MOVEMENT ECOLOGY OF GEMSBOK IN THE CENTRAL KALAHARI IN RESPONSE TO VEGETATION GREENNESS AS ASSESSED BY SATELLITE IMAGERY

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DECLARATION

I declare that this dissertation is my own, unaided, original work. It is being submitted for the Master of Science degree 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)

8 August 2015

ABSTRACT

Arid African savannas experience seasonal, variable rainfall, resulting in unpredictable patterns in vegetation distribution. Understanding the spatio-temporal variability in primary productivity and the resulting behavioural responses of native herbivores is essential for the analysis of the vulnerability of savanna ecosystems to climatic and human-induced threats. The Central Kalahari Game Reserve (CKGR), Botswana, is open to free-ranging wildlife to its south and west. The mostly homogeneous dune landscape is interspersed with valley and pan systems, which deviate considerably from dune regions in their soil and vegetation structures. I assessed the phenology of green vegetation across the pan-valley and dune habitats of the northern CKGR, using Normalized Difference Vegetation Index (NDVI) imagery, and related variations in greenness to the ecology of gemsbok (*Oryx gazella*), a herbivore species that is highly adapted to arid conditions. Eight female gemsbok were collared in the northern CKGR, and their patterns of habitat selection and responses to three greenness measures (NDVI, ΔNDVI and Relative Greenness) were assessed using logistic regression models. Gemsbok 12-hour displacement distances for each herd were compared seasonally to assess whether gemsbok in the northern CKGR differ in their movement strategies depending on the prevailing environmental conditions at that point in time and space.

The northern CKGR experiences high inter-annual variability in NDVI greenness and phenology. Pan-valley and dune habitats did not have significantly different rates of green-up or green season durations, but dune habitats had higher NDVI levels. Patches with the highest greenness levels showed little spatial persistence from year to year. Gemsbok did not select for higher NDVI or ΔNDVI, but they selected for categories of relative greenness that were higher than the lowest relative greenness level. Gemsbok selected pan-valleys over dunes during the green season, but were not selective during the brown season, probably as a result of the loss of green grasses in pan-valley habitats during this period. Finally, gemsbok had no specific general trend in seasonal displacement distances. Gemsbok in the CKGR are likely to be opportunistic feeders, and herds probably made varying behavioural decisions based on their immediate environmental conditions.

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CHAPTER 1: GENERAL INTRODUCTION

Broad project aim

To relate the movement patterns and habitat selection of an arid-adapted herbivore to spatio-temporal variability in grazing resources, and to predict the behavioural responses of this species to amplified climate variability and resource scarcity.

Motivation of study

The compounding influences of anthropogenic climate change, in association with human-induced impacts, such as the erection of fences, habitat degradation and landscape transformation, threaten the ecosystem dynamics of native wildlife populations throughout arid African savannas (Thuiller, 2007; Meadows, 2006; Parmesan & Yohe, 2003). These accumulating threats jeopardise ecosystem functionality by altering forage and water availability, and disrupting natural movements and migrations of wildlife (Knight, 1995b; Western et al., 2009; Okello & Kiringe, 2004). The southern and central Kalahari is an expansive, unique system, spanning a large proportion of southern Africa (Knight, 1991; Verlinden, 1998), and remains relatively unrestricted by fences. The region is home to a large biomass of wildlife species, but also to human populations and their associated livestock (Bergström & Skarpe, 1999). It is the variability in food resources and vegetation phenology that allows such an array of herbivores to coexist in the Kalahari environment (Campbell, 1981). The Central Kalahari Game Reserve (CKGR), Botswana, is open to free-ranging wildlife to its south and west, and the Kalahari system is a mosaic of Wildlife Management Areas, communal lands, fenced ranches and National Parks (Thouless, 1998). Herbivore populations in the arid Kalahari ecosystem experience significant spatial and temporal variability in primary productivity as a result of fluctuating rainfall regimes (Makhabu et al., 2002; Bergström & Skarpe. 1999; Verlinden & Masogo, 1997). To cope with this variability, native ungulates must respond to the prevailing environmental conditions through movement strategies, and cannot rely on physiological adaptations alone (Parris, 1972).

The Kalahari region (Figure 1.1) has experienced a gradual decline in surface water over the last century, resulting in the permanent loss of species such as buffalo (*Syncerus caffer*), white rhino (*Ceratotherium simum*) and zebra (*Equus quagga*) (Campbell, 1981). Other large herbivore species in the Kalahari are believed to persist as a consequence of their ability to traverse large distances in search of forage resources that meet their energetic requirements (Verlinden, 1997). However, these herbivore species show significant inter-annual fluctuations in population numbers as a consequence of spatial and temporal variability in rainfall and forage availability (Spinage & Matlhare, 1992). Throughout the 1900s, pans and river valleys outside of protected areas were utilised increasingly by local people for their better quality pasture and ephemeral water for livestock, resulting in the development of more permanent human settlements in these areas (Campbell, 1981). Certain studies have suggested that the significant decline in native ungulates during the drought period of the 1980s was caused by the erection of fences along the northern and eastern boundaries of the park, the provision of artificial waterholes (Knight, 1995b) and the presence of human settlements in the region of the Kalahari between the CKGR and Kgalagadi Transfrontier Park (KTP) (previously the South African Kalahari Gemsbok National Park and the Botswana Gemsbok National Park) (Campbell, 1981; Williamson & Williamson, 1981). These factors hindered the natural movements of herbivores towards regions with more widely available forage and water (Campbell, 1981; Williamson & Williamson, 1981). Artificial waterholes in the KTP were thought to have attracted herbivores towards regions of unsustainable forage (Knight 1995b). Increased human disturbance in these regions led to land transformation, overgrazing and the threat of poaching and, consequently, much of the landscape has become uninhabitable for indigenous herbivores (Campbell, 1981). The unfenced southern and western boundaries of the CKGR allow populations to migrate and move in and out of the protected area freely in search of necessary resources, such as water and better quality forage (Verlinden, 1998). Many human-related pressures that originate outside of national parks are not solely limited to wildlife in unprotected areas, but also impact the community structure of the entire, interlinked Kalahari region (Thouless, 1998). Continued expansion of human settlements and livestock grazing areas threatens to isolate wildlife populations within national parks (Verlinden, 1998), thus severely risking the long-term survival and fitness of native species (Newmark, 2008). The unpredictability of this environment combined with the climate change predictions of increased aridity and rainfall variability (Hulme et al., 2001); progressively amplify the vulnerability of the Kalahari to human disturbances. Naturally-occurring and cyclic threats, such as drought, are also common events in the Kalahari. Drought can dramatically reduce the carrying capacity of the region’s herbivores (Knight, 1995b; Coe et al., 1976) through a decline in the availability of water and forage.

Gemsbok (*Oryx gazella*) are exceedingly well-adapted to arid conditions and, although commonly described as grazers (Cerling et al., 2003), they feed on browse material to supplement their diet and survive permanently in the water-scarce Kalahari environment (Knight, 1991; Cain et al., 2006; pers. obs.) (Figure 1.2). Few studies have been conducted on gemsbok, and those that have were concentrated in the southern Kalahari or in Namibia (Knight, 1991; Lehmann et al., 2013; Osmers et al., 2012; Mills & Retief, 1984), therefore little is known about the population dynamics and movements of gemsbok in the CKGR. Discerning gemsbok movement responses and resource selection in relation to changes in resource availability through space and time could shed light on the ecological mechanisms that determine the movement patterns of these herbivores and allow subsequent inference of how they are able to survive in highly arid and variable conditions.

Recently developed technologies, such as satellite-derived vegetation indices, are a valuable means of monitoring the spatio-temporal variability and availability of primary productivity over large spatial and temporal scales (Kerr & Ostrovsky, 2003). These methods, used in conjunction with GPS satellite tracking, enable ecologists to assess movement and habitat selection patterns of individuals remotely, over extended time periods, and without continuous, costly fieldwork (Musiega & Kazadi, 2004; Pettorelli et al., 2006; Mueller et al., 2007). The advancing discipline of movement ecology allows ecologists to quantify the relationship between animals and their natural environments, explain and predict the responses of animals to environmental variability, and hopefully, aid in the development of ecosystem-scale conservation strategies. This study specifically investigates the movements and habitat selection of an ungulate exceedingly well-adapted to the Kalahari region during a period of limited rainfall.

Literature review

African savannas and spatio-temporal variability

African savanna ecosystems function through a number of interacting factors, such as rainfall, temperature, vegetation structure, soil composition, fire, topography and herbivory (Skarpe, 1992; van Langevelde et al., 2003). Climate and, in particular, rainfall, is the most important factor affecting the spatial and temporal distribution of vegetation across African savanna ecosystems (Fensholt et al. 2012). Rainfall has a positive relationship with primary productivity, which has been demonstrated in a number of semi-arid and arid regions (Rosenzweig, 1968; Nicholson & Farrar, 1994; Phillipson, 1975). Seasonal environments experience large fluctuations in precipitation, temperature and length of the growing season, thus vegetation phenology and the associated changes in plant quality are more pronounced than in more temporally-stable environments (van der Wal, et al., 2000). Phenology, combined with vegetation composition and structure, controls the availability of primary productivity for primary consumers (Pettorelli et al., 2007; Wiegand et al., 2008). It is the seasonality, inter-annual variability and instability of rainfall in arid African regions that results in a highly unpredictable vegetation distribution (Skarpe & Bergström, 1986). Vegetation quality relates to the protein concentration and energetic digestibility of forage materials (van der Wal et al., 2000), and is known to decrease with increasing biomass (Mueller et al., 2007). Fibre content and auxiliary metabolites accumulate within plants as they senesce and increase in quantity (Mysterud et al., 2001).

Drought conditions often lead to rapid declines in herbivore populations as a result of limited rainfall and, consequently, the loss of forage biomass and quality (Williamson & Mbano, 1988; Knight, 1995b). The impact of the drought depends on its duration and severity, as well as on compounding anthropogenic threats (Caughley et al.,1985). Changing climatic conditions could negatively impact wildlife, as well as the livelihoods of countless human populations dependent upon cattle farming. Du Toit (1995) reported that indigenous wild herbivores make up less than 10% of the overall biomass of large herbivores in Africa, whereas domestic cattle form the largest proportion. Although, Botswana has designated a significant proportion of its land for wildlife protected areas, indigenous animals are still at risk from human-influenced pressures and climate-related threats (Campbell, 1981).

Satellite Vegetation Indices

Satellite remote-sensing technologies have been beneficial for ecological research, specifically at a landscape scale of analysis and over long temporal periods (Kerr & Ostrovsky, 2003). Satellite vegetation indices, calculated with instruments such as the MODerate resolution Imaging Spectroradiometer (MODIS), and its predecessor, the Advanced Very High Resolution Radiometer (AVHRR), have been used for the assessment of spatio-temporal trends in primary productivity (Huete et al., 2002). Vegetation Indices can be utilised as proxies for vegetation productivity, biomass and nutritional quality (Paruelo et al., 1997; Box et al., 1989). The Normalized Difference Vegetation Index (NDVI) correlates closely with leaf area index (leaf thickness) and the amount of chlorophyll in the leaf (van Bommel et al., 2006). NDVI is calculated using the formula:

$$\text{NDVI} = \frac{(\text{NIR}-\text{RED})}{(\text{NIR}+\text{RED})}$$

where NIR is near infrared reflected radiation and RED is reflected red radiation (Pettorelli, et al., 2005). The formula is based on the characteristics of chlorophyll, which absorbs RED but reflects NIR, thus expressing a “greenness index” (Box et al., 1989; Pettorelli et al., 2005). The Enhanced Vegetation Index (EVI) is principally used over areas with high vegetation biomass because of its acute sensitivity to variations in canopy cover (Huete et al., 2002; Pettorelli, et al., 2005) and enhanced ability to cope with atmospheric aerosol interferences (Fensholt et al., 2006). EVI is calculated using the following formula:

$$\text{EVI} = \frac{\text{NIR}-\text{RED}}{\text{NIR}+\text{C1 x RED} - \text{C2 X BLUE} + L} \,.\, (1.5 + L)$$

where L is the canopy background correction factor, and C1 and C2 are constants of aerosol resistance (Fensholt et al., 2006; Huete et al., 2002). With the use of a soil adjustment parameter (L), the Soil Adjusted Vegetation Index (SAVI) was developed to control the effects of soil reflection and brightness in areas where vegetation biomass is low or background soil reflectance causes interference (Huete et al., 1992). The following formula is used to calculate SAVI:

$$\text{SAVI} = \frac{\text{NIR}-\text{RED}}{(\text{NIR}+\text{RED}+L)} .\, (1 + L)$$

Satellite vegetation indices are an efficient means of investigating the phenology of vegetation over large spatial and temporal scales (Reed et al., 1994). Phenological metrics, such as the onset and offset of greenness, duration of greenness, and peak greenness are valuable measures for assessing and mapping long-term trends and seasonality, particularly highly variable areas.

NDVI is a valuable measure for assessing the prevailing rainfall regimes as it has been found to closely relate to precipitation conditions, and can be used as a proxy for spatial and temporal rainfall variability (Anyamba & Eastman, 1996). NDVI measured over the Kalahari correlated with precipitation with a lag period of one to two months (Richard & Poccard, 1998), and is known to be influenced by soil composition (Nicholson & Farrar, 1994). AVHRR NDVI images at a resolution of 4 km x 4 km, and with a temporal resolution of 10 days were positively correlated to aircraft-based, visually-measured grass greenness in a study conducted by Verlinden & Masogo (1997) in the southern Kalahari. Additionally, AVHRR NDVI had a positive relationship with precipitation in the Kalahari (Grist et al., 1996). The more recently-developed MODIS NDVI, which is measured at a spatial resolution of 250 m or 500 m and provides temporal composites of 16 or 8 days respectively, was chosen as the most suitable vegetation index for this study. MODIS NDVI has been successful in a number of studies, including the evaluation of spatial variability of vegetation across a semi-arid region of Brazil (Schucknecht et al., 2013), the estimation of herbivore forage quality in a semi-arid region of Mongolia (Kawamura et al., 2005) and in the description of phenology (Zhang et al., 2003). Additionally, MODIS NDVI was found to accurately mirror *in situ* NDVI measurements within semi-arid habitats (Fensholt et al., 2006).

Herbivore movements

The movement ecology and habitat selection patterns of large herbivores must be understood by comparing movement patterns to the environmental conditions experienced by the animal (Nathan et al., 2008). Since these conditions differ through space and time, a spatio-temporal outlook is necessary to assess habitat variability and seasonality. Nathan et al. (2008) incorporate four important components to develop a theoretical framework for animal movement ecology. Firstly, the internal (physiological and neurological) state of the organism infers the incentive of movement (Nathan et al., 2008). The second and third factors include the capabilities of the organism for movement and navigation (Nathan et al., 2008), and explain where, how and when movement should take place (Holyoak et al., 2008). Finally, all external environmental variables make up the fourth component (Nathan et al., 2008). These include abiotic and biotic factors, such as food quality and quantity, reproduction, water, soil minerals, shelter and predation avoidance (Holyoak et al., 2008), which often place conflicting demands on the animal (Morris 2003; Gaillard et al., 2010). Seasonal growth rates, phenology and the spatial arrangement of primary productivity play vital roles in the resource selection, home ranges and landscape-scale movement patterns of wild ungulates (Fryxell, 1991; White, 1983: Wiegand et al., 2008; Albon & Langvatn, 1992).

Optimal foraging theory refers to the choices herbivores face between persisting in a particular foraging area and relocating to another area that is possibly more nutritionally advantageous (Gross et al., 1995). Herbivores face a range of costs and benefits relating to occupying a particular site at a specific point in time (Beyer et al., 2010). Costs include factors such as predation risk, or the energetic expenditure of movement or feeding; while benefits include reproduction opportunities, shelter, and the acquisition of necessary minerals, moisture and nutrients (Beyer et al., 2010; Gross et al., 1995; Parker et al., 1996). Large mammalian herbivores are able to forage on vegetation of lower quality than smaller ungulates, but they require larger quantities of plant biomass to ingest adequate nutrition and energy (Illius & Gordon, 1987; Demment & van Soest, 1985). Small-bodied herbivores feed more selectively on better quality forage (Jarman, 1974). Dry season conditions in arid environments are the most costly to herbivores because the quality and availability of forage declines considerably in comparison to wet season conditions, and travelling between adequate foraging locations is often time-consuming and energetically-expensive, and can put herbivores at risk of increased water loss. When faced with depleted food resources, herbivores either remain where they are and expand their diets to include lower quality forage, or they disperse in search of better quality forage elsewhere (Holdo et al., 2009; Augustine, 2010; Shannon et al., 2013). For example, buffalo in Klaserie Private Nature Reserve (KPNR) increased their travel distances and occupied much larger home ranges during dry conditions, when high quality forage availability was limited (Ryan et al., 2006). Verlinden (1998) suggested that, during dry periods or drought conditions, herbivores in the Kalahari would be expected to traverse greater distances in search of adequate resources. However, in a contrasting case, herbivores in arid southern Australia were forced to adjust their diets in response to forage depletion during dry season conditions, leading to increased interspecies competition (Dawson & Ellis, 1994). In most cases, the low availability of high quality vegetation in the dry season forces herbivores to alter their diets by consuming less favourable forage material (Bailey et al., 1996; Macandza et al., 2004).

During the drought period of the 1980s, tens of thousands of wildebeest (*Connochaetes taurinus*) died from starvation in the southern and central Kalahari, many as a result of fences that prevented their natural migration to areas of greater water and forage availability (Knight, 1995b; Spinage & Matlhare, 1992; Thouless, 1998). Other species, such as red hartebeest (*Alcelaphus buselaphus*), eland (*Taurotragus oryx*) and giraffe (*Giraffa camelopardalis*), also showed considerable population declines during this period (Thouless, 1998). Contrastingly, resident gemsbok populations were less affected by the drought, and this is thought to be related to their ability to meet their water requirements from sources other than fresh drinking water (Knight, 1991), and to their different movement and foraging strategies (Knight, 1995b). The availability and variability of rainfall is believed to drive wildlife movements in the Kalahari (Parris, 1972; Williamson et al., 1988), where herbivores are believed to track rainfall with their sense of smell (Campbell, 1981).

Movement analyses and GPS tracking

Habitat or resource use is defined as the proportion of time or quantity of the resource that an individual (or population) utilises in a specific place over a defined period (Manly et al., 2002). Habitat (or resource) selection is defined as the action of actively choosing one habitat (or resource) over another (Johnson, 1980). Habitat (or resource) use is described as being selective only when it is used significantly more abundantly compared to its availability (Johnson, 1980). Habitat (or resource) availability includes the habitats (or resources) that are accessible to the individual (or population) (Johnson, 1980; Aarts et al., 2008). Habitat use varies with availability (Manly et al., 2002), and, therefore, it is only by comparing usage with availability that one is able to quantify an individual's habitat (or resource) selection (Manly et al., 2002). Habitat selection models are beneficial for the analysis of the relationship between individuals (or populations) and their environments and for the identification of important resource hotspots within the landscape (Johnson, 1980).

A species closely related to gemsbok, the Arabian oryx (*O. leucoryx*) modified its space use in response to spatially-stochastic precipitation (Spalton, 1993). Spalton (1993) found that Arabian oryx utilise small areas, which occasionally overlap, and form part of a larger, expanding home range. The time lag between rainfall events and the green-up responses of primary productivity is an important consideration in herbivore movement ecology. For example, an obvious lag period was evident between rainfall events that increased forage biomass and the enhanced utilisation of that forage by female eland, which had migrated into the Nairobi National Park, Kenya (Hillman, 1988).

GPS technology provides higher frequency and more accurate location and movement data than *in situ* observations (Tomkiewicz et al., 2010), and enables ecologists to develop more elaborate habitat selection models (Beyers et al., 2010). It is only by understanding the mechanisms that regulate movement and behaviour patterns that ecologists will be able to define environmental trade-offs and predict how wildlife may react to threats such as climate change, vegetation loss, habitat degradation and the enhanced unpredictability in the quantity and distribution of rainfall.

Study area

The CKGR (Figure 1.1), established in 1961 in central Botswana (Hitchcock, 2002), extends over an area of approximately 52 800 km². The unfenced boundaries of the reserve allow wildlife to roam extensively across the Kalahari region in pursuit of required resources (Makhabu & Marotsi, 2012). Ambient temperatures range from extreme lows of -1 °C during the winter months to extreme highs of 40 °C in summer (Makhabu et al., 2002; Owens & Owens, 1978). Following the Kalahari rainfall gradient, from the southwest to the northeast, the Kgalagadi Transfrontier Park receives 200-250 mm of average rainfall per year (Mills & Retief, 1984; Nicholson & Farrar, 1994), Khutse Game Reserve (directly south of CKGR) experiences an average annual rainfall of 300 mm, while yearly rainfall in the north-eastern sections of the CKGR is approximately 400 mm (Nicholson & Farrar, 1994). Rain falls predominantly during the summer months (October to April), but significant inter- and intra-annual variations in rainfall characterise the Kalahari as a highly unpredictable environment (Makhabu et al., 2002; Scalon et al., 2002). The fluctuating rainfall regime results in a large degree of spatial and temporal variability in primary productivity (Nicholson & Farrar, 1994). Movements in pursuit of unpredictable resources, are essential for herbivore population sustainability during adverse environmental conditions, and often lead to the flow of populations between protected and unprotected areas in the Kalahari (Crowe, 1995; Thouless, 1998).

The Kalahari is made up of undulating sandy dunes, which hold just enough moisture near the soil surface to support open grasslands, and scattered trees and shrubs (Campbell, 1981). Small, sparse woodland savanna regions also exist (Campbell, 1981).The fairly homogeneous dune landscape is comprised of deep, mostly infertile, mineral-deficient soils (Thomas & Shaw, 1991; Knight, 1991). Due to the considerable lack of water and soil nutrients, the dry Kalahari region is devoid of agricultural crops, but large proportions of the environment are exploited for livestock grazing (Darkoh, 2003). Scattered throughout the region are large, saline pans, which contrast with the extensive dune regions (Campbell, 1981) (Figure 1.3). Pans have firm soils, with high concentrations of clay (and, in some places, calcrete), which hold nutrients and, occasionally, surface water after rainfall events (Parris & Child, 1973; Knight, 1995a). The northern CKGR has three well-known fossil river valleys: Deception (Figure 1.4), Passarge and Letiahau, which have soils with a similar composition to pans (Bergström & Skarpe, 1999). Due to their clay-rich soils and ability to retain some moisture, pan and valleys produce pastures of short, nutritious, green grasses during the summer months, which attract large hosts of native herbivores (Campbell, 1981; Parris & Child, 1973; Verlinden, 1997). Scattered tree islands exist within and along the borders of pans and valleys, providing adequate shade for wildlife during the hottest times of day (Knight, 1991; pers. obs.). The dominant dune areas have fast infiltration and evapotranspiration rates (Knight, 1995a), and the vegetation composition differs considerably from pans and valleys (Makhabu et al., 2002). The vegetation is described as shrub savanna (Verlinden, 1998), with occasional scattered trees, of mostly *Vachellia* spp. (previously *Acacia*) and *Boscia albitrunca* (Skarpe, 1986). Tall, perennial grasses include species such as *Stipagrostis* spp., *Eragrostis* spp. and *Aristida* spp. (Skarpe, 1986). The dune grasses are often less nutritious and lower in protein content than pan and valley grasses, but are considerably higher in biomass (Knight, 1991). Herbivores are sporadically attracted to pan regions for resources other than just grasses; these include surface waters and soil minerals, which they lick from the soil surface (Bergström & Skarpe, 1999; Parris & Child, 1973) (Figure 1.5).

Natural drinking water is only present occasionally during the summer rainfall period, immediately after rainfall events within pan and valley habitats (Knight, 1995b). Hence, during the dry season, the Kalahari lacks natural drinking water, and wildlife is either forced to move to other regions, where water is more readily available, or acquire moisture from other resources, such as underground roots and tubers (Williamson, 1987), or water-rich fruits that occur above-ground (Knight, 1995a). Three species of the Cucurbitaceae family occur in the Kalahari region, the gemsbok cucumber (*Acanthosicyos naudinianus*), the wild cucumber (*Cucumis africanus*) and the most prevalent, frost-resistant, tsamma melon (*Citrullus lanatus*) (Lovegrove & Knight-Eloff, 1988; Knight, 1995a). Tsamma melons, which mature during the dry, winter months, are an important alternative water source for native wildlife in the Kalahari (Knight, 1995a). Tsamma melons are utilised by a number of species, from rodents to carnivores, and, most frequently, by large herbivores (Knight, 1995a).Gemsbok used tsamma melons even while near to surface water, suggesting that these resources could contain other valuable nutrients that supplement their diets (Knight, 1995a). The availability of tsamma melons is also highly variable, and as a result, their utilization by herbivores remains inconsistent (Knight, 1995a). Gemsbok cucumbers are, however, more predictable in their annual growth patterns than tsamma melons (Keith & Renew, 1975). Wildlife species are thought to locate underground storage organs with their keen sense of smell, and gemsbok have been observed with their noses to the ground, smelling out roots and tubers that they dig up using their hooves (Williamson, 1987).

