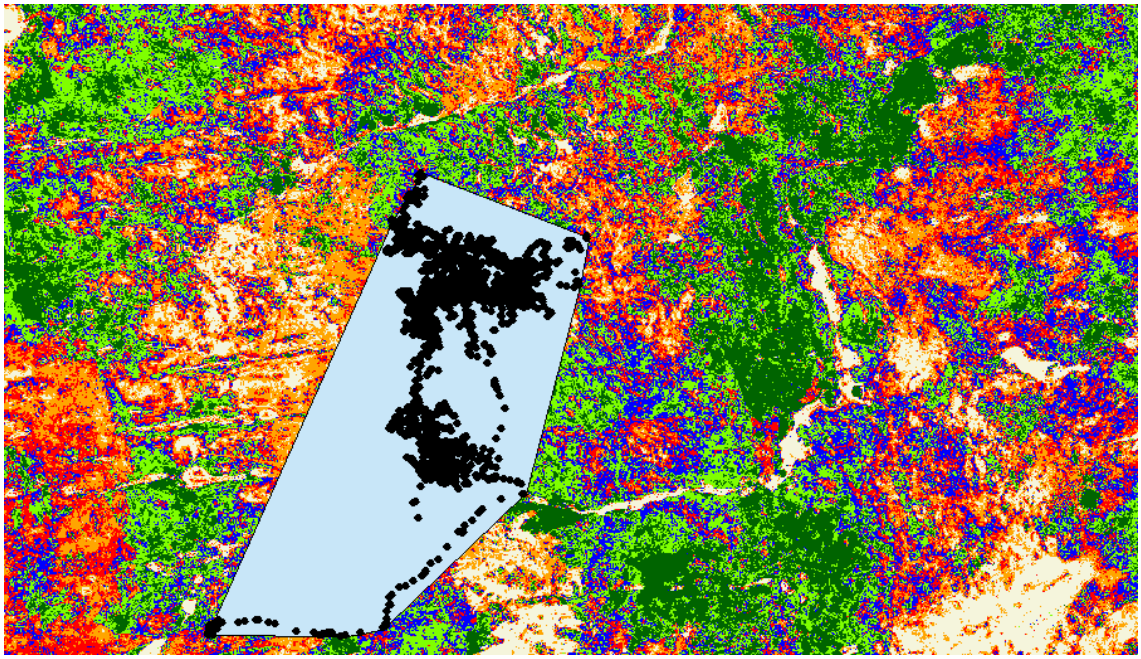

Figure C7.1 – SAT565 locations and home range

C7.1 Usage and Availability – SAT565

The usage of patch classes by Gemsbok SAT565, and the availability of landscape patch classes to this animal, is shown in Table C7.1 and Figure C7.2 below. This animal displayed a disproportionately high usage of Class 5 and Class 6.

Table C7.1 – Usage and Availability SAT565

Class	Class 1	Class 2	Class 3	Class 4	Class 5	Class 6
Usage %	3.5	12.4	11.0	12.4	32.2	19.2
Availability %	10.1	22.6	17.6	13.6	21.1	15.2