Study species

Gemsbok are exceptionally well-adapted, both behaviourally and physiologically, to harsh southern African arid regions (Cain et al., 2006; Skinner & Chimimba, 2005) and are distributed throughout the arid territories of southern Africa (Skinner & Chimimba, 2005). Males are generally heavier than females, weighing on average 240 kg, whereas the slighter-built females have a mass of approximately 210 kg (Skinner & Chimimba, 2005). Gemsbok are predominantly grazers, but are known to forage occasionally on browse material (Cerling et al., 2003). When compared to wildebeest, Knight (1991) described gemsbok as having a narrower muzzle, which aids in forage selection and the consumption of succulent plant species, underground roots, storage organs and fruit (Knight, 1991; Williamson, 1987). They obtain the majority of their water from grasses and alternative forage resources and, therefore are not dependent on permanent sources of drinking water for survival (Knight, 1991; Knight, 1995a). Gemsbok, like the closely-related Arabian oryx (Spalton, 1993), are opportunistic breeders that give birth throughout the year (Eloff, 1959).

Gemsbok do not show seasonal trends in their movements, and are considered to be non-migratory (Williamson, 1987), nomadic ungulates (Kreulen, 1985). They appear to avoid communal areas as much as possible (Thouless, 1998), and usually remain further than 66 km from settlements and livestock (Bergström & Skarpe, 1999). In fact, aerial surveys of Botswana in 1992 concluded that gemsbok are increasingly restricted to protected areas (Bonifica, 1992), which do not necessarily contain the most suitable foraging conditions (Verlinden & Masogo, 1997). Expansion of cattle grazing zones would likely constrict gemsbok and other indigenous herbivore ranges, resulting in increased competition for resources between wild ungulates. Knight (1991) proposed that, throughout the year, in the southern Kalahari, gemsbok actively select greener grasses. On the other hand, Verlinden & Masogo (1997) established that gemsbok populations use areas of low NDVI greenness, perhaps to avoid human settlements in unprotected areas, where the most suitable grazing sites are selected by cattle. Their ability to utilise regions of low greenness could also be attributed to their supplementary consumption of browse material, water-rich fruits and underground storage organs (Verlinden & Masogo, 1997; Knight, 1991; Dieckmann, 1980). During the 1970s and 80s, a study conducted in the southern Kalahari found that, when compared to hartebeest and wildebeest, gemsbok population distributions showed the strongest correlation with rainfall events, following a lag period of one to two months (Mills & Retief, 1984). Hartebeest also responded to rainfall events after a one to two month lag period, but this response was considerably less pronounced than that of gemsbok (Mills & Retief, 1984). The relationship between gemsbok presence and rainfall was strongest in riverbed habitats (Mills & Retief, 1984), which, like pans, contained soils and vegetation richer in minerals and of higher quality than dune regions (Leistner, 1967). During dry conditions, gemsbok populations showed a rapid movement into dune areas, where grasses had a lower protein concentration in the riverbed habitats but were considerably more abundant (Mills & Retief, 1984).

Gemsbok populations in south-western and central Kalahari displayed similar trends, as they used pans more during rainy periods, when they were found in greater concentrations, than during the dry, winter months (Bergström & Skarpe, 1999; Owens & Owens, 1978). Gemsbok require between 2.4 and 3.9 litres of water per day, depending on the ambient temperature (Taylor, 1968). This water is acquired through various means, such as natural or artificial water supplies, grazing forage, succulent plants, fruit or underground plant storage organs (Knight, 1991). Hitchcock (1996) found that gemsbok can tolerate water high in salinity, but this tolerance is known to decline during drought conditions, when drinking highly saline water can lead to an increased risk of dehydration (Knight, 1995b). Pan habitats are attractive to gemsbok for a number of resources other than palatable grazing and occasional surface water succeeding rainy conditions (Knight, 1991; Eloff, 1959). These include soil mineral and salts, which gemsbok have been observed to acquire by actively digging into pan soils with their front hooves (Eloff, 1959, pers obs. (Figure. 1.5)).

Thesis structure

The aim of this thesis is to investigate the degree of spatial and temporal variability in green vegetation across the northern CKGR during a low rainfall year, and subsequently to determine how gemsbok, herbivores well-adapted to aridity, respond to this environmental variability with behavioural movements and habitat selection. Three distinct habitat types were defined: pans, valleys and dunes. Pans and valleys were combined into one habitat type because of their similar soil and vegetation compositions, and are referred to as pan-valley habitats.

The study has been separated into two research chapters, which are integrated in the final conclusion chapter. The first research question involves the regional long- and short-term NDVI greenness patterns of the northern CKGR.

The main objectives were:

1. To assess long-term greenness changes from 2000 to 2013 across pan-valleys and dunes.
2. To assess the short-term greenness variations from November 2012 until July 2013.
3. To compare the timing of greening up between pan-valley habitats and dune habitats.
4. To compare the duration of green periods between pan-valley habitats and dune habitats.

These objectives were achieved by investigating trends in NDVI at bimonthly and annual temporal scales. Annual phenological metrics were calculated using a method adapted from Reed et al., (1994). Cluster analyses were performed to identify areas of high, low and persistent greenness at bimonthly and annual temporal scales.

The second research chapter focuses on the movement ecology of gemsbok in the northern CKGR, and examines the relationship between gemsbok foraging locations, habitat type and satellite-measured vegetation greenness.

The main objectives were:

1. To determine whether gemsbok foraging locations coincided with greener areas compared to less green areas during transition periods, when the landscape is neither homogeneously green nor homogeneously brown.

2. To determine whether gemsbok favour green regions in one habitat type over green regions in another.
3. To assess the seasonal variation between 12-hour displacement distances of gemsbok.

The first two objectives were achieved with the use of use-availability generalized linear mixed models, following Manly et al. (2002)'s Design III, which states that each individual animal and its available resources are separately identified. Three different measures were used to represent greenness: NDVI, ΔNDVI (change in NDVI between one 16-day time period and the previous 16-day time period, i.e. T_n and T_{n-1}) and relative greenness, which was defined on a pixel-by-pixel basis through time. Relative greenness uses the NDVI distribution through time during the collar period to establish the relative level of greenness for each individual pixel, thus omitting the effect of spatial variation in soil and vegetation structure. These three measures of greenness assisted in evaluating the use of satellite-measured NDVI to identify habitat and resource selection by gemsbok in an arid savanna. Finally, objective 3 was achieved using Wilcoxon rank sum tests for comparing two repeated measures to investigate seasonal changes in 12-hour gemsbok displacement distances.

The final chapter (Chapter 4) forms an integral component of the study, linking the main concluding statements from the two research chapters and providing an overall synopsis and evaluation of the key findings.

Figures

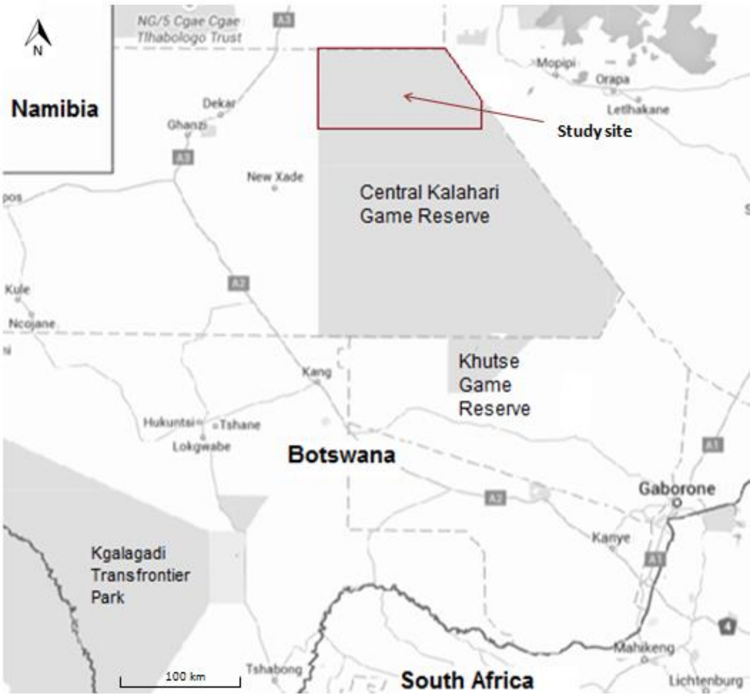

Figure 1.1 Map of the Central Kalahari Game Reserve, Botswana showing the study site depicted in the northern region of the reserve. (Adapted from Map data ©2015 AfriGIS (Pty) Ltd, Google)

Figure 1.2 Gemsbok (*Oryx gazella*) feeding on browse material in the northern region of the Central Kalahari Game Reserve. This photograph was taken in May 2014.

Figure 1.3 Photograph of a pan in the northern region of the Central Kalahari Game Reserve, taken from a helicopter in November 2012, revealing the clear contrast between pan regions and dune regions in the late brown season.

Figure 1.4 Photograph of Deception Valley, Central Kalahari Game Reserve, taken from a helicopter in May 2014, revealing the clear distinction between valley regions (top right of the photograph) and dune regions (bottom of the photograph) in the late green season.

Figure 1.5 Gemsbok (*Oryx gazella*) utilizing a pan habitat in the Kgalagadi region of Botswana. This photograph was taken in March 2014, and gemsbok were seen digging with their front hooves into the pan sands.

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CHAPTER 2: SPATIO-TEMPORAL VARIABILITY IN SATELLITE-MEASURED GREENNESS ACROSS THE NORTHERN CENTRAL KALAHARI GAME RESERVE

Introduction

The harsh, water-restricted savanna regions of southern Africa are both highly diverse and remarkably dynamic. There are a number of intrinsically-linked natural factors affecting savanna systems, such as rainfall, temperature, soil, vegetation type, topography, herbivory and fire (Skarpe, 1992; van Langevelde et al., 2003; Bergström and Skarpe, 1999). The intensity and dispersal of rainfall is, by far, the most important factor determining the distribution of local flora and fauna within arid/semi-arid savannas (Fensholt et al. 2012; Coe et al., 1976). The Kalahari ecosystem, which is the focus of this study, supports a considerable number of wild, well-adapted animal and plant species. The availability of palatable forage material is vital for the survival of the native herbivores, and in turn, their predators. Only once scientists have comprehensively understood the variability and diversity that exists in these dry savanna ecosystems, can we begin to comprehend the conditions that arid-adapted herbivores and their predators experience on an inter-annual and seasonal basis. A holistic understanding of the greenness trends over the past decade is essential before one can accurately predict how a potential change in climate might affect the future of forage availability in the central Kalahari.

Satellite imagery provides valuable, spatially-consistent data that cover large spatial and temporal scales (Huete et al., 2002). The MODerate resolution Imaging Spectroradiometer (MODIS) instruments situated on the Terra satellite (launched in 1999) and the Aqua satellite (launched in 2002) collect comprehensive data on the earth’s oceans, land, ice and atmosphere (Tucker & Yager, 2011). MODIS, the successor to Advanced Very High Resolution Radiometer (AVHRR), acquires data in 36 spectral bands (Tucker &Yager, 2011). Among the many MODIS products are the vegetation indices: the Normalized Difference Vegetation Index (NDVI) and the Enhanced Vegetation Index (EVI), which enable the observation of variability in the degree and distribution of vegetation greenness. (Tucker & Yager, 2011). Greenness has been described as a proxy for vegetation cover and above-ground net primary productivity (ANPP) (Paruelo et al., 1997; Fensholt et al. 2012; Box et al., 1989), and shows a correlation with biomass (Shippert et al., 1995) and the timing of high quality forage growth (Pettorelli et al., 2011).

The relationship between satellite-measured NDVI and rainfall has been referred to as the ‘rain-use efficiency’ (Nicholson & Farrar, 1994), which is defined as the ANPP per unit rainfall (Bai et al., 2008). A global study into the relations between annual climate and the seasonal change in NDVI showed that the timing of NDVI extremes were closely related to seasonal trends in temperature and rainfall, with a lag period of one to two months between rainfall and NDVI (Potter & Brooks, 1998). On a smaller spatial scale, a study conducted in Botswana during the 1980s found that NDVI patterns appear to parallel the oscillations of seasonal rainfall, and also experienced an approximate lag of two months between rainfall events and peaks in NDVI (Nicholson & Farrar, 1994). The rainfall-NDVI relationship was found to be much stronger in Botswana than other savanna regions further north and in West and East Africa, which have a similar climatic regime to Botswana (Nicholson & Farrar, 1994; Scanlon et al. 2002; Goward & Prince 1995; Richard & Poccard 1998). A linear relationship between rainfall and NDVI existed in the semi-arid regions of Botswana, when rainfall did not surpass 500 mm per annum (Nichoson & Farrar, 1994). Beyond this threshold, a level of “saturation” occurred, after which NDVI increased with rainfall only very marginally (Nicholson & Farrar, 1994). Above a certain threshold, rainfall events can surpass the level necessary for grass growth (Scanlon et al., 2002). This relationship between NDVI and precipitation is not simple, however, and soil and vegetation types also play an important role in rain-use efficiency (Nicholson & Farrar, 1994).

In a study following that of Nicholson & Farrar (1994), it was established that the NDVI-rainfall relationship varied with soil type (Farrar et al., 1994). The soils with the highest level of productivity were vertisols, rich in clay, while the least productive were arenosols, which are sandy with low levels of organic matter (Farrar et al., 1994). Soil type also had some effect on the duration of the lag period between the rainfall events and the subsequent peak in NDVI (Nicholson & Farrar, 1994). Soil type affects water retention rates (Nicholson & Farrar, 1994), and so has a substantial impact on the relationship between rainfall and the availability of water for vegetation (Méndez-Barroso et al., 2009). Vegetation type also influenced the relationship between NDVI and precipitation in Botswana (Nicholson & Farrar, 1994). In general, woodlands showed very slight inter-annual variability in NDVI (Nicholson & Farrar, 1994), and produced considerably higher NDVI values than grassland-dominated regions (Scanlon et al., 2002). The drier sandveld regions, classified as the thornveld, and characterised by large grassland areas, produced moderate NDVI values compared to trees (Scalon et al., 2002) and experienced great annual instability in the degree and duration of NDVI greenness (Nicholson & Farrar, 1994). In savanna regions, grasses show a more expansive areal biomass following precipitation events than trees (Scalon et al., 2002). Bare soil produced low NDVI values, with an equally low sensitivity to inter-annual variations in precipitation (Scanlon et al., 2002).

As the second largest nature reserve in the world, the extensive Central Kalahari Game Reserve (CKGR) makes up 1/11th of Botswana's entire surface area. The region is classified as semi-arid, which, by definition, refers to an area where water is a major limiting factor for plant productivity (Fensholt et al., 2012). The CKGR was originally established in 1961 by British colonials as a reserve for the Basarwa (San or bushmen) to continue their traditional, nomadic, hunter-gatherer lifestyle, without disturbance from other peoples (Wiessner, 1984; Hitchcock, 2002). It covers an area of 52 800 km², and is distinguished by its unpredictable supply of surface water (Thomas & Shaw, 1991). The mostly homogeneous dune landscape is interspersed with vastly different features: the valley and pan systems (Makhabu et al., 2002). Pans in southern Africa are defined as depressions that hold water following a rainfall event (Lancaster 1978). In the Kalahari, pans are believed to be a result of aeolian formation (Grove 1969, Rogers 1934, Wayland 1953; Lancaster 1978). Pans and valleys, with their soils high in clay and calcrete, support open grasslands. With their fertile soils and higher capacity to hold soil moisture, pans provide greater productivity than dune habitats during wetter months (Knight, 1991). On the other hand, dune regions, which consist of sandier, less fertile soils, are believed to be more productive during the months of low rainfall (Knight, 1991).

This study provides a regional investigation of the vegetation greenness trends in one of the most remote semi-arid regions of southern Africa, the northern CKGR. Particular attention was paid to the contrasts between habitat types. Since pan and valley regions display very similar soil and vegetation structures (Knight, 1991), they have been grouped together into one habitat type, the pan-valley habitat, and are compared to the divergent dune habitats. Four objectives and hypotheses were formulated to assess long- and short-term changes in greenness. The first objective was to assess long-term greenness changes from 2000 to 2013 across pan-valleys and dunes, and the corresponding hypothesis (H_1) is that green regions do not recur in the same area every year or season, yielding high inter-annual spatial and temporal variability. The second objective was to assess short-term greenness changes, from November 2012 until July 2013, with the hypothesis (H_2) that, within habitats, relative greenness would be patchily distributed across space and time during the wet season conditions and the location of green regions would be directly attributed to isolated thunderstorms. The third objective was to compare the timing of *green up* between dune and pan-valley habitats. I hypothesized (H_3) that, following periods of rainfall, green patches in pan-valley habitats would green up earlier in the season than patches in the dune habitats. The fourth and final objective was to assess the duration of green periods between the pan-valley and dune habitats. It was hypothesized (H_4) that green regions within dune habitats would remain greener for longer in the season than those in the pans and river valleys. Increases and decreases in NDVI over time will be referred to as *greening* and *browning*, respectively. The mean NDVI over time was calculated on a pixel-by-pixel basis. When each pixel is compared to itself through time, it will be referred to as *brown* or *green* on the occassions when the value of that pixel is lower or higher than its mean, respectively.

Methods

Study area

The study was conducted in the northern region of the CKGR (Figure 2.1 and 2.2) and comprised a total area of approximately 16 853 km². The landscape is predominantly flat and made up of gradually undulating, immobile sand dunes dominated by an arid sandveld vegetation (Makhabu et al., 2002). The dune systems are interspersed with three prominent fossil river valleys: Deception, Passarge (Owens & Owens, 1978) and Letiahau Valleys, and by several large pans (Figure 2.2). The major pans and the valley systems are made up of paler, harder clay- and calcrete-dominated soils than the dunes (Knight, 1991; Makhabu et al., 2002), and usually support short, green grasses during the rainy season (Makhabu et al., 2002). In this study, I assessed the spatial and temporal variation of greenness across two major habitat types. Dunes were compared to valley and pan habitats, which were grouped because of the similar soil and vegetation structures in these habitats. The region receives a variable annual rainfall of approximately 400 mm (Makhabu et al., 2002; Owens & Owens, 1978), which falls mainly during the summer months from October to April (Makhabu et al., 2002), in the form of ephemeral convective storms (Scanlon et al., 2002). The vegetation structure is characterised by open shrub savanna with scattered trees and shrubs, particularly the evergreen *Boscia albitrunca*, semi-evergreen *Vachellia* (previously *Acacia*) *haematoxylon* and deciduous *Vachellia* (previously *Acacia*) *erioloba* (Knight, 1991).

Data Acquisition

For the 2000-2013 period, MODIS 13 Q1 NDVI time series satellite data, for southern Africa was sourced from the MODIS Reprojection Tool Web Interface (MRTWeb, https://mrtweb.cr.usgs.gov/). The data are freely available and are corrected for factors such as aerosols, water vapour, cloud shadows and orbital drift (de Jong et al., 2012). The images are taken daily and, every 16 days, the highest NDVI value per pixel is chosen as the measure of vegetation greenness to reduce the effects of contamination, such as cloud cover, in the final composite image. The satellite images downloaded for this study were at a spatial resolution of 250m with 16 day (bi-monthly) composites. These data were used to analyse long- and short-term vegetation variability and trends in the northern CKGR. The major pan and valley regions were separated from the rest for the study site with the use of a shapefile made by hand in ArcGIS 10.1 and Google Earth. The entire study site was made up of 269

648 pixels, but only 2 642 of those pixels were classified as pan-valley habitats, which make up a much smaller surface area (1%) than the immense dune regions.

Temporal analysis

The temporal analyses in this study were divided into two components (1st and 2nd objectives). The first assessed the long-term annual variability in greenness from the year 2000 to 2013. The second looked at short-term variability from November 2012 to July 2013 (Table 2.1) when eight female gemsbok were collared in this area and their GPS satellite positions were recorded (see Chapter 3). NDVI rasters compiled every 16 days from mid-February 2000 until the end of November 2013 were used in the long-term study. This means that the years 2001 to 2012 were made up of 23 16-day rasters each, but 2000 and 2013 contained only 20 and 21 rasters, respectively.

Analyses of greenness

The NDVI raster images in this study were compared in two distinct manners. Firstly (objectives 1 and 2), on a pixel-by-pixel basis through time, whereby each individual pixel was compared to itself through time, as a relative greenness measure. The assumption was that vegetation structure and soil type remained fairly homogeneous over time, and so changes in greenness over time should rather be a result of rainfall variation. Secondly (objectives 3 and 4), the pixels were compared through space to the other pixels across the habitat, using cluster analyses. These analyses were valuable as assessments of the change in the degree of greenness across space, and described what a potential herbivore might have experienced at a particular point in time. Both methods were essential because the variability of greenness across the spatial and temporal scales form major elements of this study. Vegetation structure was expected to differ more significantly across space than time, and as such patches of high greenness that remained consistently green throughout both the green and brown seasons were likely to have been dominated by evergreen tree species, which do not lose their leaves during the dry season.

Data Analysis

H_1: Long-term annual trends in greenness:

I calculated the mean, sum, maximum, standard deviation and co-efficient of variation for each 16-day, 250m NDVI raster, and then averaged those across space and time for each year from 2000 to 2013. The “Raster Calculator” tool in ArcGIS® 10.1 (Esri®, 380 New York Street, Redlands, CA, United States) was used to create a single output raster for each year from a list of input rasters with each type of descriptive statistic. The input rasters included the 16-day NDVI rasters for each year, and the output rasters provided me with pixel-by-pixel values, calculated across time. The major pan-valley habitats of each output raster were distinguished from the dune pixels to determine whether the two habitat types showed variation in their long-term annual greenness trends. All pixels in each habitat type were averaged to produce one value for each year and each habitat. These results were then plotted against time.

Cluster Analyses:

Cluster and outlier analyses (Anselin’s Moran I similarity index) were performed on each mean annual raster from 2000-2013. A cluster in this study was defined as a group of adjacent pixels that exhibited a statistically significant similarity in their greenness values, be it high or low. The cluster analysis was performed in ArcGIS 10.1, where the ‘Inverse distance’ was used as the conceptualization of spatial relationships based on the idea of spatial autocorrelation, that “nearby neighbouring features have larger influences on the computations for a target feature, than features far away” (ArcGIS 10.1). Euclidean distance provides the straight-line distance between two points, and was selected as the most suitable distance method for continuous NDVI raster data. Binary rasters of HH clusters (areas of high NDVI) and LL clusters (areas of low NDVI) were created for each year. This tool was able to identify clusters of high and low greenness, as well as outliers, which are pixels surrounded by pixels exhibiting drastically different values. However, only the HH and LL clusters were necessary for these analyses. In total, 28 binary rasters were produced, 14 each of HH and LL clusters per year. From these two sets of 14 rasters, two more rasters were produced, using the ‘Equal to Frequency’ tool in ArcGIS 10.1, to determine how many times during the 14 year period each pixel fell within a HH or LL cluster.

Phenological metrics and seasonal fluctuations:

Spatially-averaged NDVI greenness was plotted against time to show seasonal trends in greenness from 2000 to 2013. Six simplified phenological measures were derived from spatially-averaged MODIS NDVI trend data, using a method adapted from Reed et al. (1994), whereby a rapid, sustained peak in NDVI was identified to signal the onset of greenness.

These basic metrics defined the green and brown seasons for each year, and included temporal metrics for the onset, offset and duration of the green season, as well as NDVI metrics, which included the NDVI value at onset, offset and peak greenness. This procedure is useful for the analysis of phenology, but it is important to acknowledge that in this study the metrics did not correspond to specific dates in the calendar year because the data had a bi-monthly temporal resolution. The results were therefore limited in their precision, and rather indicated which of the 16-day periods fell in the green season, and which in the brown season. The onset of greenness was determined by comparing the seasonally-oscillating NDVI trend to a moving average graph of the time series. The moving average was calculated using the equation:

$$A_t = (B_t + B_{t-1} + B_{t-2} + \ldots B_{t-(x-1)}) / x$$

where A_t is the value of the moving average at time t, B_t is the NDVI value at time t, and x is the time interval of the moving average. The moving average time interval is an important component of the analysis, and needs to be selected with caution (Reed et al. 1994). A small period generates a highly oscillating curve that could identify irrelevant fluctuations in the data. On the other hand, a large period produces a flattened curve, which is less sensitive to the trend data (Maxwell, 1976). Several moving average periods were tested, varying from 3 to 23. A period of 12 was selected because it produced a semi-annual lag, which best corresponded to the data’s 16-day resolution (23 periods per annum). The onset of greenness was identified as the first data point of the NDVI series that fell above the intersection point between the NDVI trend and the moving average curve, with at least the next two subsequent NDVI points remaining above the moving average curve as well (Figure 2.3). The end of the green period was defined using an analogous process, whereby a second moving average curve (also with a period of 12) was produced, which lagged behind the NDVI trend, rather than in front. This time, the offset of greenness was identified as the last data point of the NDVI series that lay above the intersection point between the NDVI trend and the second moving average curve (Figure 2.3). Duration was easily calculated by adding the number of 16-day periods that fell within the green season for each year. The maximum NDVI value for each season was taken to be the value at the highest inflection point of each green season. Rainfall in the Kalahari predominantly begins in October and ends in the following April, and greenness trends reflect those of rainfall. As a result of this, the green season was predicted to span from the end of one year into the beginning of another. For example, the 2001 green season began in November 2000 and ended in June 2001. The brown season of 2001 would then follow its green season.

Once the green and brown seasons for each year had been defined, rasters depicting the seasonal greenness for each year were produced to assess whether green patches occurred in the same area each green season. The sum of all NDVI rasters in the brown season were subtracted from the sum of all NDVI rasters in the green season to omit areas of persistent greenness (probably regions containing evergreen tree species) and portray seasonally green patches for each year. This analysis was performed using the ‘Raster Calculator’ tool in ArcGIS 10.1. Twelve rasters showing seasonally green patches were produced for the years 2001 – 2012.

H_2: Short-term trends in greenness (Nov 2012 – Jul 2013):

NDVI mean and standard deviation were calculated using 16-day rasters from the beginning of 2011 to the end of November 2013, and will be referred to as the short-term mean and standard deviation ($Mean_{st}$ and $Stdev._{st}$). The collar period (Nov 2012 – July 2013) was comprised of 16 NDVI rasters, each of which was compared to $Mean_{st}$. I created binary rasters, whereby pixels with a value of 0 and 1 were areas where the NDVI value was less than and greater than the $Mean_{st}$, respectively. A second set of 16 binary rasters were created whereby pixels with a value of 0 and 1 depicted areas where the NDVI value was less than and greater than the $Mean_{st}$ + 1 standard deviation above the mean ($Stdev._{st}$), respectively. For each of the 16 time periods, the binary raster depicting green areas was added to the corresponding $Mean_{st}$ + $Stdev._{st}$ raster. This produced 16 rasters where 0=pixels with values below the mean, 1=pixels with values above the mean and 2=pixels with values greater than $Mean_{st}$ + $Stdev._{st}$. All pixels equal to 0, 1 and 2 were classified as brown, green and very green, respectively (Table 2.1). In certain cases whereby pixels were explained as only either green or brown, the very green pixels were included with the green pixels. Each pixel had its own $Mean_{st}$ and $Stdev._{st}$ value and as a result, periods of greenness or brownness were relative to that specific pixel across time, and did not illustrate the greenness of a pixel relative to the surrounding pixels. This was a temporal change, and as such vegetation type was expected to have little influence on whether a pixel was green or brown. $Mean_{st}$ was chosen as the baseline comparative mean because NDVI was found to decrease considerably between 2011 and 2013 (Figure 2.4), therefore a mean taken from 2000 – 2013 would be an overestimate of greenness for this period, while the collar period (Nov 2012 – Jul 2013) was believed to be too short to accurately represent greenness and would probably underestimate average greenness experienced by each pixel in the region. The "equal to frequency" tool in ArcGIS 10.1 was used to calculate the frequency of occurrence of green pixels during the collar period. Since the collar period was made up of 16 16-day periods, the maximum number of times that a pixel could be green is 16, and the minimum is 0.

To express greenness relative to surrounding areas, Cluster and Outlier Analyses (Anselin's Moran 1 similarity index) were performed on each 16-day raster during the collar period. Binary Rasters of HH and LL clusters were created for each 16-day period, similar to the methods during the long-term annual trends in greenness. Two additional rasters were calculated from these 16-day binary cluster rasters using the equal to frequency tool in ArcGIS 10.1, which indicated the number of times a corresponding pixel in the list of rasters lay within a HH or LL cluster.

H_3 and H_4: Short-term temporal change in greenness between habitats:

Percentage greenness during the collar period was calculated by determining the number of green pixels compared to the total number of pixels for that habitat type. At a smaller spatial scale, two areas were chosen along two of the prominent valley systems, namely Zone A, along the Passarge fossil river valley, and Zone B, along the Letiahau fossil river valley (Figure 2.5). The zones included major proportions of the valley systems and the adjacent dune areas. It was expected that if the valley regions in either of these zones experienced rainfall, so would the surrounding dune regions, due to their proximity. In this way, no rainfall bias was expected across either of the two habitat types. Mean NDVI and standard deviation was calculated across all valley pixels and all dune pixels for each 16-day period and plotted against time for Zones A and B. The aim of this analysis was to discern whether one of the habitat types became greener earlier in the season, and whether one remained greener for longer.

Results

H_1: Long-term annual trends in greenness:

The annual sum, mean and maximum of NDVI greenness trends appeared to follow a very similar pattern of high annual variability, with the highest values in 2006 and clear declines from 2001 to 2003, and from 2011 to 2013 in both pan-valleys and dunes (Figure 2.4 (a-c)). Although the general trend appeared to oscillate over time, it was clear that across all years, the mean, maximum and sum of NDVI greenness values were greater in dune than the pan-valley habitats (Figure 2.4 (a-c)). Standard deviation in NDVI greenness also showed a similar trend, but variation across time was more distinct, and in 2000 and 2006, the pan-valley habitats showed higher deviation than those of the dunes (Figure 2.4 (d)). The annual co-efficient of variation trend showed a reasonably high annual variability in to relation the mean (Figure 2.4 (e)).

Cluster Analyses:

Since similar annual trends were exhibited by the statistical calculations (mean, maximum and sum), only mean NDVI was used for the cluster analysis. Due to the much greater proportion of dune pixels, in relation to pan-valley pixels, these data were expressed as a ratio of number of pixels in the cluster: non-clustered pixels. Dune habitats exhibited a similar ratio of HH clustered: non-clustered pixels and LL clustered: non-clustered pixels, and the annual variability of these ratios were low (Figure 2.6). Pan-valley habitats, however, had a much larger proportion of LL clusters than HH clusters, and there was a high annual variability (Figure 2.6). Dune regions, which covered a significantly greater proportion of the overall landscape, were made up of stable and equal proportions of low and high NDVI clusters, whereas the considerably smaller pan-valley regions were mostly comprised of low NDVI clusters, which varied substantially from year to year. Over the 14-year period, the highest frequencies of HH clusters were found in very specific dune habitats (Figure 2.7), while high frequencies of LL clusters were located in pan-valley habitats, as well as the region south of Letiahau and Deception valleys (Figure 2.8). It is likely that these areas of high frequency greenness were areas of constant tree cover, which was why those pixels continually exhibited clusters of high greenness throughout the 14-year period (Figure 2.7).

Phenological metrics and seasonal fluctuations:

Timing of the onset of greenness between 2000 and 2012 proved to be reasonably predictable, occurring between early November and December, and the offset taking place between early June and late July (Table 2.2; Figure 2.3). In terms of phenology, it was the duration of the green season that showed most considerable inter-annual variability, with the green season ranging from a low of 13 bi-monthly periods (208 days) in 2012 to a high of 17 bi-monthly periods (272 days) in 2010. The level of maximum NDVI greenness ranged from a low of 3894.37 units in 2003 to a high of 6607.6 units in 2008 (Table 2.2).

Seasonal greenness maps for each year indicated that patches of highest greenness did not reoccur in the same area each year, and inter-annual variability did exist, but there did appear to be a distinct bias towards the locality of green patches in the north-east of the region (Figure 2.9(a-l)). Two years that deviated from this trend were 2007 and 2012 (Figure 2.9(g,l)), which, surprisingly, were both years that experienced lower annual NDVI values and shorter green seasons (Table 2.2, Figure 2.3).

H_2: Short-term 16-day trends in greenness:

When the short-term collar period between November 2012 and July 2013 was assessed, a seasonal change in greenness was clearly evident from the 16 rasters showing brown, green and very green pixels (Figure 2.10). The spatial extent of greenness increased by 75% between November 2012 and January 2013 (Figure 2.10 & 2.11). Greenness was initially patchy, developing from the south-west of the study area, and increasing towards the north-east (Figure 2.10). By mid-January to early February, the landscape was relatively homogeneously green, with 60% of the area being greater than one standard deviation above the mean i.e. classified as very green. Towards the end of February, the greenness had already begun to subside, starting to decline from the east towards the west (Table 2.1, Figure 2.10). By May 2013 only a small extent (< 1%) of greenness remained in the east of the study area. Over the entire collar period, it is clear that green pixels appeared more frequently in the western section of the study site than in the eastern (Figure 2.10). This is surprising considering that, in previous years, there were more green patches in the north and eastern sections of the study region (Figures 2.7 & 2.9). The areal extent of greenness increased linearly from November until reaching a plateau between the months of December and February 2013 (Figures 2.11 & 2.12). Very few pixels (< 1%) remained green for more than twelve of the sixteen periods (Figure 2.12). By mid-January the green pixels reached a maximum areal cover of 15 372.60 km² (94% of the study area) (Figure 2.11). A gradual decrease in areal extent of greenness ensued until the end of the collar period, with May, June and July supporting a green cover of less than 1% (Figure 2.11). The distribution of HH clusters (Figure 2.13) during the collar period depicts a very similar pattern to that of the HH clusters during the long-term annual trend (Figure 2.7). This is a clear indication that those areas are, in fact, dominated by evergreen tree cover. The frequency of LL clusters during the collar period was greatest across the south eastern portion of the study region, and in the pan-valley habitat (Figure 2.14).

H_3 and H_4: Change in short-term temporal greenness between habitats:

Dune and pan-valley habitats exhibited similar onset and duration of greenness, but differed in amplitude (Figures 2.4, 2.15, 2.16); this was true on a larger scale as well (Figure 2.17). It was expected that, following periods of rainfall, green patches in the pan-valley habitat would become greener earlier in the season than in dune habitats. By averaging the data over such a large spatial scale, certain temporal variations might have been filtered out and hence the data were re-evaluated at a much smaller spatial scale (Figure 2.15, 2.16); however results were similar to the previous large scale analysis.

Discussion

In agreement with previous research (Poporato et al., 2002; Fensholt et al., 2012; Nicholson & Farrar, 1994), this study validated the high inter-annual and seasonal variability in NDVI, characteristic of an arid African savanna. This variability was expected because of the annually-inconsistent and seasonally-fluctuating rainfall regime associated with these regions (Nicholson & Farrar, 1994). Rainfall data sourced from Matswere gate (eastern border of the CKGR) from 2006 – 2013 provided valuable insight into the level of monthly rainfall experienced by the region over the last eight years (Figure 2.18). The northern region of the Central Kalahari traditionally lies between the 350 and 400 mm isohyets (Figure 2.19), but in 2007 and 2012, only 238.8 and 155.7 mm of rain fell, respectively. These low rainfall events are believed to be cause for the decline in mean, maximum and sum of NDVI greenness during these two years (Figure 2.4). Additionally, these two years showed major deviation in the location of seasonally-green patches, where green patches predominantly found in the north-east shifted towards the north-west of the region (Figure 2.9).

Besides inter-annual variability in greenness, striking seasonal fluctuations were also evident, due to seasonal rainfall trends, with over 80% of precipitation falling between October and April (Poporato et al., 2002). The consequent relationship between rainfall and NDVI greenness was most clearly demonstrated during low rainfall years, in particular 2007 and 2012, when spatially-averaged NDVI declined considerably (Figure 2.3), and the duration of the green season was shorter than other years (Table 2.2). Peak NDVI was most commonly recorded in January, but variations in the timing of NDVI maximum ranged between December and March. Rainfall usually ceased between April and May and a *browning* trend would follow until the end of the green season in June/July. July and August were usually the driest months of the year, and NDVI remained consistently low, until the *greening* period commenced again around November (Table 2.2, Figure 2.3). These results were consistent with Nicholson & Farrar, (1994) who showed that, between 1982 and 1987, trends in NDVI tended to spike in January and February, and declined until September and October.

The short-term collar period (November 2012 – July 2013), which fell within a stage of drought, experienced a seasonal rainfall of only 163.1 mm (Figure 2.18), a decline in mean and maximum NDVI (Figure 2.3, 2.4), and also exhibited a green season of only 13 periods (approximately 208 days, the shortest of all 13 years) (Table 2.2). These conditions would suggest a highly stressed environment for herbivores, with limited available forage. During this period, relative greenness across the northern CKGR initially developed in the western region of the study area, suggesting that rainfall events initially took place in the west. Rainfall commenced in November 2012 and peaked in January 2013, while maximum observed relative greenness was exhibited in late January/early February 2012 (Figure 2.10, 18). This suggested a lag period of approximately two months between onset of rainfall and maximum NDVI greenness.

Refuting Hypotheses 3 and 4, the pan-valley habitat did not show any difference in rate of *greening* or duration of green season, when compared to the vast dune habitats. There are a number of possible explanations for this. Firstly, I hypothesised that the spatial scale of the analysis was too large and as a consequence, the temporal fluctuations in the data were being disguised. This was ruled out when the analysis was repeated at a much smaller spatial scale (Figure 2.5, 2.15 & 2.16), and the results did not change. Secondly, it was proposed that the collar period, being a drought year, was merely an anomaly. However, when the greenness time series for the two habitats were extended all the way back to 2008, yet again, no temporal deviations were found between the two habitat types (Appendix A). Thirdly, a possible explanation for this result could have been related to the temporal resolution of the imagery (16-day), which could have been too large to pick up any temporal divergence between the habitat types. Future studies might be able to pick up phenological variations between habitat types using satellite images captured at a finer temporal resolution. A fourth and final possible option was that the soil and vegetation differences between these habitats have far less control over phenology than the prevailing rainfall events.

Pan-valley habitats did, however, diverge from dune regions in their amplitude of greenness, and ratios of high and low clusters. Since pan and valley regions are comprised of clay-rich soils, which support highly palatable short grasses, during wet season conditions, while dune regions are comprised predominantly of shrub savanna, and a tall grass layer of *Stipagrostis* spp., *Aristida* spp., and *Eragrostis* spp. (Skarpe, 1986), it is possible that differences in greenness values between these habitats was a result of major biomass differences. Vegetation biomass is considered to be correlated to NDVI (Shippert et al., 1995). Additionally, since palatability is thought to decrease with grass length, and increase in soils high in clay content (Nicholson & Farrar, 1994), the shorter greener grasses in pans and valley regions, would be expected to experience a higher degree of grazing pressure, thus keeping them short, and maintaining the lower biomass. During brown seasons, however, pans and valleys are often bare, thus it is expected that NDVI would be affected by soil background reflectance, as found by Huete et al. (1985) and Huete & Tucker (1991). NDVI has been known to decrease with increasing soil brightness (Nicholson & Farrar, 1994), and is only independent of the effects of soil background when the areal extent of vegetation cover is greater than 70% (Nicholson & Farrar, 1994). This suggests that during the brown season and early green season , when pan and valley regions either present bare soil or short, green grasses, the NDVI values of these regions may be affected by background soil reflectance, thus revealing a distinct deviation from the degree of greenness across the dune regions.

Since alterations of land management are minimal in the CKGR, natural conditions are largely considered to control vegetation productivity, and as such, trends in NDVI greenness. Other than rainfall, herbivore pressure, soil type and vegetation structure, an additional natural factor influencing greenness in savanna regions is fire (Holdo, 2007). Fire in the central Kalahari, however, is usually low-intensity, and not known to result in large-scale mortality of trees (Scanlon et al., 2007). A major bush fire originated in late August 2008 on the western boundary of the CKGR and spread across 80% of the reserve. NDVI greenness was substantially affected by this fire, and low greenness values were exhibited in a pattern equivalent to that of the fire (Figure 2.20, 2.21). However, following the rainfall event in November 2008, greenness appeared to return to normal and the distinct burn scars were no longer evident (Figure 2.21). When assessing the yearly data, 2008 did not show any significant declines in greenness compared to the other years, and, consequently, although fire results in an immediate effect on NDVI, this event in particular did not appear to have any long lasting impact on the annual NDVI degree or duration. Once again, the dominant role of rainfall and the control it has over vegetation dynamics was revealed.

In summary, as a result of the unpredictable rainfall regime, high inter-annual variability in vegetation phenology metrics was observed in the northern region of the CKGR. Additionally, annual variation in location of seasonal green patches was evident. The collar period (November 2012 - July 2013) was during drought conditions, with low annual and seasonal greenness values, and a short green season. This suggested that herbivores would have been faced with heightened stress levels, and a low availability of highly palatable forage material. Surprisingly, pan-valley habitats showed similar temporal trends to dune regions, suggesting that soil and vegetation type could have little effect on the rate of *greening* or *browning*, nor on the duration of the green season. The degree of greenness, however, did differ between habitats: dune regions displayed higher greenness, more clusters of high greenness and fewer clusters of low greenness than pan-valley habitats. It is expected that pan-valley regions, which consist of soils rich in clay, are devoid of most vegetation during the brown season. Dune regions, however, produce tall, dry grasses with scattered seasonal and evergreen trees and shrubs during the brown season, and therefore continue to retain certain amounts of NDVI-measured greenness throughout the year.

Tables

Table 2.1 Dates and codes of each 16-day period correlating to NDVI images during the gemsbok collar period (Nov 2012 – July 2013).

Time Period	Raster Code	Dates
T_1	2012321	16 November 2012 – 1 December 2012
T_2	2012337	2 December 2012 – 17 December 2012
T_3	2012353	18 December 2012 – 31 December 2012
T_4	2013001	1 January 2013 – 16 January 2013
T_5	2013017	17 January 2013 – 1 February 2013
T_6	2013033	2 February 2013 – 17 February 2013
T_7	2013049	18 February 2013 – 5 March 2013
T_8	2013065	6 March 2013 – 21 March 2013
T_9	2013081	22 March 2013 – 6 April 2013
T_{10}	2013097	7 April 2013 – 22 April 2013
T_{11}	2013113	23 April 2013 – 8 May 2013
T_{12}	2013129	9 May 2013 – 24 May 2013
T_{13}	2013145	25 May 2013 – 9 June 2013
T_{14}	2013161	10 June 2013 – 25 June 2013
T_{15}	2013177	26 June 2013 – 11 July 2013
T_{16}	2013193	12 July 2013 – 27 July 2013

Table 2.2 Temporal and NDVI metrics derived from spatially-averaged NDVI trend data from 2000-2012.

Year	Temporal Metrics				NDVI metrics		
	Time period of greenness onset	Time period of green offset	Time period of peak greenness	Greenness duration (no. of 16-day periods)	Value at greenness onset	Value at greenness offset	NDVI max
2001	late Nov 2000	late June 2001	late Mar 2001	14	3013.05	3467.27	5605.37
2002	early Nov 2001	early July 2002	early Dec 2001	16	3356.49	2207.07	4410.79
2003	early Dec 2002	early July 2003	early Mar 2003	14	2349.87	2210.54	3894.37
2004	late Nov 2003	early July 2004	late Mar 2004	15	2196.63	2676.18	5881.82
2005	early Dec 2004	mid June 2005	late Feb 2005	13	2900.37	2410.55	4525.47
2006	late Nov 2005	early July 2006	late Jan 2006	15	2245.83	2890.74	6176.77
2007	late Nov 2006	mid June 2007	early Jan 2007	14	3169.95	2472.44	5141.91
2008	late Nov 2007	early July 2008	late Jan 2008	15	2266.62	2662.84	6607.6
2009	late Nov 2008	early July 2009	late Jan 2009	15	2868.59	2562.7	5134.72
2010	early Nov 2009	late July 2010	early Jan 2010	17	2449.81	2560.51	4748.3
2011	early Dec 2010	late July 2011	early Feb 2011	15	2935.72	2753.48	4855.57
2012	early Dec 2011	mid June	late Jan 2012	13	3392.14	2237.2	4766.43

Figures

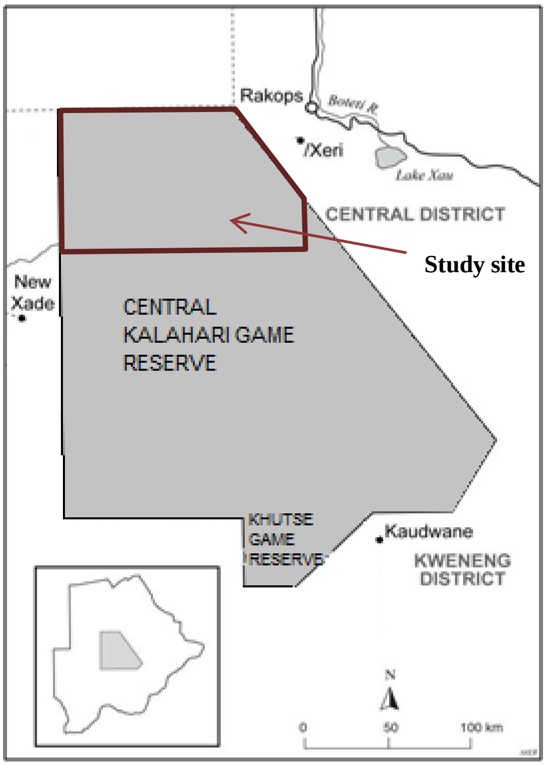


Figure 2.1 Map of the Central Kalahari Game Reserve (CKGR), and Khutse Game Reserve (KGR) to the south, central Botswana. The study site is the northern region of the CKGR and has been outlined in red.

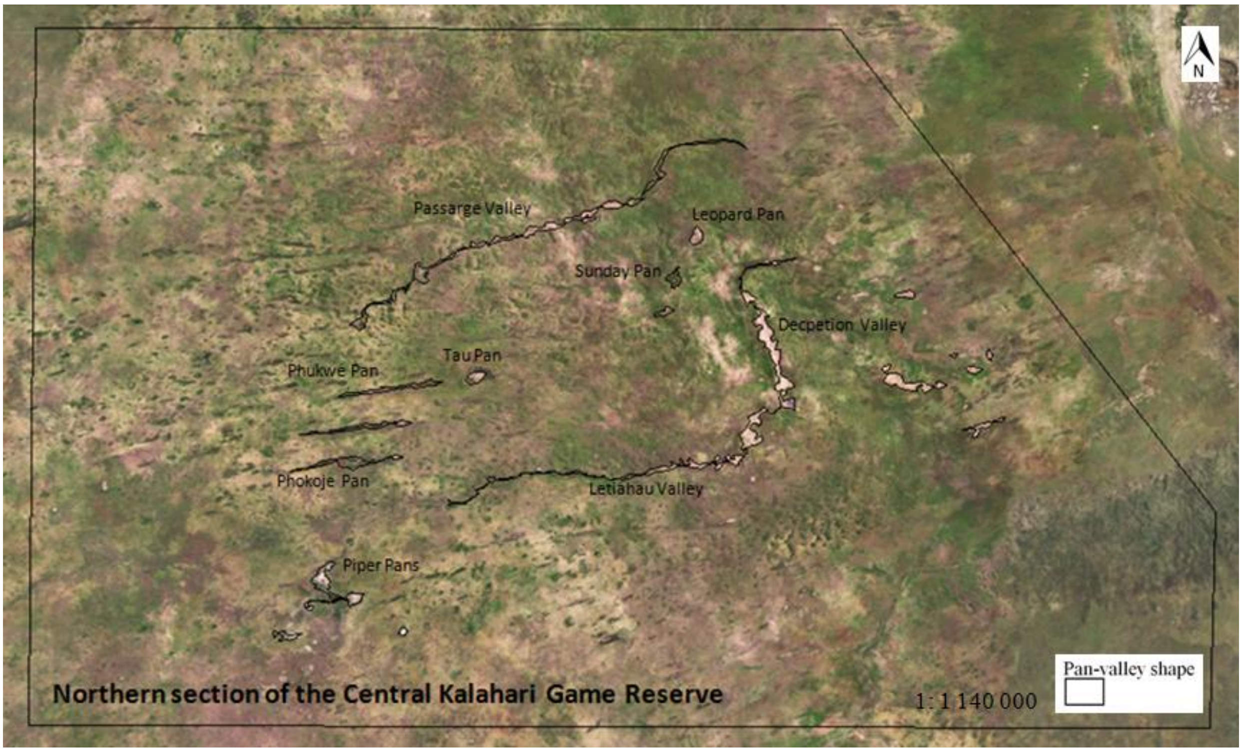


Figure 2.2 Satellite image depicting the study site for this research, the northern section of the Central Kalahari Game Reserve. The major pans and river valley systems have been outlined in black. Everything surrounding these regions is classified as dune regions. These two habitat types (pan-valleys and dunes) form an imporant component of this study.