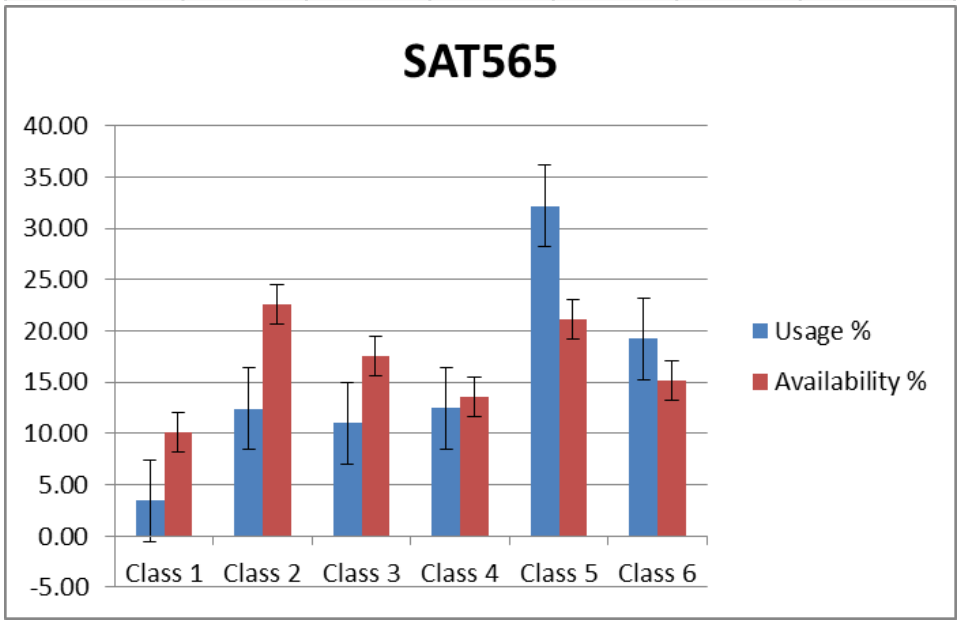

Figure C7.2 – SAT565 Usage and Availability, with Std. error bars

Gemsbok SAT565 Summary

- Predominant use of Class 5 (sparse cover, with some shrubs)
- Disproportionately high use of Class 6 (pans and valleys)

C8 SAT566

SAT566 was collared and released on 9 November 2012 and continued to be tracked only until 12 January 2013, resulting in just 1044 location observations. 96.5% of all location observations for SAT566 were allocated to a classification class in ERDAS. This animal formed part of a herd of 6 Gemsbok tracked in the NE region of the research area.

The temperature sensor on this animal failed on 22 December 2012. As the temperature record in particular landscape patch classes formed the key focus of this research report, location data that did not have corresponding temperature data had to be excluded from the analysis. Gemsbok SAT566 has therefore significantly less data available for analysis that the other animals in the study (1044 locations vs a mean number of locations of 6034 for the other animals in the study, resulting in an overall mean of 5410 locations for all 8 Gemsbok).

The locations of Gemsbok SAT566 over the period of the study, together with its estimated home range, are shown in Figure C8.1 below:

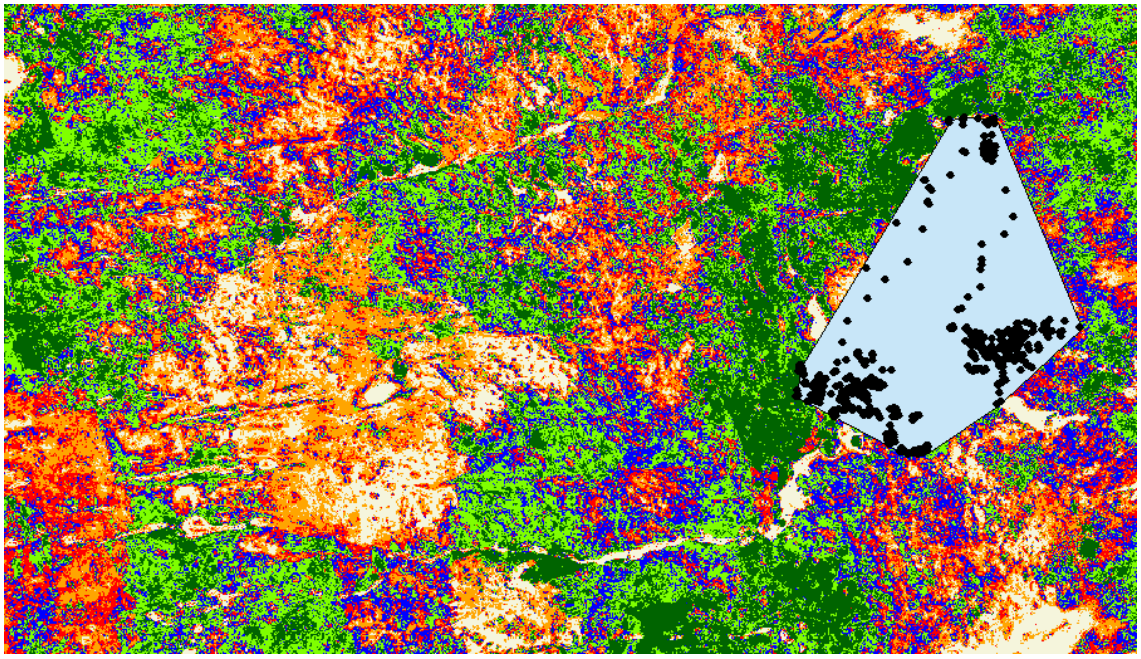

Figure C8.1 – SAT566 locations and home range

C8.1 Usage and Availability – SAT566

The usage of patch classes by Gemsbok SAT566, and the availability of landscape patch classes to this animal, is shown in Table C8.1 and Figure C8.2 below. Although usage was highest in Class 5, there was disproportionately high usage of Class 1 and Class 2, relative to the availability in these patch classes with more structure, cover and shade.

Table C8.1 – Usage and Availability SAT566

Class	**Class 1**	**Class 2**	**Class 3**	**Class 4**	**Class 5**	**Class 6**
Usage %	16.8	16.5	16.6	12.2	23.5	11.0
Availability %	6.3	13.0	22.4	26.4	23.1	8.8

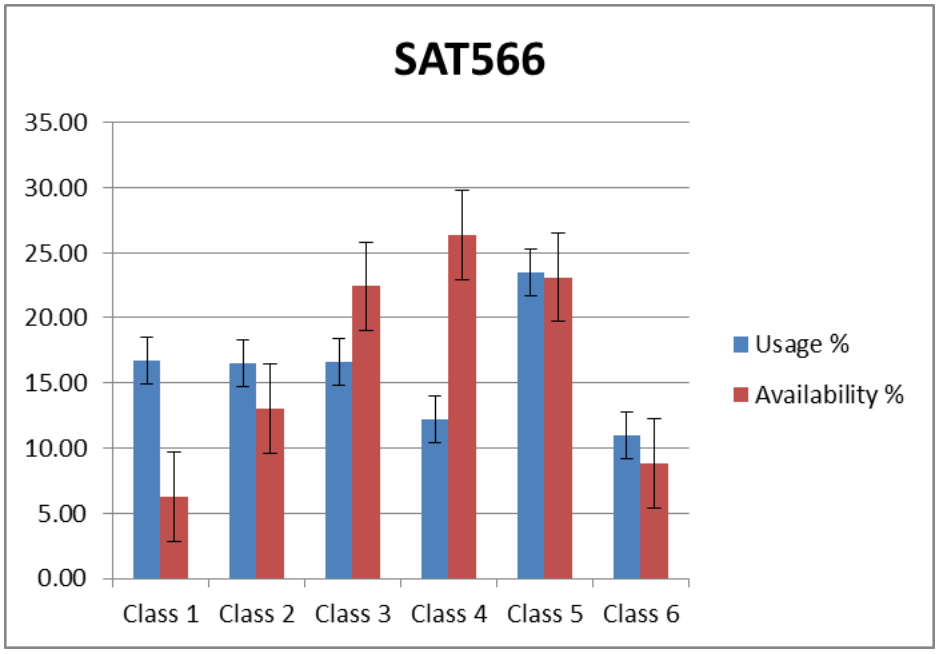

Figure C8.2 – SAT566 Usage and Availability, with Std. error bars

Gemsbok SAT566 Summary

- High use and high availability in Class 5 (sparse cover, with some shrubs)
- Less use of grasslands (Class 3 and Class 4)
- Disproportionately high use of limited structure and cover (Class 1)