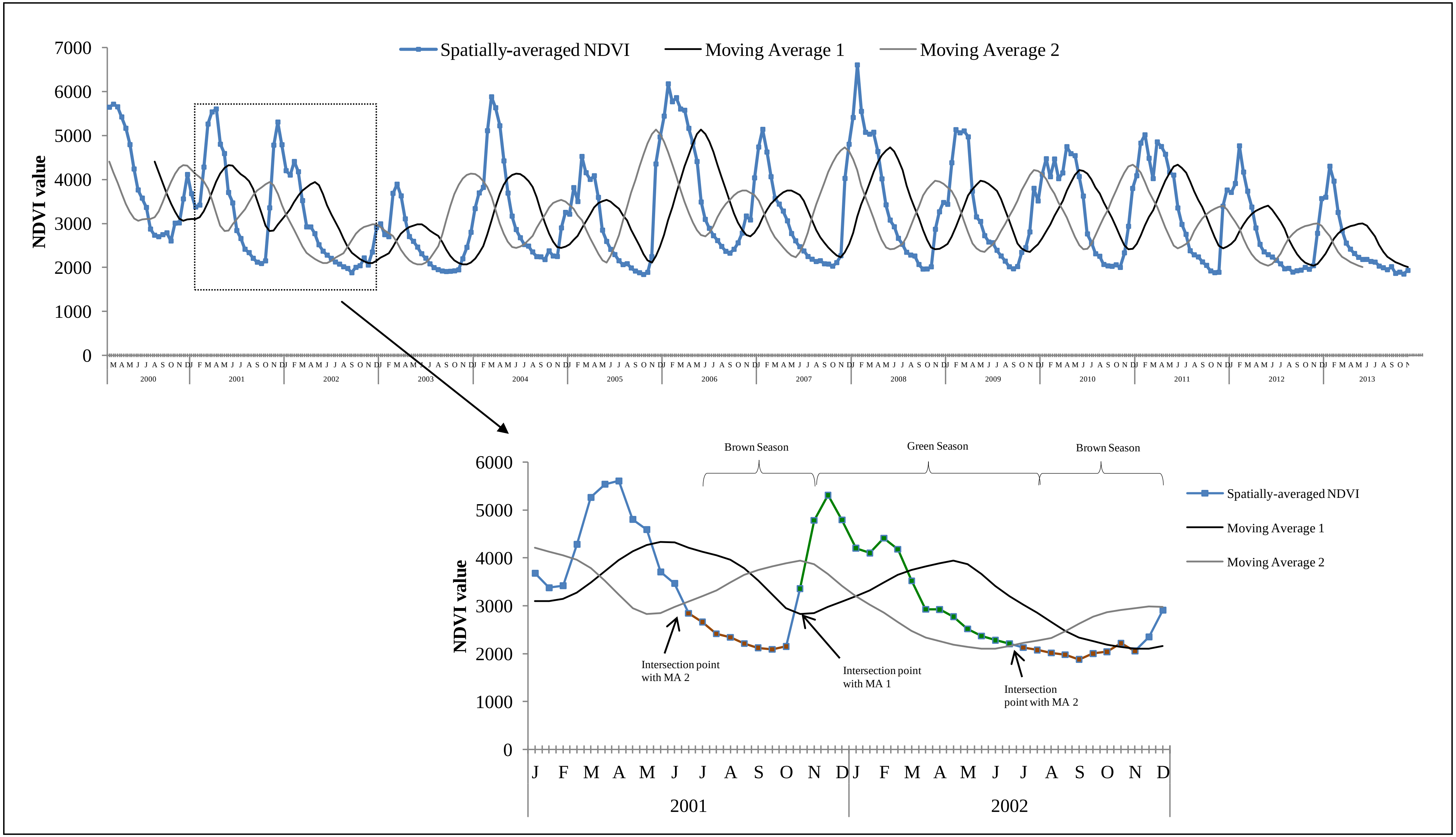
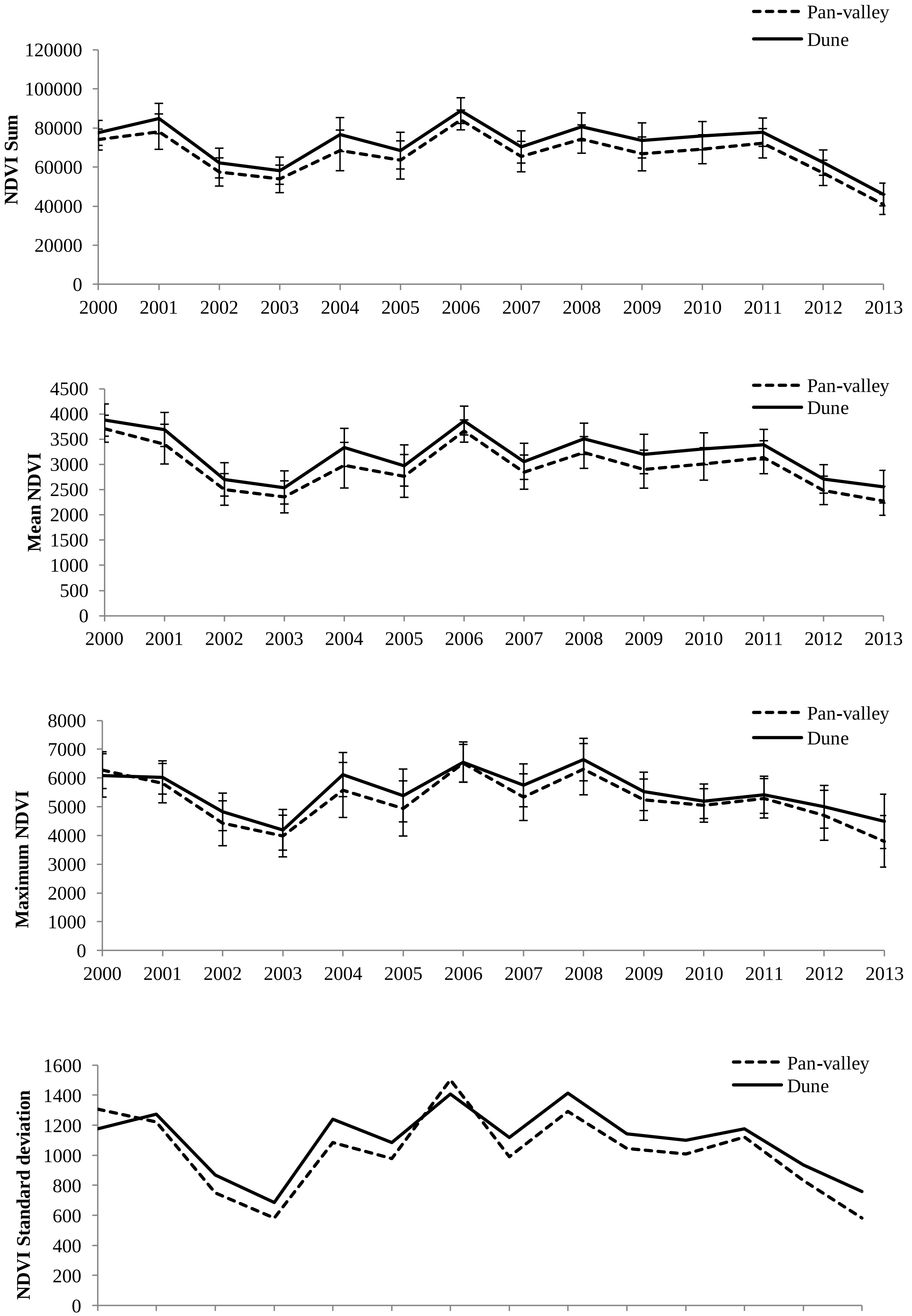


Figure 2.3 Spatially-averaged NDVI temporal profile and moving average 1 & 2 curves for 2000 – 2013, indicating the derivation of green and brown seasons for the northern region of the Central Kalahari Game Reserve. This method has been adapted from Reed et al. (1994).


Pan-valley
Dune
NDVI Sum
120000
100000
80000
60000
40000
20000
0
2000 2001 2002 2003 2004 2005 2006 2007 2008 2009 2010 2011 2012 2013
a
Pan-valley
Dune
Mean NDVI
4500
4000
3500
3000
2500
2000
1500
1000
500
0
2000 2001 2002 2003 2004 2005 2006 2007 2008 2009 2010 2011 2012 2013
b
Pan-valley
Dune
Maximum NDVI
8000
7000
6000
5000
4000
3000
2000
1000
0
2000 2001 2002 2003 2004 2005 2006 2007 2008 2009 2010 2011 2012 2013
c
Pan-valley
Dune
NDVI Standard deviation
1600
1400
1200
1000
800
600
400
200
0
2000 2001 2002 2003 2004 2005 2006 2007 2008 2009 2010 2011 2012 2013
d

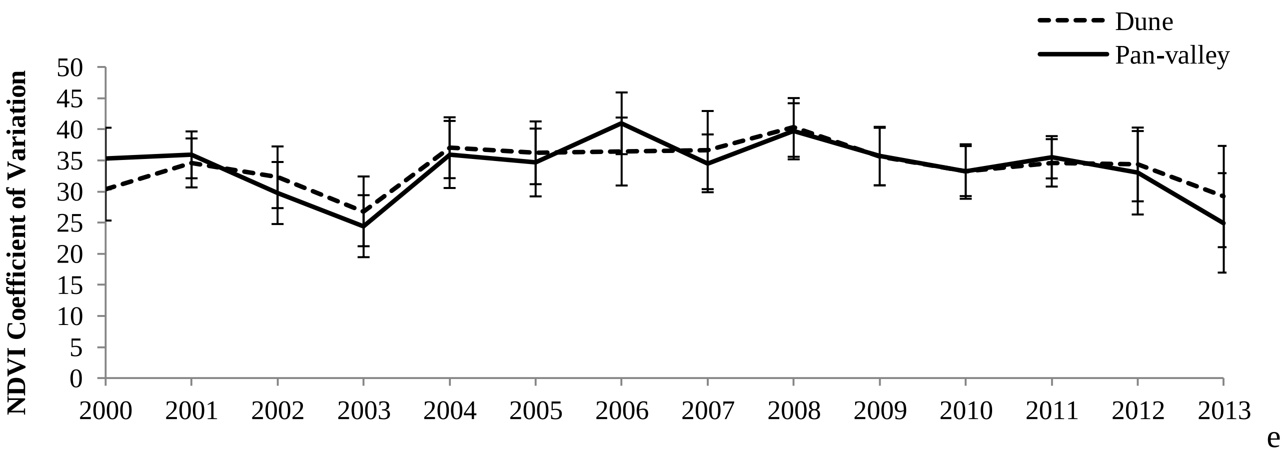


Figure 2.4 (a-e) Average annual NDVI sum, mean, maximum, standard deviation and co-efficient of variation across all pixels in the dune and pan-valley habitats of northern Central Kalahari Game Reserve from 2000-2013.

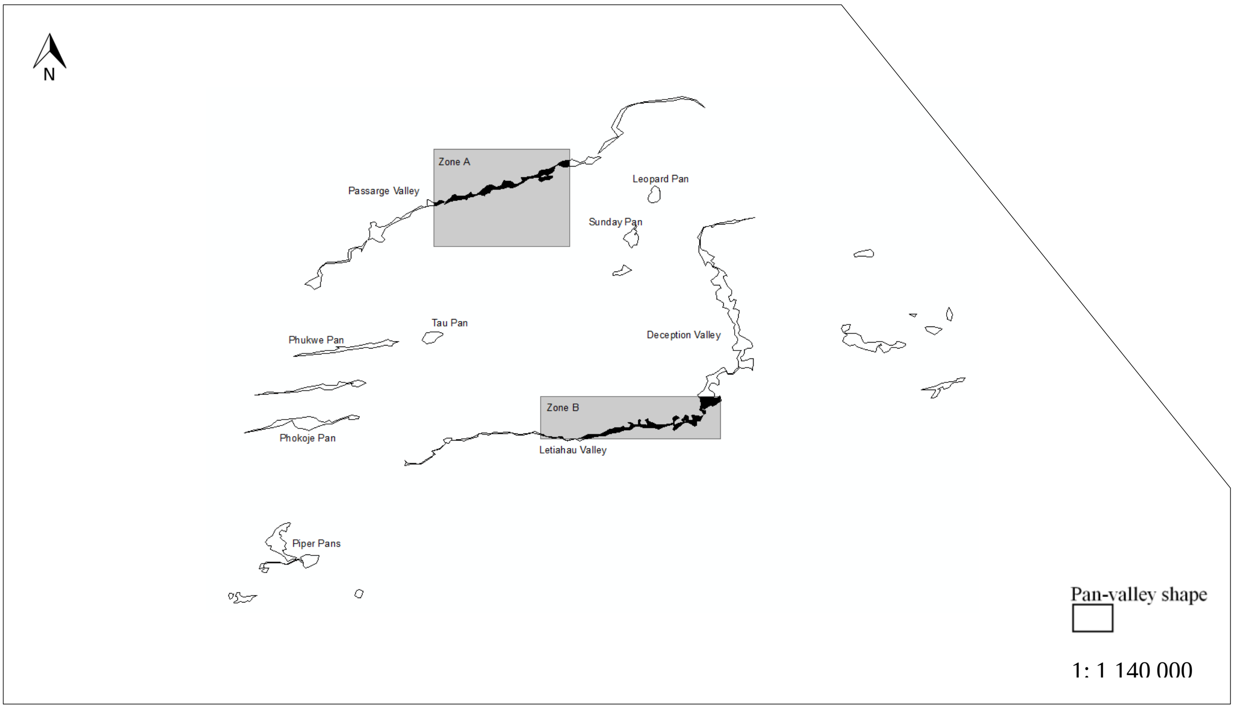


Figure 2.5 The position of Zone A and Zone B, which were used to assess temporal differences in mean NDVI across dune and valley habitats at a much smaller spatial scale compared to the entire study site.

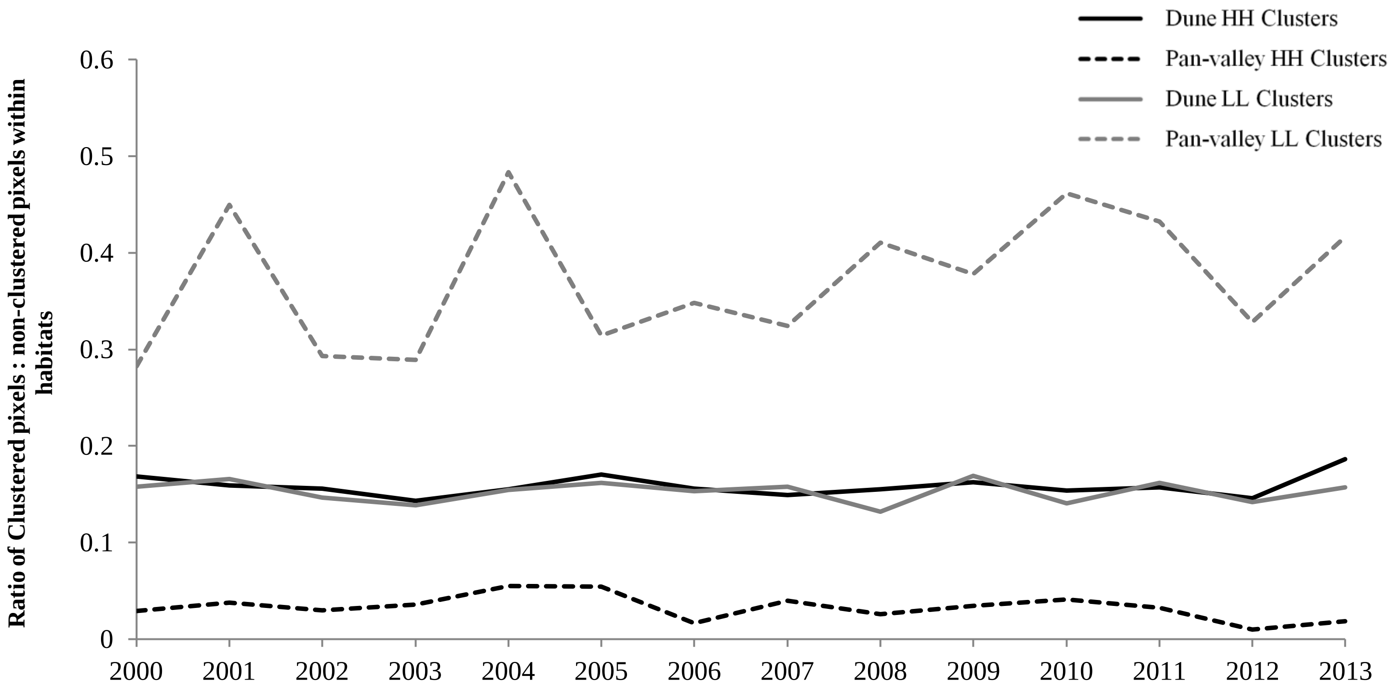


Figure 2.6 Ratio of HH (high NDVI) and LL (low NDVI) clustered pixels in the dune habitats and pan-valley habitats of the northern Central Kalahari Game Reserve from 2000-2013.

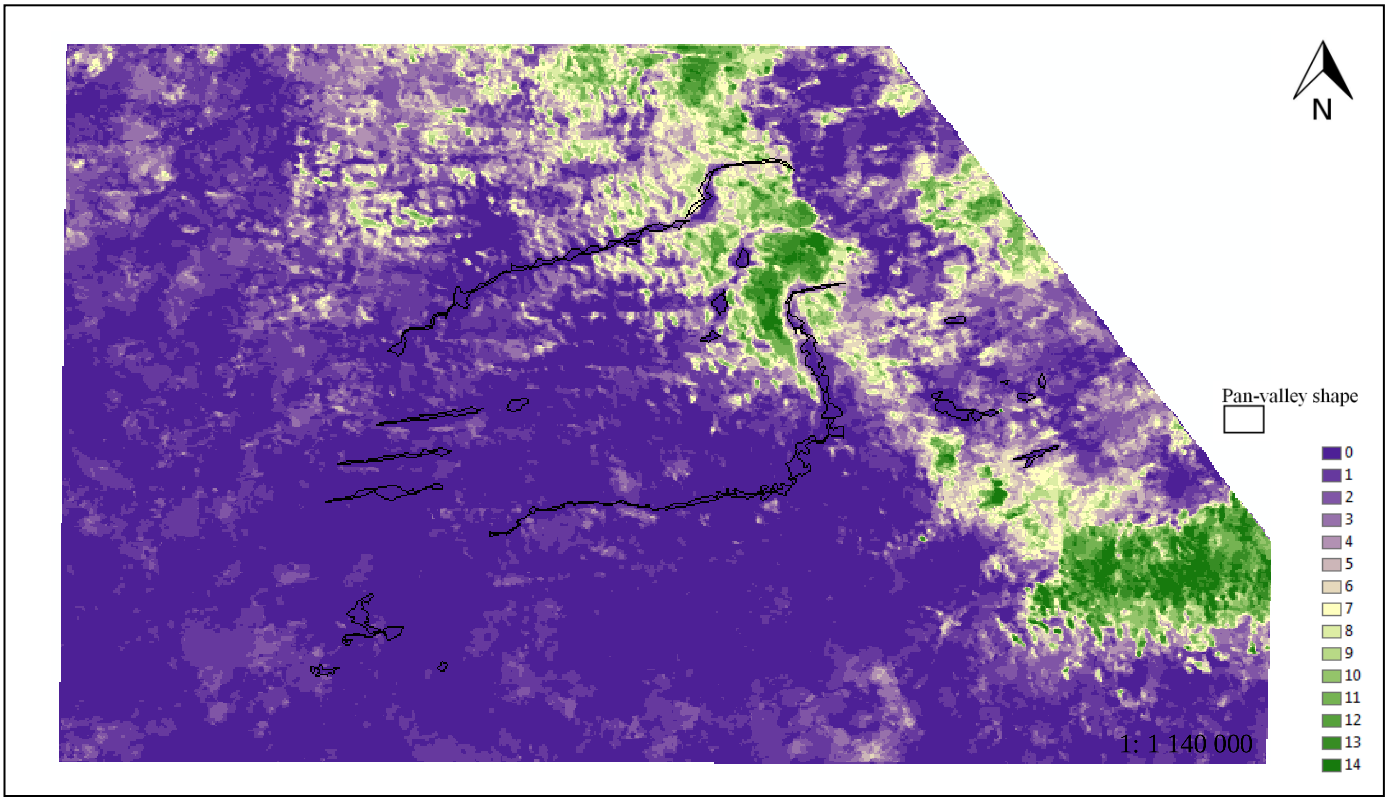


Figure 2.7 Frequency of HH clusters from 2000-2013 in the northern Central Kalahari Game Reserve. Dark green areas depict regions that remained green (within high NDVI clusters) for 12 or more years, during the 14 year period.

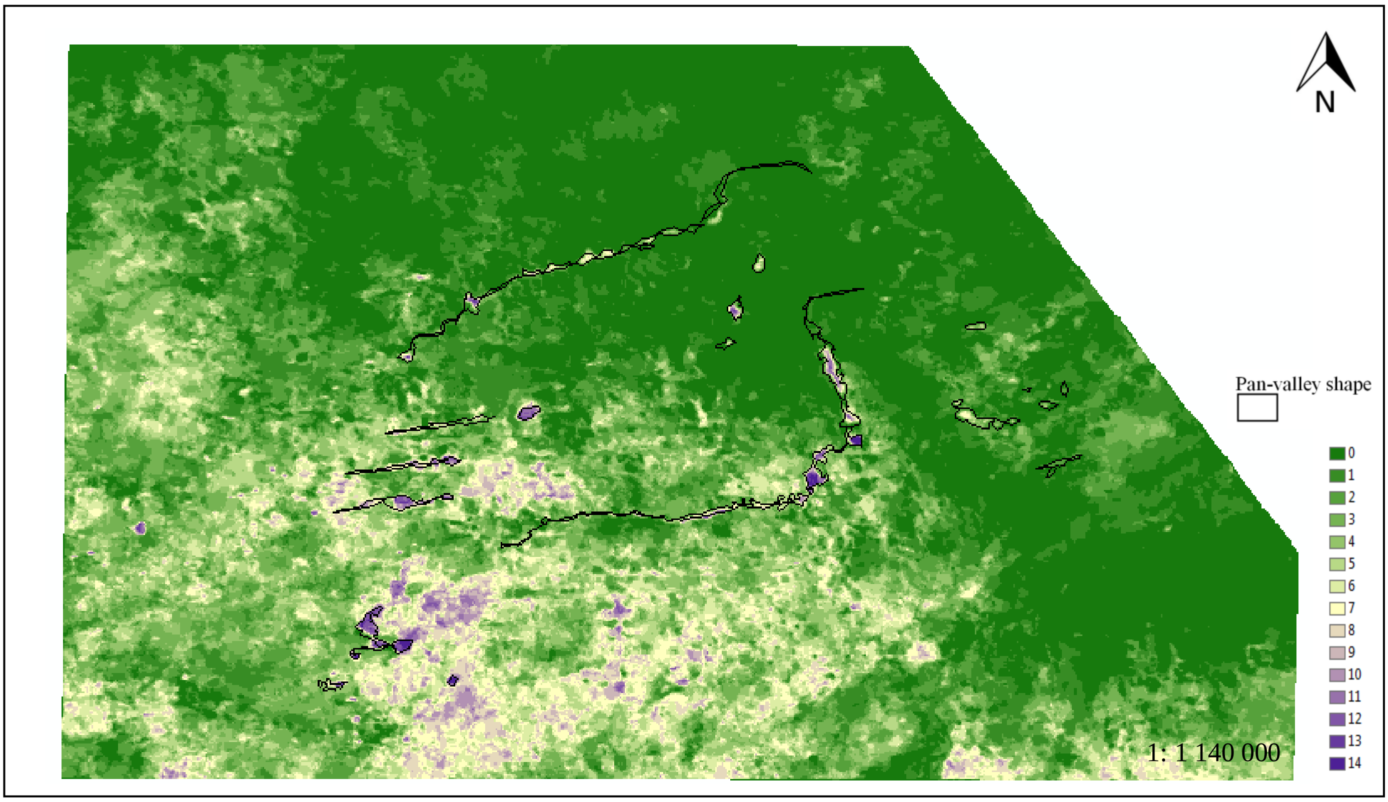
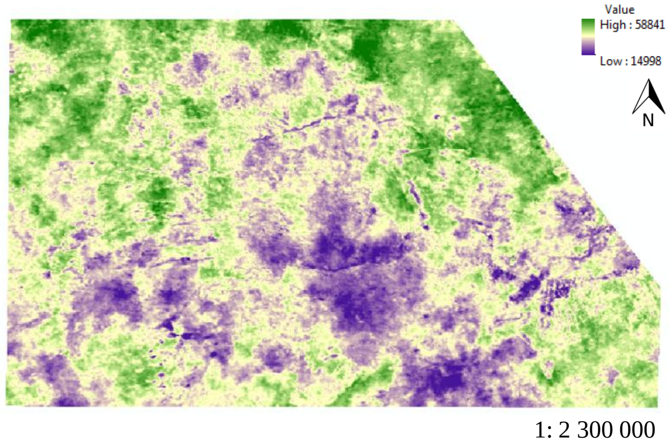
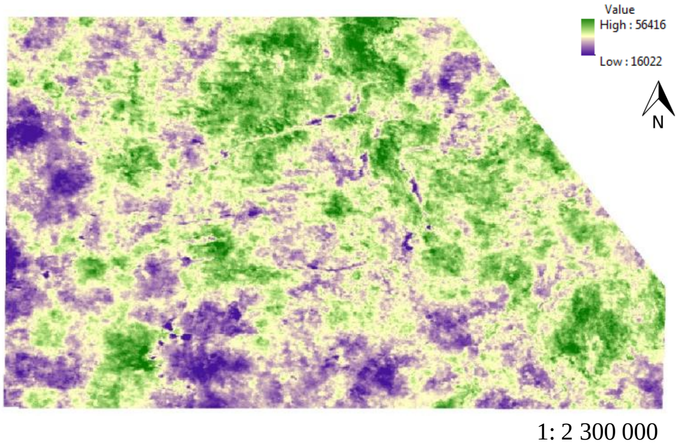


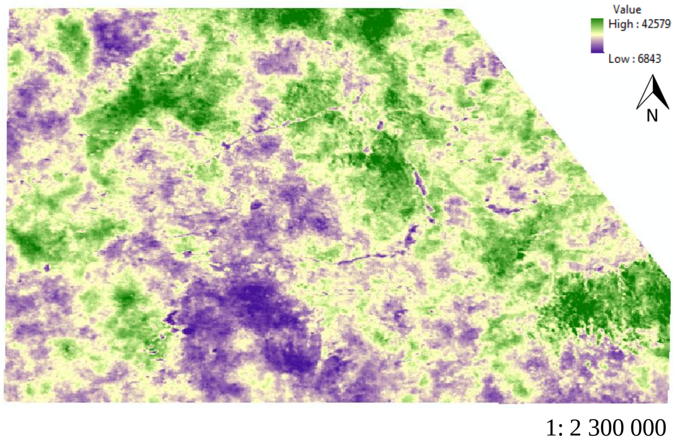
Figure 2.8 Frequency of LL clusters from 2000-2013 in the northern Central Kalahari Game Reserve. Dark purple areas depict regions that remained brown (within low NDVI clusters) for 12 or more years during the 14 year period.



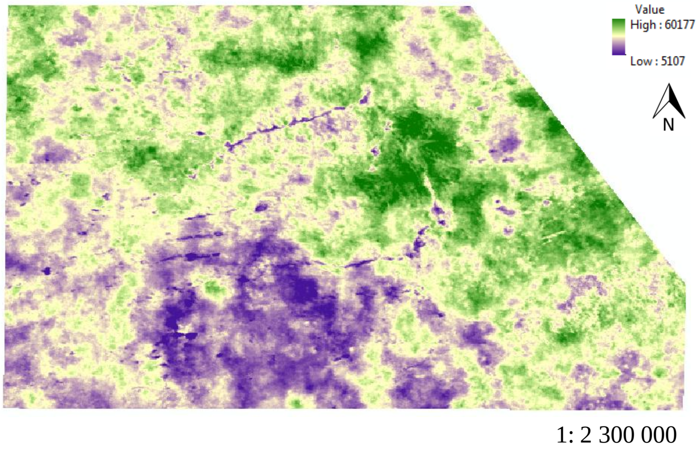
a: 2001



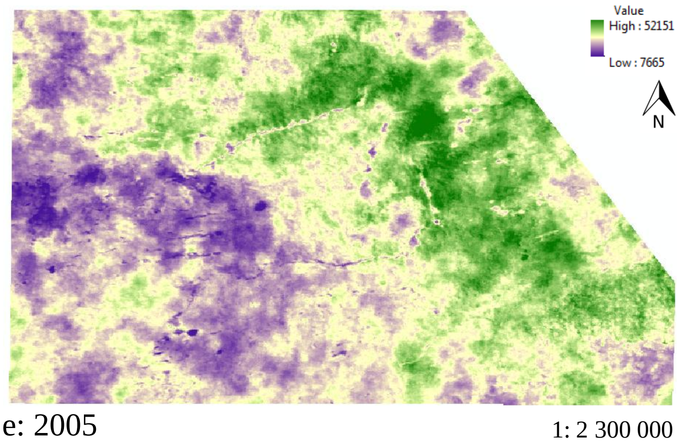
b: 2002



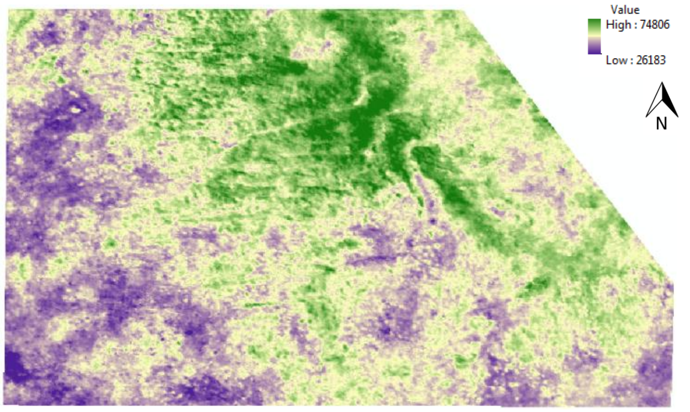
c: 2003



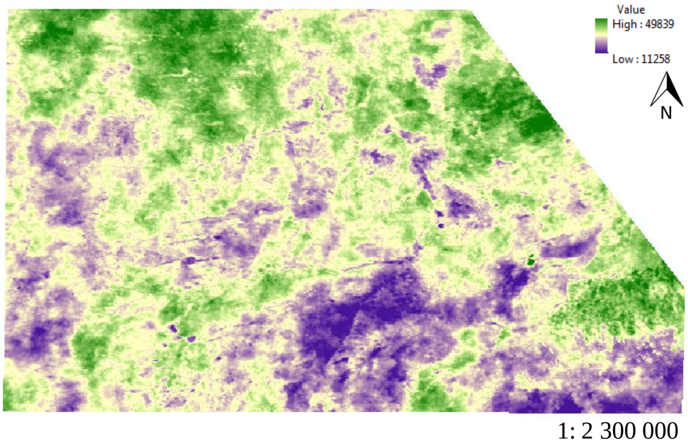
d: 2004



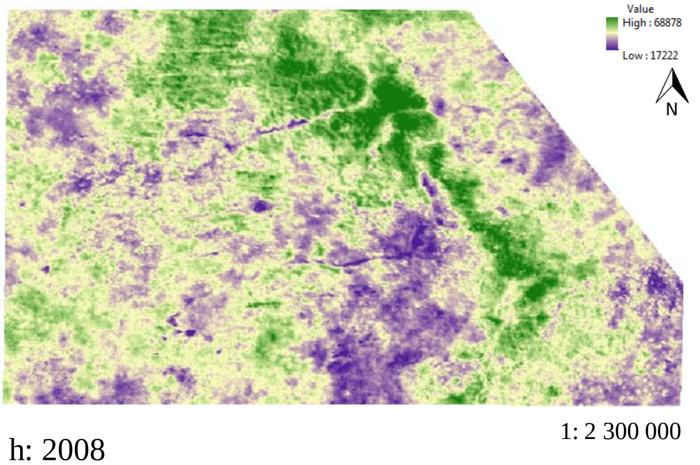
e: 2005



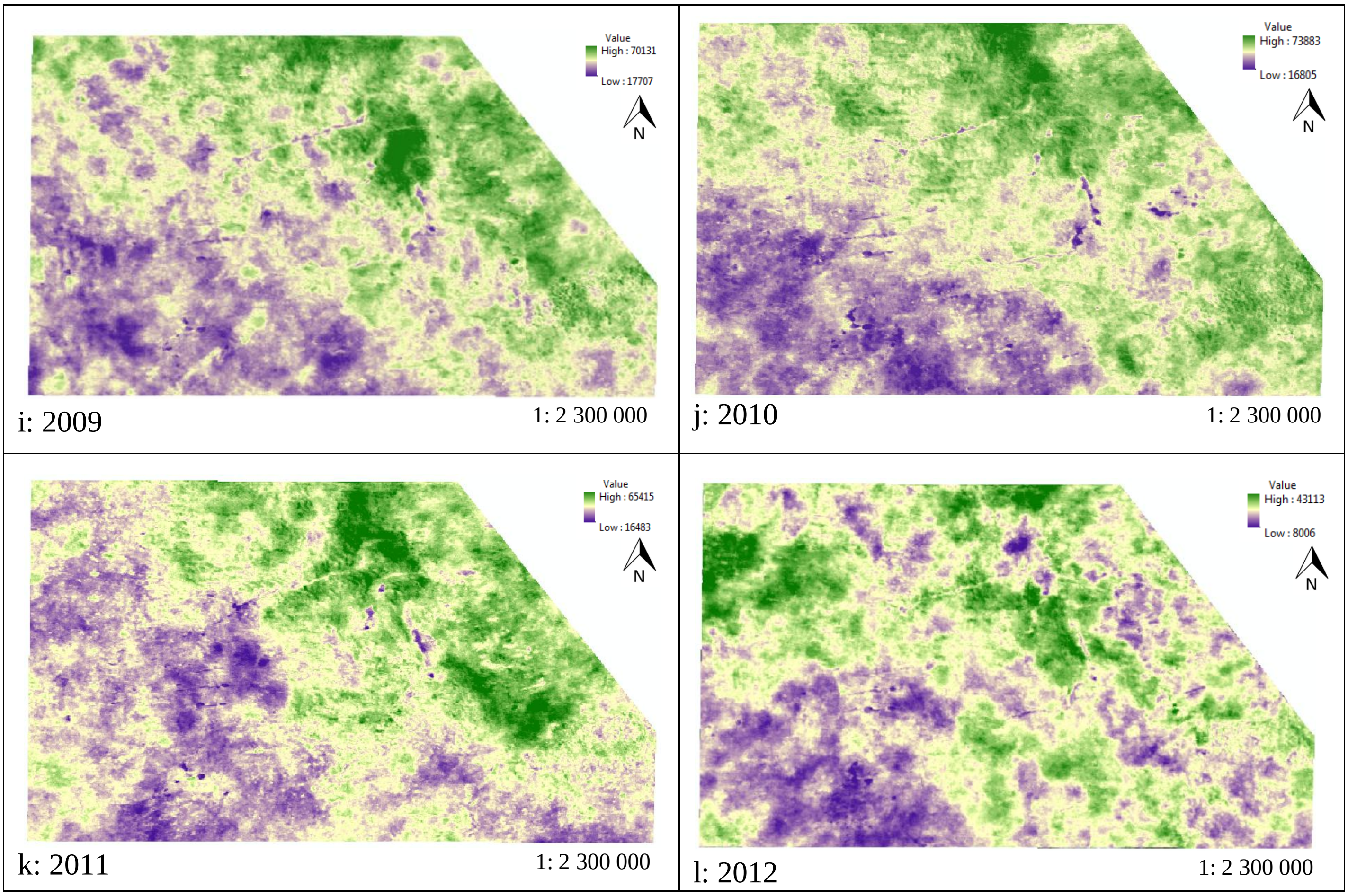
f: 2006



g: 2007



h: 2008



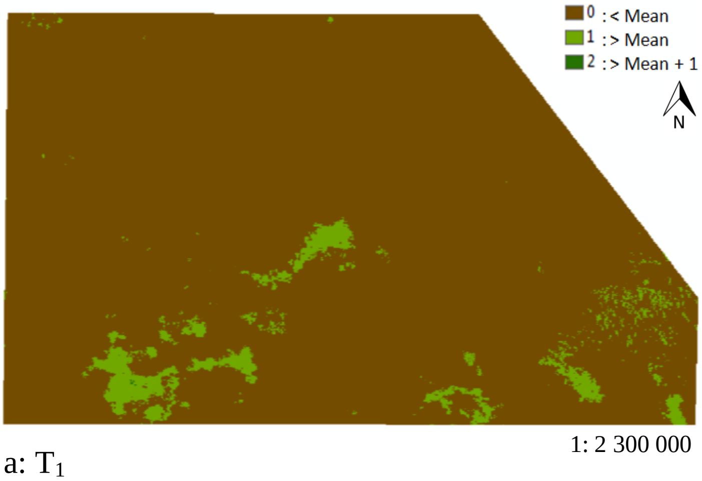
i: 2009 1: 2 300 000

j: 2010 1: 2 300 000

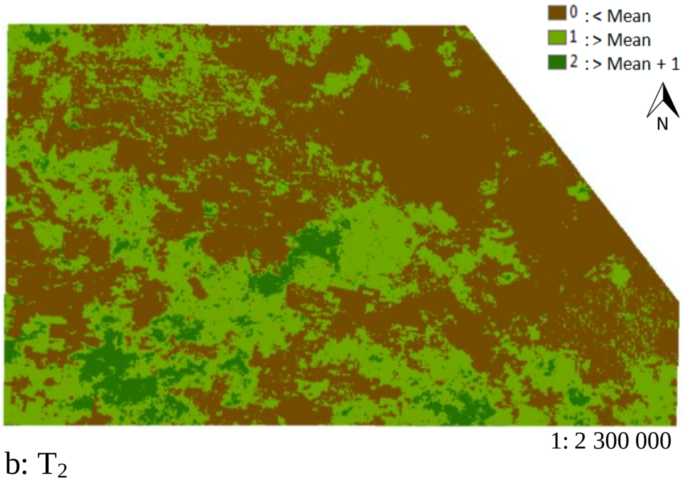
k: 2011 1: 2 300 000

l: 2012 1: 2 300 000

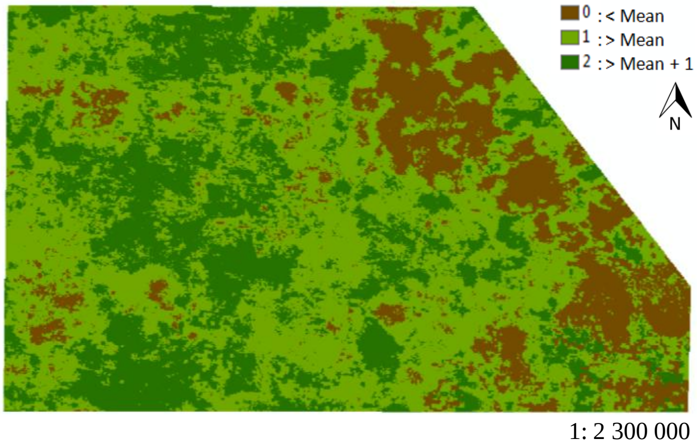
Figure 2. 9 (a-l) Rasters depicting inter-annual variation in seasonal greenness from 2001 – 2012 of the northern region of the Central Kalahari Game Reserve. Seasonal greenness is calculated on a pixel-by-pixel basis, by subtracting the sum of all brown season rasters from the sum of all green season rasters for each year.



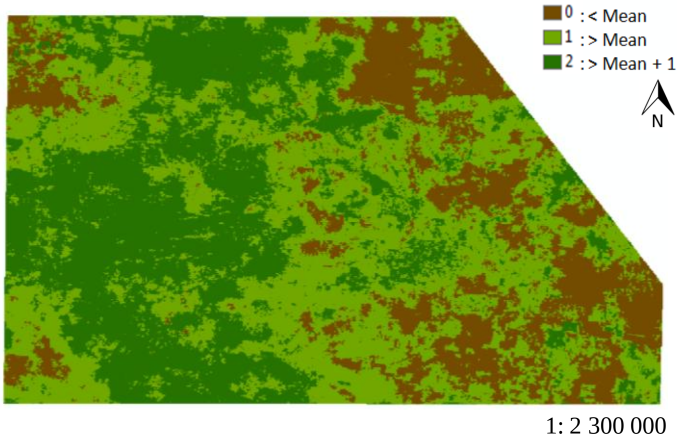
a: T_1



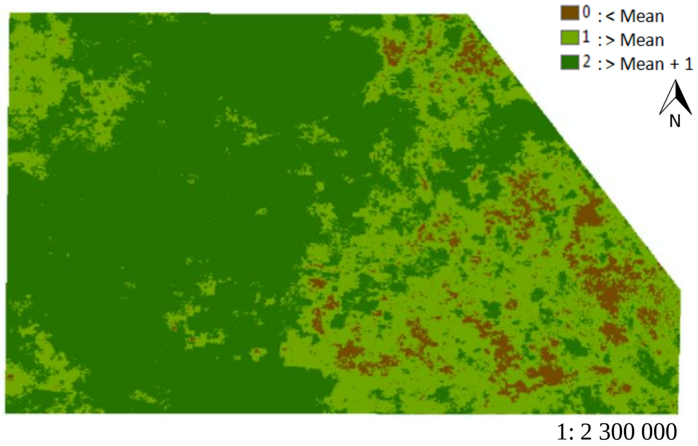
b: T_2



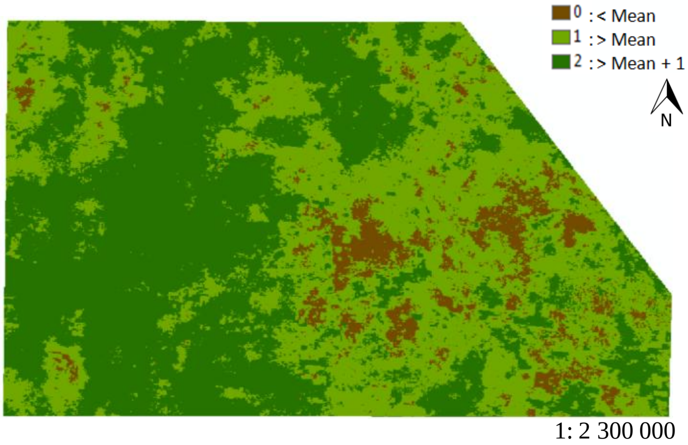
c: T_3



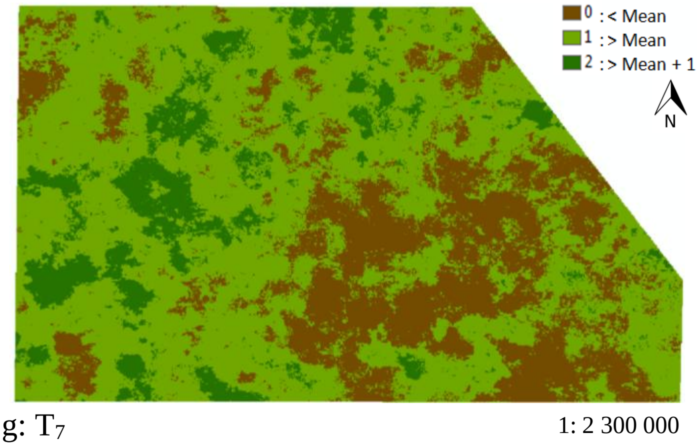
d: T_4



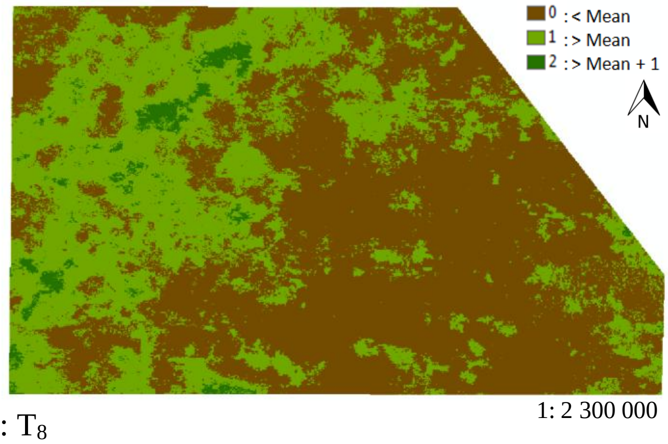
e: T_5



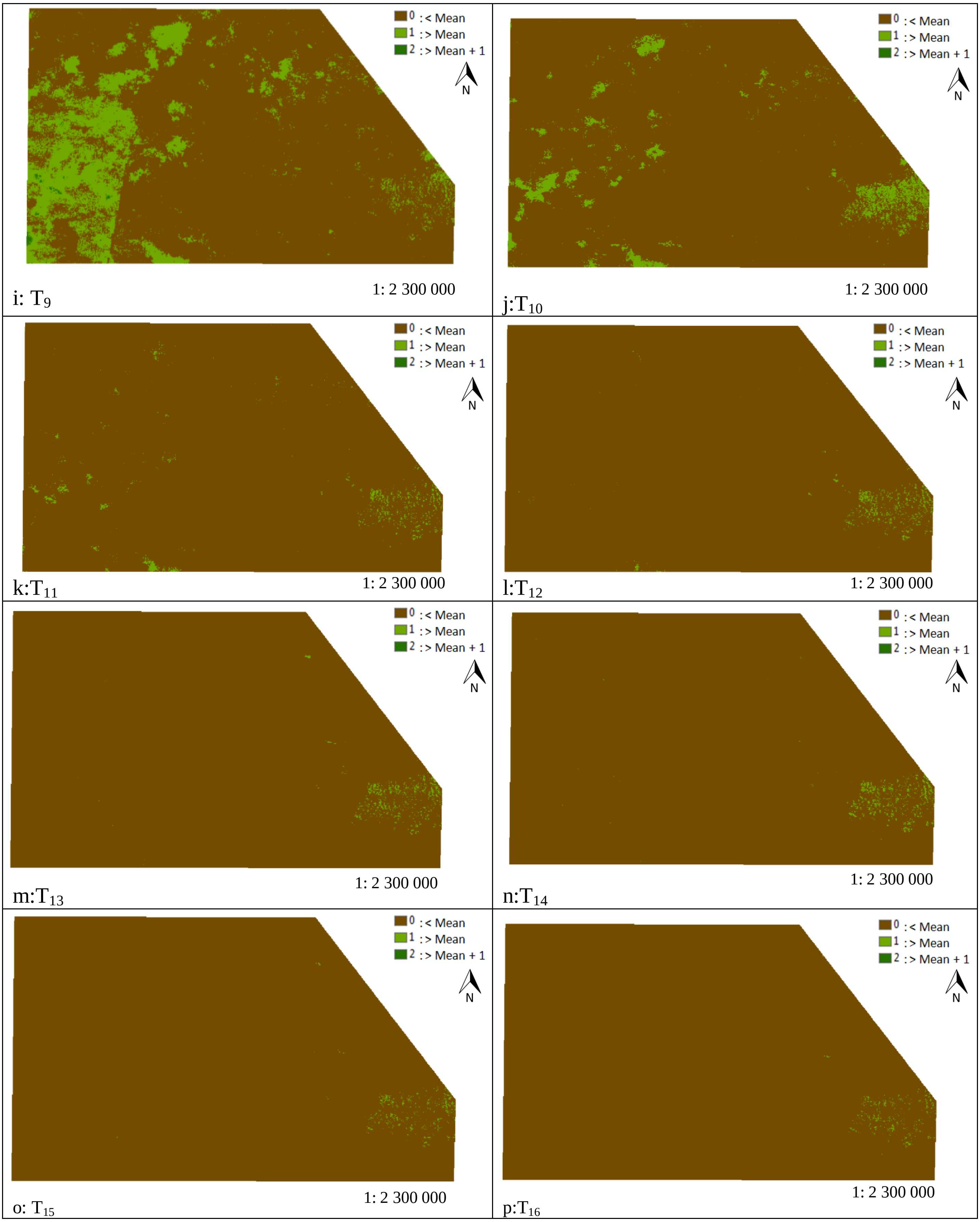
f: T_6



g: T_7



h: T_8



i: T_9 j:T_{10} k:T_{11} l:T_{12} m:T_{13} n:T_{14} o: T_{15} p:T_{16}

Figure 2.10 (a-p) Rasters depicting change in relative greenness over time of the northern section of the Central Kalahari Game Reserve from November 2012 – July 2013. Time periods are divided into 16 x 16-day periods. 0 (brown) = areas where NDVI is less than mean NDVI from 2011 to 2013, 1 (light green) = areas where NDVI is greater than mean NDVI from 2011to 2013, and 2(dark green) = areas where NDVI is greater than mean NDVI from 2011 to 2013 + 1 standard deviation above the mean.

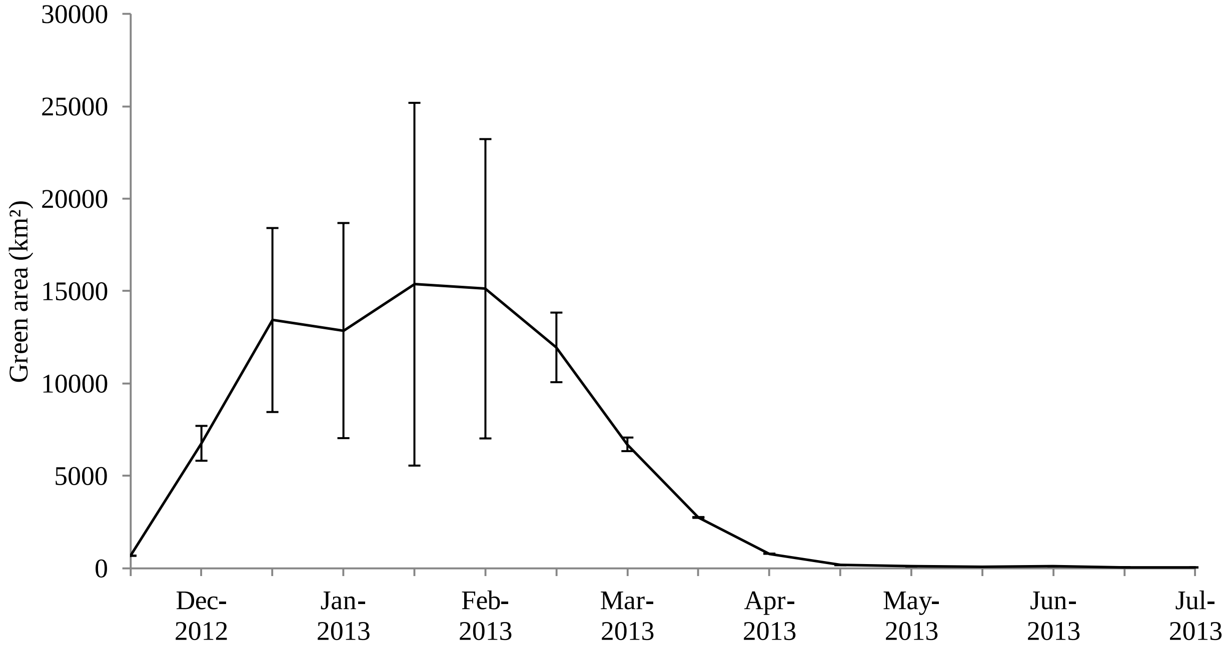


Figure 2.11 Change in areal extent (km²) of greenness in the northern section of the Central Kalahari Game Reserve through time. A pixel is classified as green when its NDVI value is greater than mean NDVI from 2011-2013.

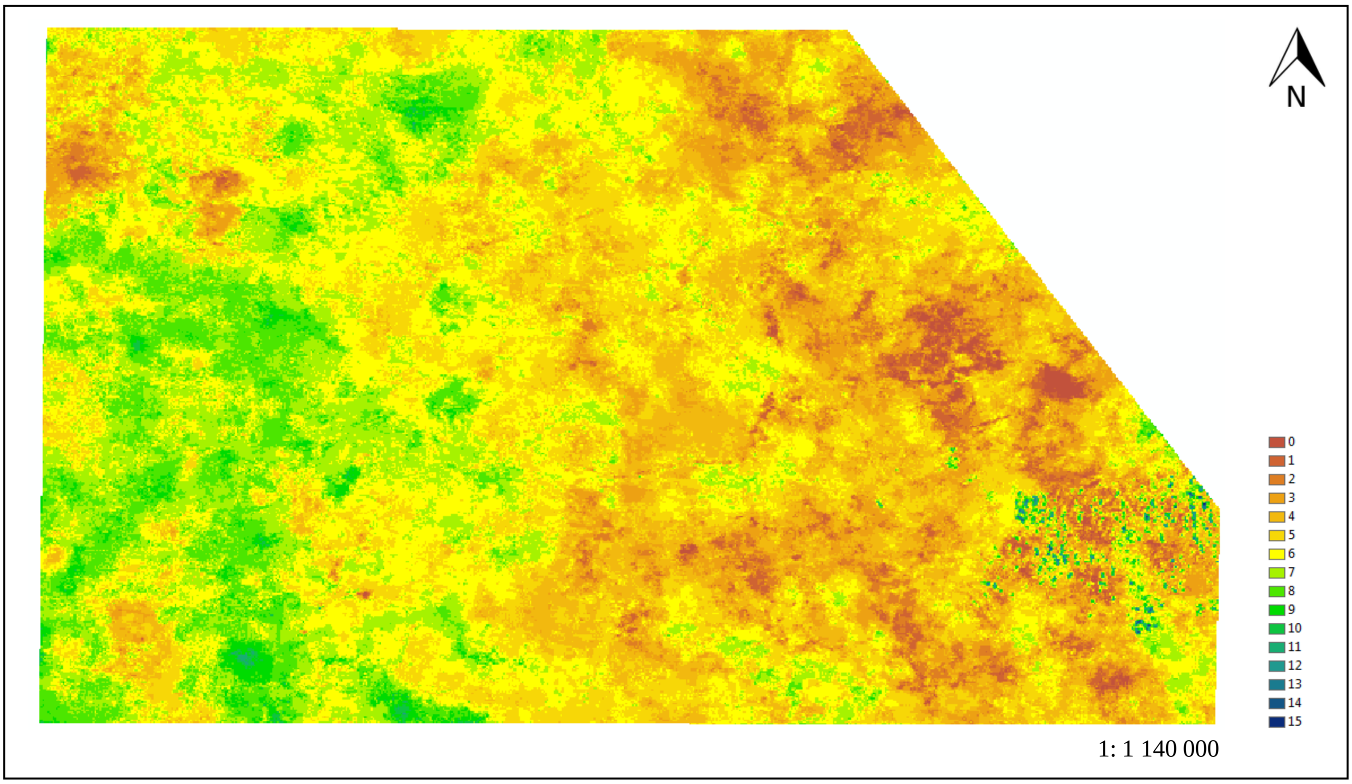


Figure 2.12 Raster displaying the frequency of greenness during 16 time periods from November 2012 – July 2013.

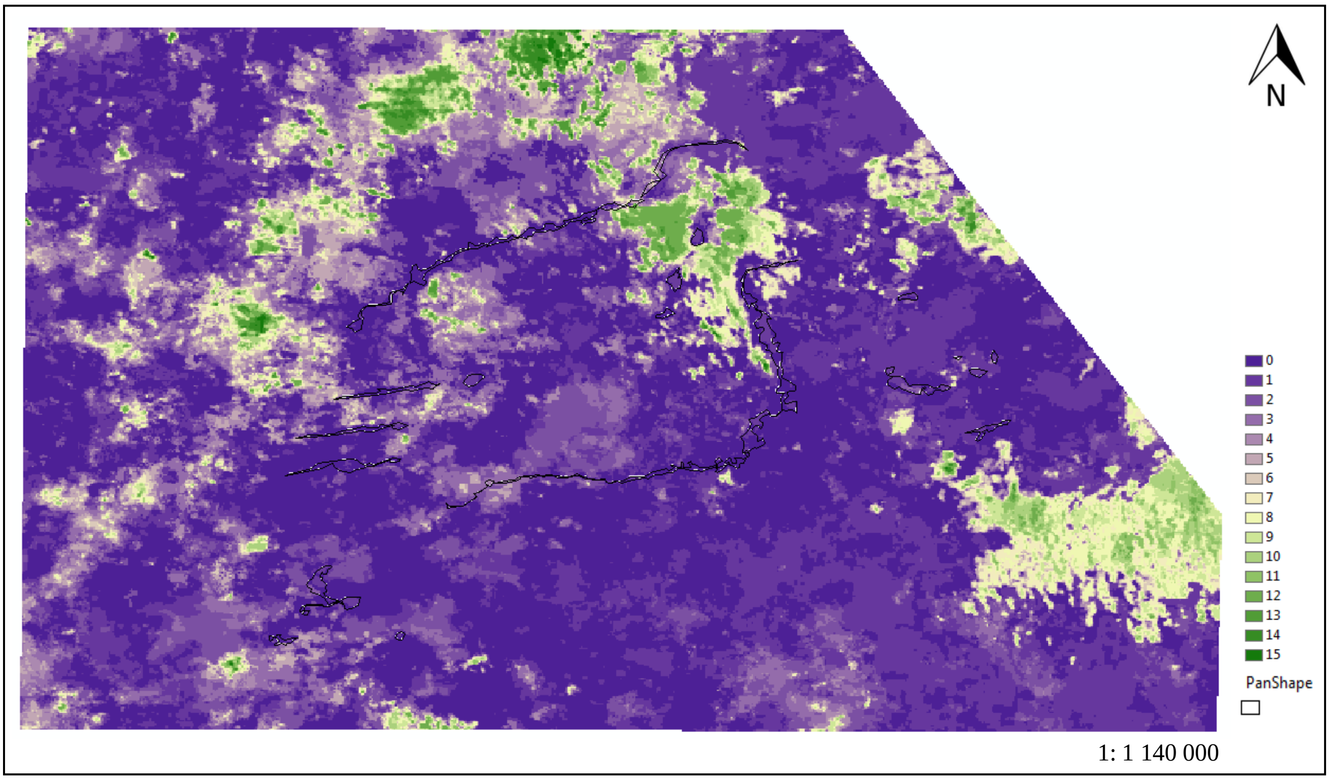


Figure 2.13 Frequency of HH clusters (high greenness) during the collar period (November 2012 – July 2013).

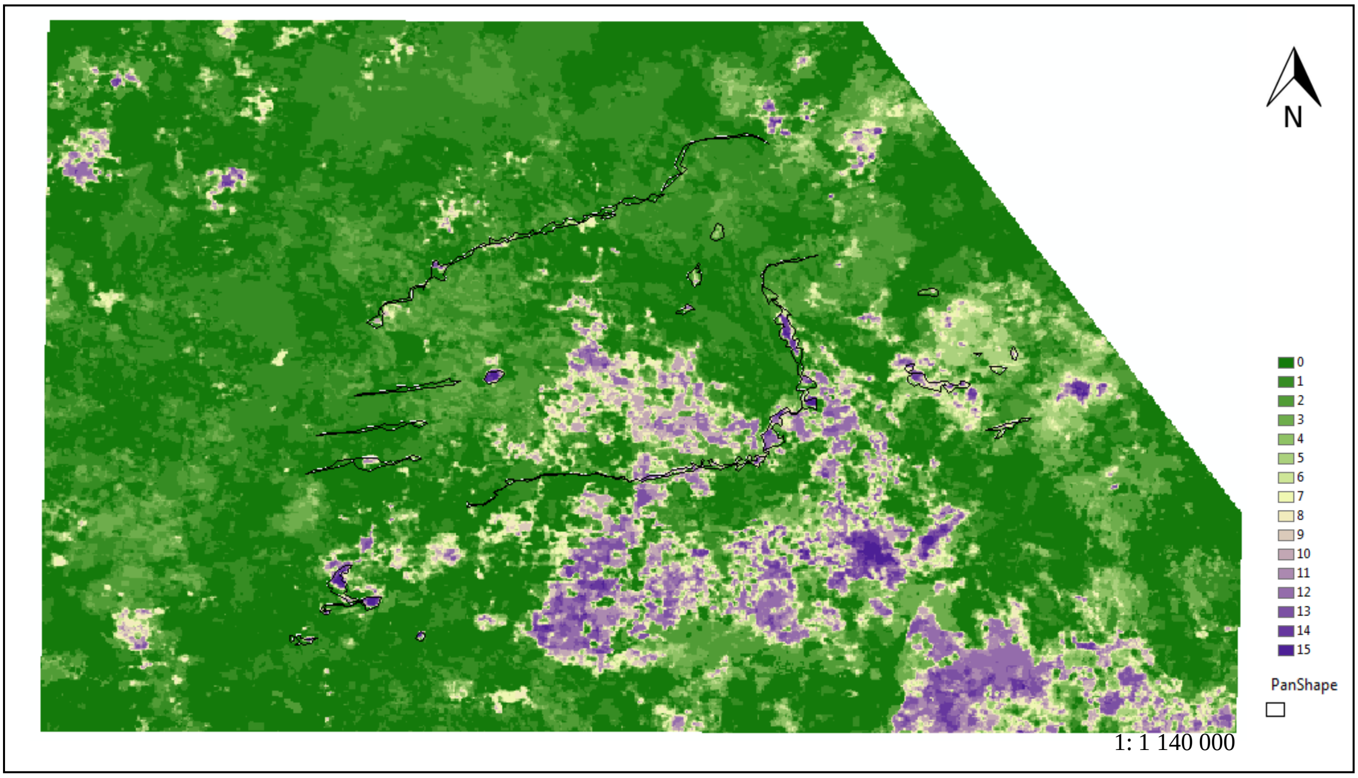


Figure 2.14 Frequency of LL clusters (low greenness) during the collar period (November 2012 – July 2013).

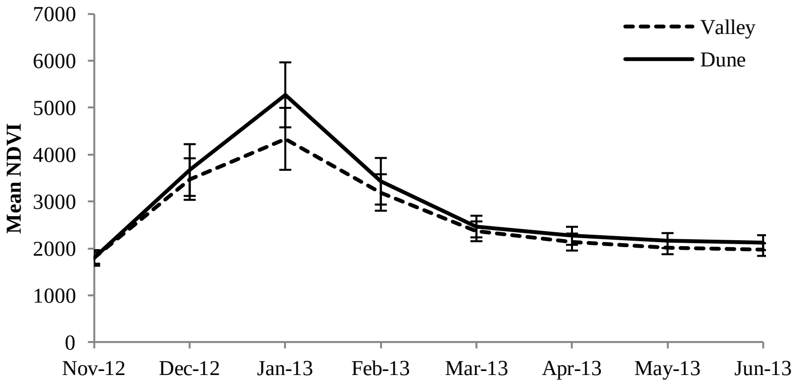


Figure 2.15 Mean NDVI over time, averaged across valley and dune habitats within Zone A (central Passarge Valley).

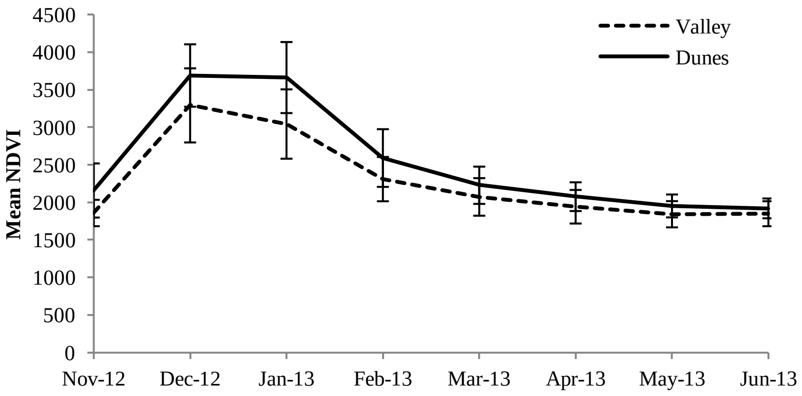


Figure 2.16 Mean NDVI over time, averaged across valley and dune pixels within Zone B (Letiahau Valley).

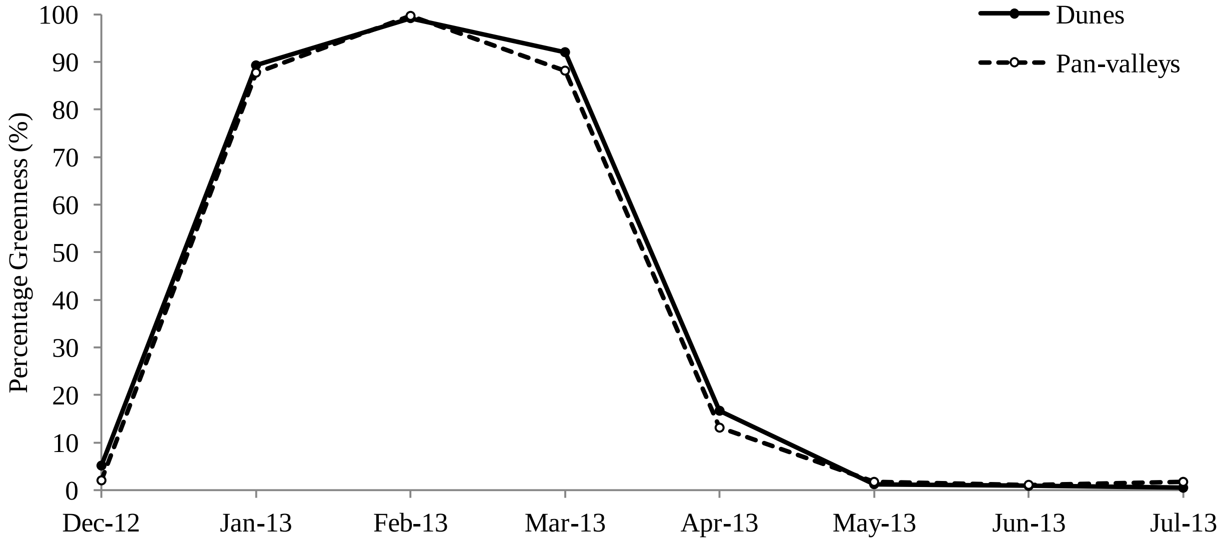


Figure 2.17 Percentage NDVI greenness across both dune and pan-valley habitats of the northern Central Kalahari Game Reserve during the collar period (November 2012 – July 2013).

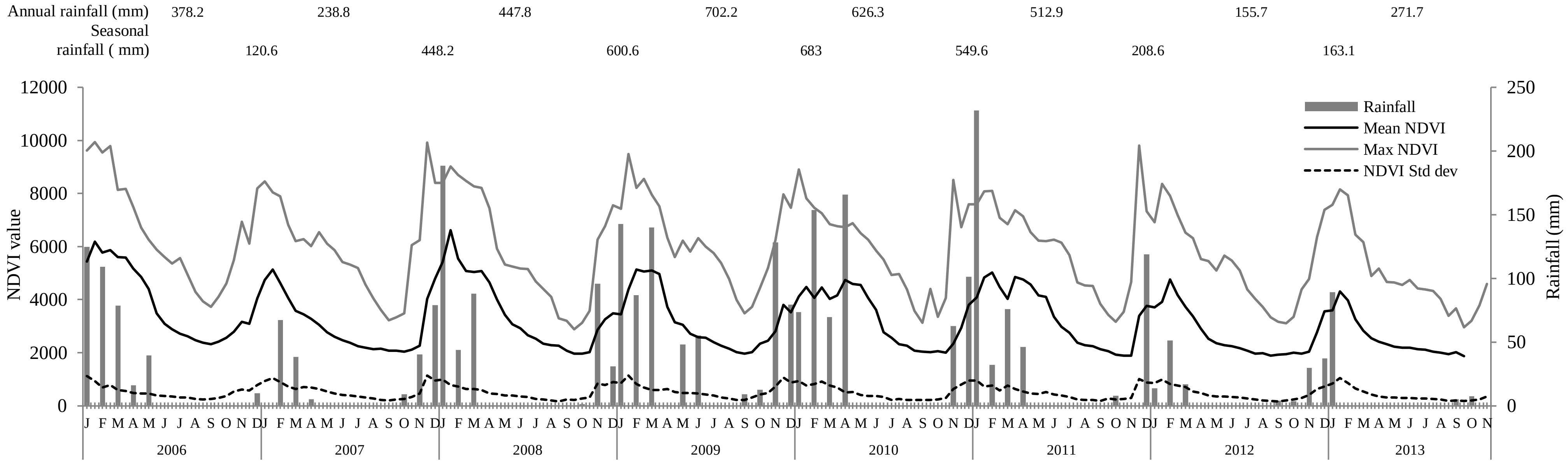


Figure 2.18 NDVI mean, maximum and standard deviation time series and monthly rainfall (mm) of the northern Central Kalahari Game Reserve from 2006 – 2013. Rainfall data were sourced from the office at Matswere gate (eastern entrance of the CKGR). The values above each peak indicate the total rainfall (mm) for that particular rainy season, and the values between each peak indicate the total rainfall (mm) for that particular year.

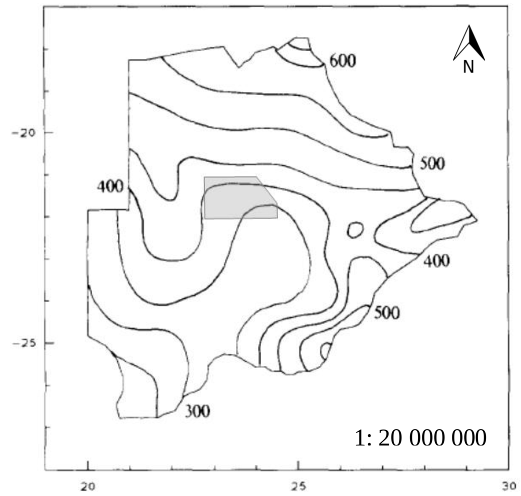


Figure 2.19 Traditional annual rainfall in Botswana (mm), indicating that the northern central Kalahari (shaded in grey) is primarily situated between the 350 and 400mm isohyets (adapted from Nicholson & Farrar, 1994).

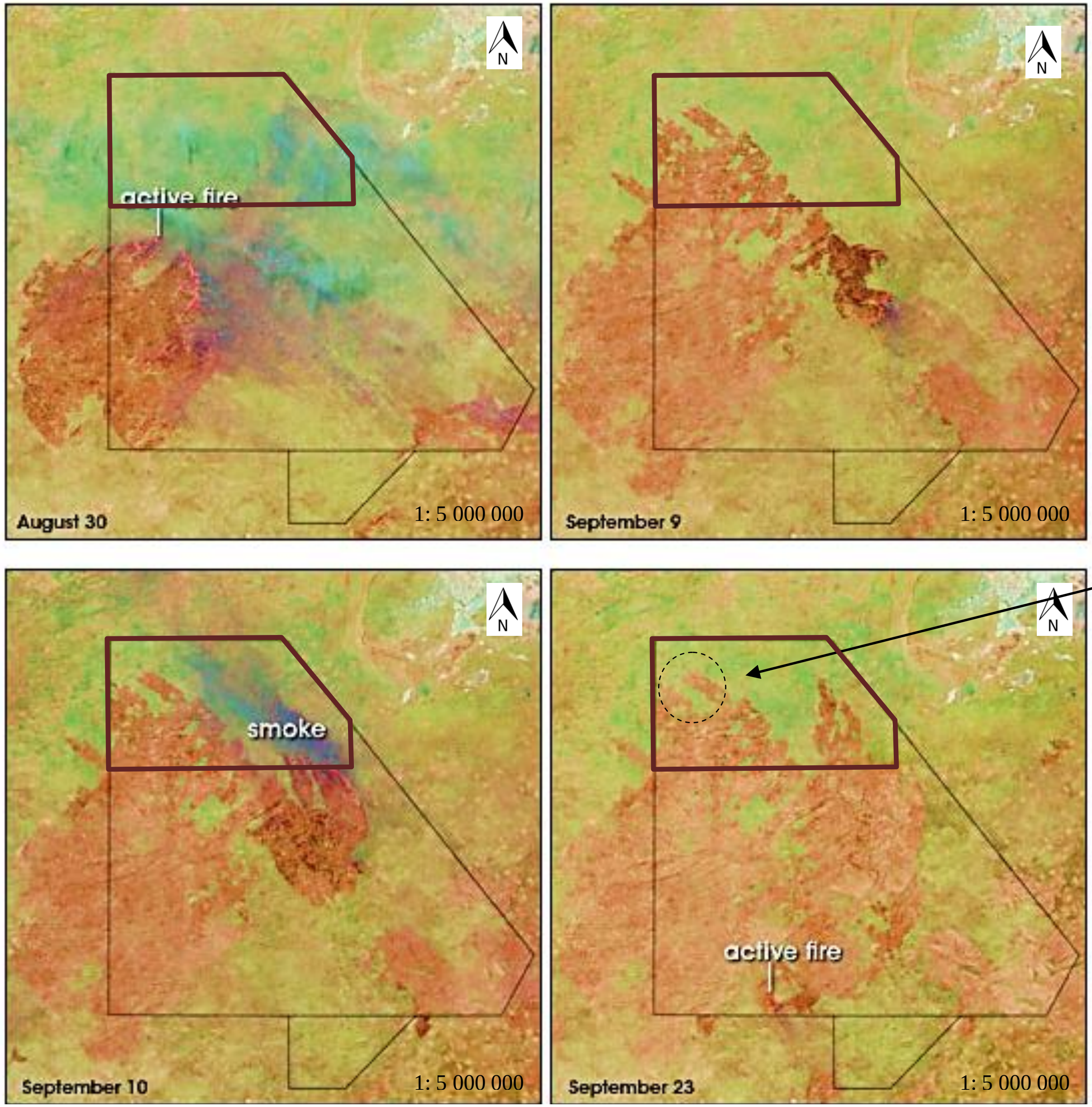
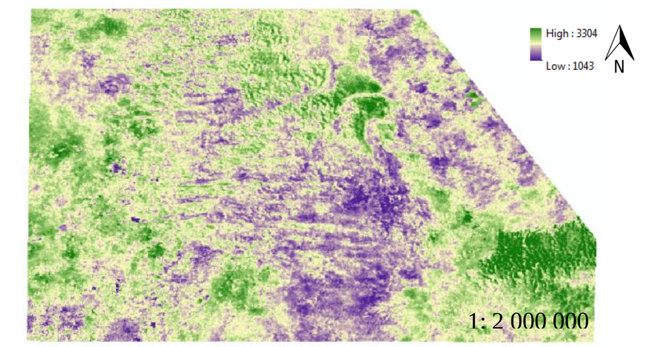
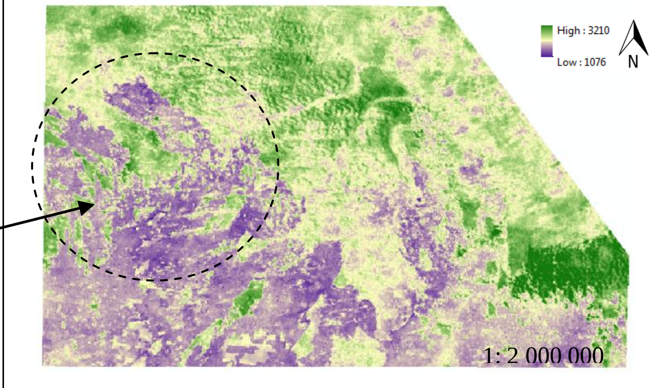


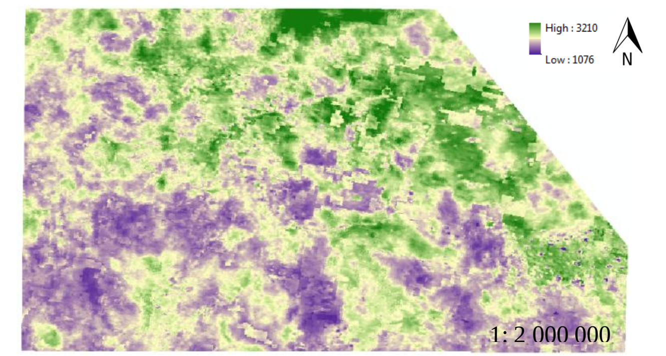
Figure 2.20 False-colour, multispectoral images captured by MODIS satellites of the large fire which spread across the Central Kalahari Game Reserve in August and September 2008.



Before the fire (29th August 2008 – 13th September 2008)



After the fire (14th September – 29th September 2008)



After the November rains (19th December 2008 – 3rd January 2008)

Figure 2.21 MODIS NDVI rasters depicting the change in vegetation greenness before and after the fire in 2008.

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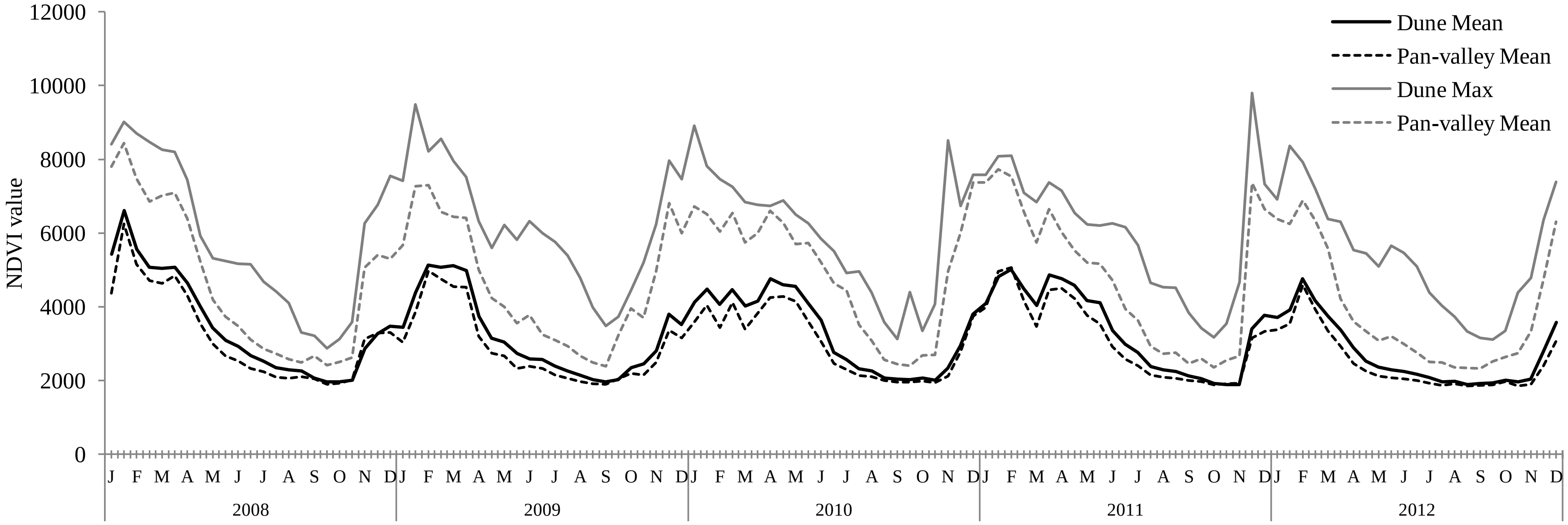
Appendices

Appendix A: Spatially-averaged mean and maximum NDVI temporal profile for pan-valley and dune habitats of the northern Central Kalahari Game Reserve from 2008 - 2012, indicating there is no temporal deviation in the rate of green-up or duration of greenness between the two habitat types.



CHAPTER 3: MOVEMENT PATTERNS AND HABITAT SELECTION BY GEMSBOK IN THE CENTRAL KALAHARI

Introduction

Spatio-temporal variability in rainfall and forage vegetation across arid savanna ecosystems is believed to drive the movements and habitat selection patterns of large herbivores (Williamson et al., 1988; Knight, 1991; Verlinden & Masogo, 1997). Acquiring a comprehensive knowledge of the movement responses of free ranging herbivores to the variability throughout these regions is essential for the provision of sustainable mitigation procedures and conservation policies to prevent species and habitat loss, should the need arise (Coughenour, 1991; Bailey et al., 1996). This is particularly true for arid southern African savannas, which are expected to become warmer and drier, with increasingly unpredictable rainfall, as a consequence of climate change (Meadows, 2006; Hannah et al., 2002). Less frequent rainfall events and amplified temperatures, in an already spatio-temporally variable habitat, could radically constrict arid savanna biomes (Meadows, 2006), thus considerably reducing herbivore carrying capacity. Migration and mobility have been identified as the most vital behavioural adaptations for herbivore survival and breeding success, particularly in spatially and temporally variable environments (Fryxell et al., 2004). Large herbivore movements are influenced by abiotic factors such as gradient, soil minerals and water, and by biotic factors such as competition, predation, and the abundance and nutritional quality of forage material (Ottichilo et al., 2001; Bailey et al., 1996, Fryxell et al., 2005; Bar-David et al., 2009).

Optimal foraging theory states that herbivores make movement decisions to capitalise on high quality forage and limit energetic loss wherever possible, often leading to behavioural trade-offs (Sæther & Andersen, 1989; Johnson et al., 2001). These trade-offs continuously influence herbivore decisions concerning where and when they should feed, and the type of forage material that they should consume. Many grazers prefer green grass during its early growth stages following rainfall events, as it is most nutritious and easily digestible during this phase (Wilmshurst et al., 1999; Owen-Smith, 1982). However, as grasses grow, their protein and energetic content progressively decreases, while fibre content increases, resulting in a decline in forage quality over time (Owen-Smith, 1982). The phenology of savanna grasses is highly dependent on seasonal rainfall, which is often unpredictable and exhibits annual and spatial variability (Fensholt et al. 2012). As such, efficient grazing choices are vital for some herbivores during both the rainy season, when physical growth and reproductive success are regulated by green season forage, and during the dry season, when reduced forage availability can limit population growth (Seagle & McNaughton, 1992; Owen-Smith, 2002; Klein, 1965). Dry, or brown, conditions usually result in habitat shifts and diet expansion as a result of vegetation quality depletion (Owen-Smith & Novellie, 1982). For example, African buffalo (*Syncerus caffer*) utilise larger areas and move further during the dry winter months, when available forage declined, than during green season conditions, when their ranges contract (Ryan et al., 2006). Wildebeest (*Connochaetes taurinus*) migrate seasonally from the Serengeti to the Maasai Mara in East Africa because of a seasonal shift in the availability of green vegetation (Musiega & Kazadi, 2004). Contrastingly, Mongolian gazelles (*Procapra gutturosa*) (Mueller et al., 2007) and Thompson gazelles (*Gazella thomsoni*) (Fryxell et al., 2005) have irregular, non-seasonal movements that allow them to exploit ephemeral, irregularly distributed forage resources. In light of these examples, it is clear that herbivores have the ability to adapt their movements and habitat choices so as to take advantage of the prevailing environmental and climatic conditions.

Remote sensing data are a valuable component of movement ecology, specifically when modelling animal movements and habitat selection (Boone et al., 2006; Holdo et al., 2009, Pettorelli et al., 2011, van Bommel et al., 2006). Satellite tracking methods, such as the Global Positioning System (GPS), are invaluable tools for ecologists around the world to track and analyse the movements of wildlife in their natural environments over large spatial and temporal scales, and without human disturbance (Musiega & Kazadi, 2004; van Bommel et al., 2006; Pettorelli et al., 2006; Mueller et al., 2007; Owen-Smith & Cain, 2007). Satellite-measured vegetation indices, such as the Normalized Difference Vegetation Index (NDVI), are able to discern the spatio-temporal distributions and variability of primary productivity across large spatial and temporal scales (Reed et al., 1994). NDVI is widely used as a proxy for greenness and hence nutritional quality and vegetation biomass (Huete et al., 2002; Pettorelli et al., 2005; Shippert et al., 1995). Greenness, as measured by NDVI, largely influences the movements of a variety of herbivores in various biomes across the globe. Studies in the semi-arid parts of southern Africa have found that herbivores such as ostrich (*Struthio camelus*) (Milton et al., 1994) and red hartebeest (*Alcelaphus buselaphus*) (Verlinden & Masogo, 1997) move to select greener forage vegetation in heterogeneous environments. Migratory red deer (*Cervus elaphus*) in Norway pursued the spatial progression of seasonal greenness, thereby capitalising on the early growth stages of forage material (Bischof et al., 2012). Contrastingly, certain studies have revealed that NDVI is not always a useful measure for studying herbivore habitat selection. The distribution of springbok and eland in the Kalahari, for example, showed no relationship with NDVI (Verlinden & Masogo, 1997). Additionally, the spatial scale of analysis and seasonality are important considerations of any resource selection study. African elephants (*Loxodonta africana*) in Kruger National Park selected for intermediate levels of greenness at the home range scale during the wet season, but showed no association with greenness at smaller spatial scales (Marshal et al., 2011). Vegetation indices, used in conjunction with GPS, can inform ecologists of the influence vegetation availability has on animal movement with minimal fieldwork, and in the most remote of environments.

The Central Kalahari Game Reserve (CKGR) is an expansive (over 52 800 km^2), remote protected area. As such, an *in situ* field study into environmental dynamics and variability would have been extremely costly and time consuming. Monitoring the vegetation dynamics across the northern region of the CKGR with the use of NDVI satellite imagery would provide insight into the degree of unpredictability and variability of primary productivity at a landscape scale. High quality vegetation is not distributed uniformly across the environment, but is principally a result of spatially-isolated convective rainfall and the prevailing soil type (Porporato et al., 2003). The Kalahari region is generally classed as a homogeneous sandy, arid dune landscape, interspersed with a number of pans and fossil river valleys (Makhabu et al., 2002). These pan and valley systems provide a notably contrasting habitat type from the dune regions, based on their hard, clay, mineral- rich soils (Knight, 1991).

As an iconic species of the Kalahari region, gemsbok (*Oryx gazella*) thrive in this harsh, arid environment thanks to their physiological and behavioural adaptations (Cain et al. 2006). Gemsbok are able to acquire all of their necessary moisture from grasses and other plant resources and, as a result, their populations are able to flourish in landscapes with no permanent sources of water (Knight, 1991; Williamson, 1987). Gemsbok allow their core temperatures to rise to reduce water loss during periods of heat stress (Taylor 1970). They are considered to be predominantly grazers of species such as *Eragrostis lehmanniana* and *Stipagrostis* spp. (Knight 1991), but have been known to consume certain ephemeral plants, fruit and pods to supplement their diets (Knight 1991). For gemsbok to meet their protein and energy requirements during dry conditions, when high quality forage becomes limited, they can move from previously nutritious short grasslands within pans and valleys into the drier dune regions, where grasses exist at a greater biomass, albeit lower quality (Knight, 1991). In these cases, it is likely that the pans and valleys, which flourish during periods high in rainfall, become barren or desiccated during the dry season, and as such, produce forage that is extremely limited in both quality and quantity. Gemsbok may return to valley and pan regions occasionally during the dry season to access underground sources of minerals in the clay-rich soils. This is done by digging with their front hooves, which additionally allows them to acquire underground storage organs rich in moisture (Williamson, 1987), and has also been observed in Fringe-eared Oryx (*Oryx beisa callotis*) in Kenya and Arabian Oryx (*Oryx leucoryx*) (Asmodé, 1990). It is this ability to acquire alternate sources of moisture that is believed to enable gemsbok in the northern CKGR not only to survive, but also to reproduce successfully, during exceptionally dry conditions when other grazers, such as wildebeest, either perish or are forced to migrate (Williamson, 1987).

Although the wildlife within the CKGR is protected from the encroaching pressure of human populations and their livestock, the southern and western boundaries of the reserve remain unfenced and, as a result, large populations of wildlife still exist throughout regions of the Kalahari that are outside of protected areas (Bergström & Skarpe, 1999). It is these wildlife populations that would experience the effects of land-use change and habitat fragmentation (Wallgren et al., 2009; Bergström & Skarpe, 1999), thus forcing them towards the confines of the protected area boundaries. Increased herbivore population numbers in the CKGR could lead to increased inter- and intra-species competition (Illius & Gordon, 1987). These pressures, in combination with a potential decline in rainfall and added thermal stress as a consequence of climate change, threaten to cause a significant depletion of forage resources available to herbivores in this unique African environment. Gemsbok are considered to be nomadic animals, with no detectable migratory pattern, but rather move nomadically in pursuit of spatially and temporally unpredictable forage resources (Knight, 1991). Furthermore, their movements are not defined by daily visits to water (Knight, 1991). The successful gemsbok populations within the Central Kalahari (East, 1998), therefore, provide an ideal opportunity to gain insight into how this remarkable species' adaptive movement behaviours and habitat selection patterns, allow it to tolerate such harsh, unpredictable environmental conditions.

This study focuses on the movement ecology of gemsbok in the northern region of the CKGR and explores the relationship between gemsbok foraging locations, habitat type and satellite-measured vegetation greenness. To achieve this, eight gemsbok were collared in different herds to test three working hypotheses. Hypothesis 1 states that during transition periods, when the landscape is neither homogeneously green nor brown, gemsbok foraging locations will coincide with greener areas, since these are expected to offer better nutrition to herbivores, particularly during the beginning of the rainy season when grass forage is developing. Hypothesis 2 is that gemsbok will favour green regions in pans and river valleys as foraging sites, over green regions in dune habitats. Finally, Hypothesis 3 states that 12-hour displacement distances for each herd will increase during the brown season because of the necessity to increase their spatial search for food when forage quality is deficient.

Methods

Study Area

The study took place in the northern region of the CKGR, located in Central Botswana (Figure 3.1). The reserve is only fenced along its northern and eastern boundary, allowing wildlife free movement towards the south and west of the country. Situated between 21 and 22 °S and 23 and 24 °E, the northern section of the reserve contains the well-known Deception, Letiahau and Passarge fossil river valleys, which provide a distinctive contrast to the expansive, flat dune regions (Makhabu et al., 2002). The pan and valley regions are often carpeted in short green grasses during the wet season, but in the winter months the pans are often bare, sandy open areas, or produce tall brown grasses (Knight, 1991; pers. obs.). As a characteristic savanna environment, the vast dune regions are composed of a continuous grass layer with scattered trees (mostly *Vachellia* (previously *Acacia*) spp.) and shrubs (particularly *Senegalia* (previously *Acacia*) *mellifera*). Temperatures can range from extremes of -1 °C to 37 °C (Makhabu, et al., 2002), but the variability in rainfall is greater (Poprorato et al., 2003). The northern region of the CKGR receives approximately 400 mm of rainfall per annum, usually in the form of convective thunderstorms during the period from October to April (Thomas & Shaw, 1991), while the dry season extends usually from May to August into October. The northern CKGR received a seasonal rainfall of only 163.1 mm during the summer of late 2012 - early 2013, and, as such, environmental conditions during the study period were considerably more limiting than usual.

Study Species

As the only grazing ruminant to be able to permanently dwell in the waterless, arid regions of the Kalahari in southern Africa, gemsbok are a valuable species for the investigation of adaptability and possible responses to habitat fragmentation and climate change. The behaviour, physiology and morphology of this species allow them to cope efficiently in this harsh, dry savanna ecosystem. Gemsbok have a light pelage colour that reflects solar radiation (Cain et al., 2006), and as the largest of all Oryx species, gemsbok males weigh on average 240 kg, with the lighter females weighing approximately 210 kg (Skinner & Chimimba, 2005). Large herbivores are able to consume large quantities of forage with a low nutritional value (Illius & Gordon, 1987; Demment & van Soest, 1985), and generally feed less selectively than smaller herbivores (Jarman, 1974). The gemsbok’s narrow muzzle aids in the selection of taller grasses, as well as underground tubers, gemsbok cucumbers

(*Acanthosicyos naudinianus*) and tsamma melons (*Citrullus lanatus*), which have extremely high water concentrations (Knight, 1991; Dieckmann, 1980). There appears to be no definite breeding season, as young are often present all year round (Eloff, 1959)

Data Acquisition

Eight female gemsbok were collared at the beginning of November 2012, with each individual a representative of a different herd. The gemsbok were darted via helicopter by Dr Larry Patterson, a wildlife veterinarian with 30 years of experience in game capture in Botswana and registered with the Botswana Veterinary Council. Research, darting, collar and supplementary permits were acquired from the Department of Wildlife and National Parks, Botswana under the initial research permit: EWT 8/36/4 xx (36), and ethical clearance (AESC 2012/24/04) was acquired from the Animal Ethics Screening Committee of the University of the Witwatersrand. The GPS collars were manufactured by Africa Wildlife Tracking (https://www.awetelemetry.com/) and fitted with satellite data upload capability, as well as VHF radio beacons, in case of GPS failure. The mass of the collars were less than 5% of the animal's body mass, and were set to record the GPS position of the individual every hour, which could then be downloaded remotely. Five of the eight individuals were collared in and around the eastern portion of Deception Valley, whereas the remaining three individuals were collared in the west of the study area, in the vicinity of Letiahau Valley. Following the collaring procedure, the collared gemsbok were relocated using the VHF radio beacons, over the course of the following 3 days, as well as during successive fieldtrips in February and April 2013, to ensure that the individuals remained in good physical condition and the collars were not hindering their survival success to any extent. Most of the collars lasted approximately eight months from the time of dispatch, resulting in a study period extending from the beginning of the wet season (November 2012) and concluding mid-dry season (July 2013). Due to an unfortunate battery failure, one of the collars (SAT566) malfunctioned within the first two months of activation. For the analysis, the study period was split into 16 x 16-day periods, labelled $T_1 – T_{16}$. This temporal resolution corresponded to that of the NDVI images derived from the MODerate Resolution Imaging Spectroradiometer (MODIS) (Table 3.1), and the extent was a result of the duration of the collars' battery life (Table 3.2).

For the collar period, MODIS 13 Q1 NDVI time series satellite data for southern Africa was sourced from the MODIS Reprojection Tool Web Interface (MRTWeb, https://mrtweb.cr.usgs.gov/). The images each have a spatial resolution of 250 m and a temporal resolution of 16 days. These data are corrected for parameters such as aerosols, cloud shadows, orbital drift, and water vapour (de Jong et al., 2012). The major pan and valley regions were separated from the rest for the study site with the use of a shapefile made by hand in ArcGIS 10.1 and Google Earth. The entire study site (northern CKGR) was made up of 269 648 pixels, however only 2 642 of those pixels were classified as belonging to the pan and valley habitats, as they make up a much smaller surface area than the immense dune regions. Valley and pan regions will henceforth be referred to as pan-valley habitats.

Data Analysis

To investigate resource selection by eight gemsbok herds in the northern CKGR, the relationship between gemsbok foraging locations, habitat type and satellite-measured greenness was examined. Minimum convex polygons (MCPs) were developed using all GPS points collected for each individual and are believed to accurately represent the habitat available to that individual during the study period, as the polygon enclosed the entire environment utilized by that individual during the study. As the size of the area representing the available habitat decreases, the bias towards selected habitats increases. In other words, using a more condensed home range method would increase the similarity between used and available locations. MCPs are thus considered to be an appropriate means with which to represent the habitat available to each gemsbok. To avoid spatial autocorrelation between neighbouring pixels, scattered random points were used to calculate the proportion of every habitat available to each individual. Spatial autocorrelation means that environmental characteristics are more similar when spatially nearer (Tobler’s First Law of Geography). To determine how many scattered random points (SRPs) were necessary to accurately represent the total area inside the MCP, a boxplot of the NDVI distribution across an entire MCP was compared to boxplots of various ratios of SRPs:Total points (i.e. the total number of point values or pixels within each MCP) (Figure 3.2). It was concluded that a ratio of at least 1 SRP:20 Total Points was required. Although each individual’s MCP differed in size, the number of scattered points used to represent the available habitat never fell below this ratio. Like other savanna herbivores (Ryan & Jordaan, 2005, Vrahimis & Kok, 1993, Jarman & Jarman, 1973), gemsbok spend more time feeding during the early morning and late afternoon, and rest during the hottest times of the day (Knight, 1991). As a result, two locations at consistent times each day, one in the early morning and the other in the evening, were selected as foraging locations. The used locations were compared to random available locations within each individual’s MCP at a ratio of 1:10 (used to random), to ensure that available habitat was sufficiently represented (Manly, 2002).

Greenness Measures:

A major limitation of NDVI data in their available format is that it is difficult to differentiate between vegetation types, such as trees, grasses and shrubs, as they often have similar absolute values and seasonal trends of green up following rainfall events (Pettorelli et al., 2005). This becomes problematical when assessing the selection by herbivores when *in situ* ground comparison is unfeasible. In this study, I used three contrasting measures to represent greenness:

1. NDVI
2. ΔNDVI (delta.ndvi)
3. Relative Greenness (RG)

NDVI is a measure of vegetation greenness, with values ranging from 0 – 1, with larger values representing greener pixels. MODIS data are converted to a range of 0 – 10 000. ΔNDVI is the change in NDVI per pixel between one 16-day time period and the previous 16-day time period, i.e. T_n and T_{n-1}. Positive values indicate areas that have shown an increase in NDVI, while negative values have shown a decrease in greenness from the previous 16-day period. Relative greenness was defined on a pixel-by-pixel basis through time, where the NDVI distribution of each pixel during the study period was used to determine the relative level of greenness for that pixel. Level 1 relative greenness represented NDVI values less than the mean NDVI – ½ standard deviation, i.e. that pixel’s lowest NDVI values during the study period. Level 3 relative greenness represented values greater than the mean + ½ standard deviation, i.e. that pixel’s highest NDVI values during the study period. Level 2 relative greenness was everything that fell between levels 1 and 3 (Figure 3.3). The use of ½ standard deviation, rather than 1 standard deviation, was necessary to form three equally represented categories, considering the shape of the NDVI distribution. This relative measure of greenness was considered to avoid limitations associated with spatial variability in soil and vegetation structure, as these factors were considered to remain constant throughout the collar period and, therefore, changes in relative greenness were considered to result from seasonal vegetation growth and decline as influenced by rainfall.

Transition Periods:

Since greenness selection is impossible when the landscape is homogeneously green or brown, only certain 16-day periods were used in this analysis. These periods are from here onwards referred to as transition periods, when the landscape was experiencing a transition between being homogeneously green and homogeneously brown. Transition periods were defined using the relative greenness measure, rather than a crude NDVI value, so as to avoid the effect of spatial variation in vegetation structure. Additionally, these transition periods were representative of only the area inside the MCPs of all of the gemsbok combined, and not the total study area, so as to prevent any bias from surrounding unused environments. Periods were considered to be homogeneously brown when >90% of the landscape was represented by level 1 relative greenness, and homogeneously green when >90% of the landscape was represented by level 3 relative greenness (Figure 3.4). Furthermore, the transition periods were separated into two categories: Green Transition, when more of the landscape was composed of level 3 relative greenness than level 1; and Brown Transition, when more of the landscape was composed of level 1 relative greenness than level 3 (Figure 3.4).

Logistic Regression:

A range of multivariate logistic regression models were fitted to the data for both the green and brown transition periods to test Hypotheses 1 and 2, which stated that gemsbok would select for greenness during transition periods, and would select for greener regions in pan-valley habitats than in dune habitats. The logistic models followed the decrees described in Manly et al. (2002)'s Design III, where used and available resources were defined for each individual. Generalized Linear Mixed Models with a binomial distribution were developed in R version 3.1.1 © (The R Foundation for Statistical Computing Platform 2014) using the lme4 package (Bates et al., 2014) and the function *glmer*. The response variable is binary, whereby 0 = available locations and 1 = used locations, at a ratio of 10:1. The explanatory variables used in the models were NDVI (categorical, consisting of 4 equal categories, where 1 is the lowest and 4 is the highest), ΔNDVI (categorical, consisting of 4 equal categories, where 1 is the lowest and 4 is the highest), Relative Greenness (categorical, consisting of 3 levels (Figure 3.3)) and Habitat (categorical, consisting of 2 categories: dunes = 0, pan-valleys =1). The originally continuous variables (NDVI and ΔNDVI), were reformatted into four equal categories to avoid convergence failures, which prevent model production (Allison, 2004). Individual ID was included as a random factor in all of the models. The models were developed using a range of combinations of the four explanatory variables and interactions between each of the three greenness variables with the habitat variable. The default setting in R uses a reference cell for each categorical variable against which the remaining variables are compared, whereby the lowest categorical variable is set as the reference category (estimate value is 0). As such, in the created logistic models, the reference categories include NDVI value 1, ΔNDVI value 1, relative greenness level 1, and dune habitats (0). Preceding model development, all greenness explanatory variables were tested for correlation.

Comparing and testing the models:

Models were compared using the statistical measures: Akaike's Information Criterion (AIC) and Bayesian Information Criterion (BIC), which are measures of model parsimony: lower values indicate a better model fit (Burnham et al., 2011) Additionally, the Akaike weights (w_i (AIC)) were calculated for each model. Akaike weight can be understood as the probability that the model with the lowest AIC value is the best model to represent the data supplied from the list of candidate models (Burnham and Anderson, 2002). The best model for each transition period was selected based on these results. These two selected models were then assessed further, where coefficient estimate values (± 95% confidence intervals) were compared to determine the degree of selection for certain greenness measures, habitat types and the interactions between them. The coefficient estimate value represents the log odds ratio of a variable relative to the reference cell. Odds describe the probability of a gemsbok selecting a particular foraging location. Odds ratios greater than 1 (positive log odds ratios) suggest that a gemsbok is more likely to select that category variable than the reference category, while odds ratios less than one (negative log odds ratios) indicate that a gemsbok is less likely to select that category variable than the reference category (Peng et al., 2002).

Displacement distances:

Twelve hour displacement distances were calculated between the morning and evening locations for each gemsbok, each day, throughout the collar period. This investigation aimed at identifying individual differences and similarities between the movement strategies of each gemsbok herd across seasons and between day and night movements. Due to the collar failure of SAT566 in January 2014, that individual was excluded from the analysis. The linear displacement distance from the GPS point location at 07h00 to the GPS point location of that individual 12 hours later, at 19h00, was measured in ArcGIS 10.1. This displacement distance was referred to as the day movement. The linear displacement distance between the 19h00 GPS point location and the 07h00 point location the subsequent day was measured in a similar fashion, and referred to as the night movement. Data were tested for normality using the Shapiro-Wilk normality test in R version 3.1.1 ©. Subsequently, Wilcoxon rank sum tests for nonparametric data were used to determine whether 12-hour displacement distances differed between day and night, and between the brown and green seasons for each individual. In this case, 12 hours was expected to be a long enough duration for an individual to traverse from one foraging area to another

Results

Habitat use versus availability was investigated during two time periods, the green transition period (T_3, T_4, T_7, T_8) and the brown transition period (T_1, T_2, T_9, T_{10}, T_{11}, T_{12}) (Figure 3.4). In total, the green transition period consisted of 906 used locations, and 9 060 available locations (ratio of 1:10, used versus available) (Table 3.3), whereas the brown transition period consisted of 1 392 used locations and 13 920 available locations (ratio of 1:10, used versus available). Three greenness measures (NDVI, ΔNDVI and Relative Greenness) were used to assess whether gemsbok showed any selection for greenness during either of the transitions periods. For both periods, I was interested in identifying the greenness measure that best described forage selection by gemsbok, if one existed. Additionally, I aimed to determine whether gemsbok showed habitat selection between pan-valley and dune regions.

Correlation:

The results of the test for correlation of fixed effects indicated that none of the three greenness measures showed any significant level of correlation. These measures could therefore all be used in the same logistic regression model, without any concern that one explanatory variable could be linearly predicted by another, with a non-negligible degree of accuracy (Tables 3.4 and 3.5).

Transition Green Period:

The hypotheses (H_1 and H_2) were tested by fitting a number of logistic regression models to the data. During the transition green period, the best model included all four fixed effects (NDVI, ΔNDVI, habitat and relative greenness), with an interaction between habitat type and NDVI (Table 3.6). This model was chosen as the best because it produced the lowest AIC value (5795.4), the lowest BIC value (5896.3), the lowest deviance value (5767.4), and the results of the Akaike weights revealed that the model had 100% probability of being the best of the candidate models given the transition green period data (Table 3.6).

The logistic regression estimates of model 19 revealed that gemsbok showed no selection for higher NDVI values or higher ΔNDVI values (Table 3.7, Figure 3.5). In fact, gemsbok showed higher selection for NDVI category 1, 2 and 3, compared with NDVI category 4. This means that the log odds of gemsbok habitat selection was negatively related to both

NDVI and ΔNDVI. Gemsbok did however, select for higher categories of relative greenness (level 2 and 3), when compared to the lowest relative greenness (level 1). Compared to relative greenness level 1, relative greenness level 2 (0.912 ± 0.349), and relative greenness level 3 (1.412 ± 0.358) were selected for more commonly (i.e. the log odds ratios were positively associated with relative greenness ($p < 0.01$; Table 3.7, Figure 3.5). In fact, the odds of a gemsbok selecting relative greenness level 2 or level 3 were respectively 2.49 and 4.10 times greater than the odds of selecting greenness level 1 (Table 3.7). Gemsbok also selected pan-valley habitats (1.428 ± 0.380) over dune habitats (0) ($p < 0.001$; Table 3.7, Figure 3.5), and the odds of a gemsbok selecting pan-valleys were 4.17 times greater, than the odds of selecting dune regions (Table 3.7). Interestingly, gemsbok selected for category 4 NDVI in pan-valley habitats (0.700 ± 0.422), rather than lower NDVI values (category 1-3) in dune habitats (Table 3.7, Figure 3.5). This means that gemsbok were 2.01 times more likely to select for NDVI category 4 (high greenness) in a pan-valley habitat, compared to NDVI category 1 (low greenness) in a dune habitat (Table 3.7).

Transition Brown Period:

The best model developed using the brown transition period data also included all four fixed effects, however this model incorporated an interaction between relative greenness and habitat type. Again, the model was selected because it provided the lowest AIC value (9269.3), the lowest BIC value (9368.6) and the lowest deviance value (9243.3) (Table 3.8). In addition, the Akaike weights revealed that model 16b had 100% probability of being the best candidate model to represent the data (Table 3.8).

Gemsbok did not select for higher NDVI or ΔNDVI values (i.e. the log odds ratios of gemsbok selectivity was negatively related to NDVI and ΔNDVI). Additionally, relative greenness level 2 (0.312± 0.073) was selected over level 1 (reference category, i.e. estimate value is 0) ($p < 0.001$; Table 3.9, Figure 3.6). The odds of selecting relative greenness level 2 were 1.37 times greater than the odds of selecting level 1 (Table 3.9). Selection for relative greenness level 3 was not significantly greater than level 1 during the brown transition period ($p = 0.407$; Figure 3.6). Contrasting the results of the transition green period, gemsbok did not show a higher degree of selection for pan-valley habitats (-0.147 ± 0.181) than for dune regions (0) during the brown transition period ($p = 0.416$; Table 3.9, Figure 3.6). Gemsbok selected for relative greenness level 3 in pan-valley habitats (1.852 ± 0.391). In fact, the odds of selecting a pan-valley habitat with a relative greenness level of 3 was 6.37 times more likely than that of selecting a dune habitat with a relative greenness level of 1 ($p < 0.001$; Table 3.9, Figure 3.6).

Displacement Distance:

Results of the twelve-hour displacement distances showed no general seasonal movement trend (Figure 3.7 – 3.13). In most cases, individuals covered highly fluctuating 12-hour displacement distances across the duration of the period, and did not collectively travel more during the brown season than the green season, suggesting that their nomadic movements continued throughout the year without an obvious seasonal pattern. SAT562 does show a significant decline in day and night movement during the green season, and an increase during the brown season (Day: W= 9025, $p < 0.05$; Night: W= 7700, $p < 0.05$ night) (Figure 3.11, Appendix A). Similarly, SAT565 also travelled significantly more during the brown season than the green season, but this difference was only revealed during the daylight hours (W= 8329, $p < 0.05$) (Figure 3.12, Appendix A). Contrastingly, SAT561 reveals the opposite trend with peaks in displacement distances during periods of rainfall and green transition, and significantly reduced movements in the dry periods (Day: W= 3873 $p < 0.05$; Night: W= 3542, $p < 0.05$) (Figure 3.9, Appendix A). All individuals travelled further during the daylight hours than the hours of darkness (Figures 3.7, 3.8, 3.10-3.13, Appendix B) except for one individual (SAT561), which showed no significant difference in 12-hour displacement distance between day and night (W= 21 696, $p = 0.137$) (Figure 3.9, Appendix B).

Discussion

The combined habitat and greenness selection of eight gemsbok herds in the northern CKGR during a low rainfall year and stressed environmental conditions are demonstrated in the results of the logistic regression analyses. Gemsbok greenness selection was tested using three measures (NDVI, ΔNDVI and relative greenness). During both transition periods, gemsbok locations had no relationship with high NDVI or high ΔNDVI. Considering that gemsbok are most predominantly grazers (Knight, 1991), this lack of selection for higher NDVI categories is not unreasonable, given that NDVI values increase over regions with higher tree and/or shrub densities, such as woodlands (Scanlon et al., 2002). It was expected that, during foraging times, gemsbok would be likely to utilize open grassland regions, which often produce lower NDVI values than surrounding areas of high tree/shrub cover. Additionally, it is important to consider that not all green vegetation is nutritionally suitable and accessible to herbivores (Wilmshurt et al., 1999; Prins & Olff, 1998). These results concur with a study conducted by Verlinden and Masogo (1997), which revealed that gemsbok presence, measured by aerial survey in the southern Kalahari, was not explained by high NDVI values, but gemsbok were noted to be marginally more abundant in lower NDVI classes.

Relative greenness was a depiction of the temporal trend in greenness on a pixel-by-pixel basis, and therefore omitted the effect of spatial variation in vegetation type. This meant that if a particular pixel showed an increase in its relative greenness, it was likely that it had experienced rainfall. Contrastingly, if a pixel experienced a decrease in its relative greenness, it suggested that the vegetation had received no rainfall, and was therefore showing some degree of desiccation. This phenomenon would have been analogous regardless of the vegetation structure in that pixel, because the rate and duration of greenness was not found to differ between habitat types. Although no relationship was found between gemsbok locations and high NDVI and ΔNDVI values, gemsbok did show significant selection for higher relative greenness levels. This could be because gemsbok select greener grasses when they are available, but this selection for higher greenness values goes unnoticed when compared spatially to other vegetation types, such as those with high tree and shrub densities. During the transition brown period, selection for relative greenness level 2 was greater than that of level 1. However, the odds of selecting for level 3 were not significantly different from the odds of selecting for level 1. This was probably a direct effect of the fact that high greenness was less available during the brown transition period than during the green transition period. Rainfall and, as a consequence, vegetation greenness (Nicholson & Farrar, 1994) generally declines from April until September, and thus level 3 relative greenness is less available for selection by herbivores compared to level 1 or level 2 during the brown transition period. The results support Hypothesis 1, that gemsbok would select greener foraging areas than less green areas during transition periods when the landscape was neither homogeneously green nor brown. These results support those found by Knight (1991), who established that gemsbok select for greener grass conditions during both wet and dry seasons. The seemingly contrasting results revealed between Knight (1991), and Verlinden and Masogo (1997) are explained by Verlinden and Masogo (1997) to not be as different as they might initially appear. The results presented by Verlinden and Masogo (1997) suggest that gemsbok may tolerate areas of lower greenness, perhaps as an avoidance of human settlements, whereas the gemsbok movements in Knight (1991)'s study reflect those of gemsbok with more stable home ranges.

During the green transition period, when the landscape was predominantly comprised of green vegetation, gemsbok showed a higher degree of selection for pan-valley habitats than dune habitats. Soils rich in clay are intrinsically more fertile than sandy soils and produce grass species with a higher nutrient and lower fibre content (Bell, 1982). Knight (1991) noted that pan and valley regions produce short, nutritious green grasses during the green season, which attracts large herds of grazing herbivores. This selection for pan-valley regions over dune habitats did not persist into the dry transition period, perhaps because the herds moved into the sandy dune regions to meet their dietary requirements once the pan and valley grasses became depleted. Bearing in mind that gemsbok showed no significant difference in their degree of selection for either pan-valleys or dunes during the transition brown period, it was likely that gemsbok returned to the pan-valley regions occasionally, in search of other resources, such as soil minerals. Based on these results, Hypothesis 2, that gemsbok would prefer greener areas in pan-valley regions over dunes, was accepted during the green transition period only, which was reasonable, considering that green grasses in pan-valley habitats diminish considerably when rainfall ceases (Knight, 1991).

Gemsbok selected for NDVI category 4 in pan-valley habitats during the green transition period. Many of the pans and valleys in the Kalahari contained tree islands made up of predominantly large Camel thorn (*Vachellia* (previously *Acacia*) *erioloba*) trees (Knight, 199; pers. obs.). These tree islands provided substantial shade and often patches of short green grasses such as *Panicum* and *Cynodon* species. In addition, Knight (1991) noted that gemsbok foraged on the pods of *V. erioloba* to supplement their diet. This interaction between NDVI category 4 and pan-valley habitats could have been an indication of areas of these tree islands that were within certain pans and valleys, and constituted a suitable micro-habitat for gemsbok. However, to confirm this, further fieldwork would be needed. A comparable result was noted during the brown transition period, when gemsbok selected for relative greenness level 3 in association with pan-valley habitats. Level 3 relative greenness was much less available during the dry season. In this case, gemsbok may have been selecting for the greenest available grasses in pans and valleys, where clay soils dominate and possibly some soil moisture was retained.

Results showed no specific general trend in the seasonal movements of the seven collared herds in the CKGR, thus I rejected Hypothesis 3, which suggested that gemsbok would travel further during brown conditions, when forage quality was limited. This was probably a result of high variation between individuals and an indication that gemsbok in the CKGR may be opportunistic feeders, and herds make varying behavioural decisions based on their immediate environmental conditions. SAT562, the individual that showed a decrease in 12-hour day and night displacement distance during the green period, and an increase during the brown period, was known to be pregnant during the time of collaring, and it is most probable that she gave birth during one of the periods when movement declined. SAT563 and SAT561 showed spikes in their displacement distances during green periods, suggesting that these individuals searched and travelled further for the best quality vegetation when nutritious forage was more readily available. Interestingly, SAT563 exhibited a decline in movement during period 5 and 6 when the landscape was homogeneously green, indicating that long-distance search efforts were unnecessary, considering that high quality forage was easily accessible. Significantly lower displacement distances were revealed by SAT561 during the brown season, possibly because the landscape was homogeneously brown, i.e. it decreased its searching behaviour so as to conserve energy and limit weight loss as much as possible.

It is important to consider that greenness measures and habitat type are definitely not the only factors affecting the movements and habitat selection by gemsbok in the CKGR. Habitat selection and movement patterns of gemsbok could be associated with many other environmental, social and behavioural variables, which were not included in these logistic models. Examples of these variables include resources such as soil minerals, tsamma melons (*Citrullus lanatus*), gemsbok cucumbers (*Acanthosicyos naudinianus*), as well as interactions such as competition and predation. The use of these models for data prediction is beyond the scope of this study, and as such, the application of the models, particularly with the use of the relative greenness measure, was a useful means of indicating gemsbok selection for satellite-measured greenness and habitat type across this heterogeneous landscape. The utilisation of underground roots, tsamma melons, gemsbok cucumbers, soil minerals and certain forb species during the dry season, when nutritious grazing material is limited, suggests that NDVI would probably not be a useful measure with which to predict gemsbok foraging locations during the late brown season, when the landscape was homogeneously brown. The environment was mostly covered with desiccating, yellow/brown grasses, and bare soils (in some valleys and pans), and much of the greenness was usually only present in the form of unpalatable evergreen trees and shrubs (Knight, 1991).

In conclusion, the habitat utilization and movement behaviour of gemsbok is a complex matter, one that differs between individuals and the immediate environmental conditions experienced by that individual. It is evident from these results that gemsbok prefer greener grasses compared to less green grasses and bare habitats during both the transition green and transition brown period. Additionally, pan and valley habitats, with their soils rich in clay and minerals, are usually preferred over savanna dune regions when green conditions proliferate. Finally, the results of this study suggest that the use of NDVI data in its original state does not accurately demonstrate gemsbok selection for greenness in the Kalahari savanna, possibly, due to spatial heterogeneity in vegetation structure. However, the use of relative greenness, as measured in this study, is a valuable means with which to assess the movement responses of gemsbok to a spatially- and temporally-dynamic environment.

Tables

Table 3.1 Dates and codes of each 16-day period correlating to NDVI images during the gemsbok study period (Nov 2012 – July 2013).

Time Period	Raster Code	Dates
T_1	2012321	16 November 2012 – 1 December 2012
T_2	2012337	2 December 2012 – 17 December 2012
T_3	2012353	18 December 2012 – 31 December 2012
T_4	2013001	1 January 2013 – 16 January 2013
T_5	2013017	17 January 2013 – 1 February 2013
T_6	2013033	2 February 2013 – 17 February 2013
T_7	2013049	18 February 2013 – 5 March 2013
T_8	2013065	6 March 2013 – 21 March 2013
T_9	2013081	22 March 2013 – 6 April 2013
T_{10}	2013097	7 April 2013 – 22 April 2013
T_{11}	2013113	23 April 2013 – 8 May 2013
T_{12}	2013129	9 May 2013 – 24 May 2013
T_{13}	2013145	25 May 2013 – 9 June 2013
T_{14}	2013161	10 June 2013 – 25 June 2013
T_{15}	2013177	26 June 2013 – 11 July 2013
T_{16}	2013193	12 July 2013 – 27 July 2013

Table 3.2 Individual collar information for each female gemsbok (*Oryx gazella*) collared in the Central Kalahari Game Reserve.

Individual	Date collared	Collar Frequency	GPS location at immobilization point	Species	Sex	Herd count	Herd count upon relocation	Date of collar battery failure	GPS location at battery failure	Date of collar retrieval	GPS point at collar retrieval	State of individual at collar retrieval
SAT563	08/11/2012	148.8800	21° 27.218' S 23° 50.305' E	Gemsbok (*Oryx gazella*)	F	6	29	27/07/2013	21° 29.480' S 23.59.252' E	13/05/2014	21° 30.335' S 23° 59.275' E	Deceased - natural causes
SAT564	08/11/2012	148.9500	21° 27.533' S 23° 51.967' E	Gemsbok (*Oryx gazella*)	F	13	16	10/07/2013	21° 17.445' S 23° 49.766' E	15/05/2014	21° 13.488' S 23° 50.592' E	Good physical condition
SAT566	09/11/2012	149.4500	21° 27.462' S 23° 51.165' E	Gemsbok (*Oryx gazella*)	F	6	15	12/01/2013	21° 25.133' S 23° 53.797' E	13/05/2014	21° 30.595' S 23° 58.457' E	Good physical condition
SAT561	09/11/2012	148.7700	21° 26.916' S 23° 51.810' E	Gemsbok (*Oryx gazella*)	F	5	12	15/06/2013	21° 29.304' S 23° 46.391' E	–	–	Individual not located
SAT560	10/11/2012	148.4900	21° 26.311' S 23° 49.171' E	Gemsbok (*Oryx gazella*)	F	17	5	10/07/2013	21° 26.150' S 23° 48.136' E	13/05/2014	21° 25.112' S 23° 46.962' E	Deceased - natural causes
SAT562	10/11/2012	148.7800	21° 36.888' S 23° 26.939' E	Gemsbok (*Oryx gazella*)	F	13	7	16/09/2013	21° 26.988' S 23° 21.179' E	08/11/2013	21° 26.988' S 23° 21.179' E	Deceased - natural causes
SAT565	11/11/2012	149.1800	21° 37.067' S 23° 25.961' E	Gemsbok (*Oryx gazella*)	F	13	8	20/07/2013	21° 43.106' S 23° 15.518' E	–	–	Individual not located
SAT559	11/11/2012	148.1300	21° 37.263' S 23° 26.079' E	Gemsbok (*Oryx gazella*)	F	45-55	36	17/12/2013	21° 14.490' S 23° 18.489' E	16/05/2014	21° 46.678' S 23° 14.605' E	Good physical condition

Table 3.3 Number of used and available locations utilised in the logistic regression analyses for each individual gemsbok (*Oryx gazella*) and each of the two transition periods.

	Transition Green Period		Transition Brown Period	
Indiv.	No. used locations	No. available locations	No. used locations	No. available locations
SAT563	123	1230	188	1880
SAT564	124	1240	190	1900
SAT566	46	460	64	640
SAT561	123	1230	190	1900
SAT560	124	1240	191	1910
SAT562	123	1230	188	1880
SAT565	121	1210	191	1910
SAT559	122	1220	190	1900
TOTAL	906	9060	1392	13920

Table 3.4 Correlation results of greenness fixed effects for the transition green period.

Transition Green Period					
	ndvi2	ndvi3	ndvi4	RG level 2	RG level3
delta.ndvi2	0.001	0.022	0.024	-0.021	-0.044
delta.ndvi3	0.019	0.019	0.02	0.014	-0.029
delta.ndvi4	-0.004	-0.005	-0.053	0.02	-0.044
RG level2	-0.349	-0.401	-0.382	▨	▨
RG level3	-0.342	-0.415	-0.436	▨	▨

ndvi Normalized Difference Vegetation Index, *delta.ndvi* Change in NDVI value between T_n and T_{n-1}, *RG* Relative Greenness

Table 3.5 Correlation results of greenness fixed effects for the transition brown period.

Transition Brown Period					
	ndvi2	ndvi3	ndvi4	RG level2	RG level3
delta.ndvi2	-0.014	0.047	0.033	0.069	-0.005
delta.ndvi3	0.049	0.116	0.068	0.004	-0.037
delta.ndvi4	-0.008	-0.002	-0.069	-0.054	-0.224
RG level2	-0.374	-0.543	-0.29	▨	▨
RG level3	-0.116	-0.248	-0.494	▨	▨

ndvi Normalized Difference Vegetation Index, *delta.ndvi* Change in NDVI value between T_n and T_{n-1}, *RG* Relative Greenness

Table 3.6 Candidate mixed models and their related statistics, describing foraging site selection of gemsbok (*Oryx gazella*) in the northern Central Kalahari Game Reserve for the green transition period ($T_{3,4,7,8}$). A combination is denoted with a + and an interaction is denoted with a *.

Model	Fixed Effects	K	AIC	ΔAIC	w_i (AIC)	BIC	LogLik	Deviance	df
model 19	ndvi*habitat + delta.ndvi + RG	14	5795.4	0	1	5896.3	-2883.7	5767.4	9951
model 20	ndvi + delta.ndvi + RG*habitat	13	5813.1	17.7	0	5906.8	-2893.6	5787.1	9952
model 18	ndvi*habitat + RG	11	5813.2	17.8	0	5892.5	-2895.6	5791.2	9954
model 21	ndvi + delta.ndvi*habitat + RG	14	5818.8	23.4	0	5919.7	-2895.4	5790.8	9951
model 14	ndvi + delta.ndvi + RG + habitat	11	5826.9	31.5	0	5906.1	-2902.4	5804.9	9954
model 15	ndvi + RG + habitat	8	5844.7	49.3	0	5902.4	-2914.4	5828.7	9957
model 6	ndvi*habitat	9	5845	49.6	0	5909.8	-2913.5	5827	9956
model 17	ndvi + delta.ndvi + habitat	9	5855	59.6	0	5919.8	-2918.5	5837	9956
model 12	ndvi + habitat	6	5870.9	75.5	0	5914.1	-2929.4	5858.9	9959
model 7	delta.ndvi*habitat	9	5902.6	107.2	0	5967.4	-2942.3	5884.6	9956
model 1	RG*habitat	7	5907	111.6	0	5957.4	-2946.5	5893	9958
model 16	delta.ndvi + RG + habitat	8	5915	119.6	0	5972.7	-2949.5	5899	9957
model 13	delta.ndvi + habitat	6	5917	121.6	0	5960.3	-2952.5	5905	9959
model11	RG + habitat	5	5929.2	133.8	0	5965.2	-2959.6	5919.2	9960
model 9	ndvi	5	5991.2	195.8	0	6027.2	-2990.6	5981.2	9960
model 10	delta.ndvi	5	6069.5	274.1	0	6105.5	-3029.8	6059.5	9960
model 8	RG	4	6074.2	278.8	0	6103.1	-3033.1	6066.2	9961
	NULL MODEL	2	6075.8	280.4	0	6090.2	-3035.9	6071.8	9963

ndvi Normalized Difference Vegetation Index, *delta.ndvi* Change in NDVI value between T_n and T_{n-1}, *RG* Relative Greenness, *K* Number of estimated parameters, *AIC* Akaike's Information Criterion, *wi (AIC)* Rounded Akaike weights, *BIC* Bayesian Information Criterion, *LogLik* Natural logarithm of the maximum likelihood, *df* Degrees of Freedom.

Table 3.7 Logistic regression estimates for gemsbok (*Oryx gazella)* in the northern Central Kalahari Game Reserve, Botswana, for the green transition period ($T_{3,4,7,8}$) representing the model: binary selection ~ ndvi*habitat + delta.ndvi + RG + (1|indiv).

Variable	Coefficient	SE	Wald's Z	p-value		Odds Ratio
Intercept	-2.889238	0.363934	-7.939	2.04E-15	***	0.05562
ndvi 2	-0.349694	0.325704	-1.074	0.28298		0.70490
ndvi 3	-0.180079	0.315627	-0.571	0.56831		0.83520
ndvi 4	-1.298143	0.330455	-3.928	8.55E-05	***	0.27304
habitat 1	1.428469	0.379911	3.76	0.00017	***	4.17231
delta.ndvi 2	-0.626778	0.145298	-4.314	1.61E-05	***	0.53431
delta.ndvi 3	-0.205133	0.147493	-1.391	0.16429		0.81454
delta.ndvi 4	0.006705	0.086888	0.077	9.38E-01		1.00673
RG level 2	0.911886	0.348872	2.614	0.00895	**	2.48901
RG level 3	1.411506	0.358488	3.937	8.24E-05	***	4.10213
ndvi 2: habitat 1	-0.240403	0.442536	-0.543	0.58696		0.78631
ndvi 3: habitat 1	-0.855179	0.410104	-2.085	3.70E-02	*	0.42521
ndvi 4: habitat 1	0.700034	0.422271	1.68	0.09736		2.01382

ndvi Normalized Difference Vegetation Index, *delta.ndvi* Change in NDVI value between T_n and T_{n-1}, *RG* Relative Greenness

Table 3.8 Candidate mixed models and their related statistics, describing foraging site selection of gemsbok (*Oryx gazella*) in the northern Central Kalahari Game Reserve for the brown transition period ($T_{1,2,9,10,11,12}$). A combination is denoted with a + and an interaction is denoted with a *.

Model	Fixed Effects	K	AIC	ΔAIC	w_i (AIC)	BIC	LogLik	Deviance	df
model16b	ndvi + delta.ndvi + RG*habitat	13	9269.3	0	1	9368.6	-4621.6	9243.3	15300
model15b	ndvi*habitat + delta.ndvi + RG	14	9282.1	12.8	0	9389.1	-4627.1	9254.1	15299
model10b	RG + ndvi + delta.ndvi + habitat	11	9288.4	19.1	0	9372.4	-4633.2	9266.4	15302
model14b	ndvi*habitat + RG	11	9294	24.7	0	9378	-4636	9272	15302
model3b	delta.ndvi*habitat	9	9297	27.7	0	9365.7	-4639.5	9279	15304
model11b	ndvi + RG + habitat	8	9300	30.7	0	9361.1	-4642	9284	15305
model13b	ndvi + delta.ndvi + habitat	9	9304	34.7	0	9372.7	-4643	9286	15304
model2b	ndvi*habitat	9	9306.7	37.4	0	9375.4	-4644.4	9288.7	15304
model1b	RG*habitat	7	9309	39.7	0	9362.5	-4647.5	9295	15306
model5b	ndvi	5	9310.6	41.3	0	9348.7	-4650.3	9300.6	15308
model 8b	ndvi + habitat	6	9312.5	43.2	0	9358.3	-4650.2	9300.5	15307
model12b	delta.ndvi + RG + habitat	8	9320.9	51.6	0	9382	-4652.5	9304.9	15305
model6b	delta.ndvi	5	9321.4	52.1	0	9359.6	-4655.7	9311.4	15308
model9b	delta.ndvi + habitat	6	9323.1	53.8	0	9368.9	-4655.6	9311.1	15307
model4b	RG	4	9330.2	60.9	0	9360.8	-4661.1	9322.2	15309
model7b	RG + habitat	5	9332.1	62.8	0	9370.3	-4661	9322.1	15308
	NULL MODEL	2	9333.4	64.1	0	9348.6	-4664.7	9329.4	15311

ndvi Normalized Difference Vegetation Index, *delta.ndvi* Change in NDVI value between T_n and T_{n-1}, *RG* Relative Greenness, *K* Number of estimated parameters, *AIC* Akaike's Information Criterion, *wi (AIC)* Rounded Akaike weights, *BIC* Bayesian Information Criterion, *LogLik* Natural logarithm of the maximum likelihood, *df* Degrees of Freedom.

Table 3.9 Logistic regression estimates for gemsbok (*Oryx gazella)* in the northern Central Kalahari Game Reserve, Botswana, for the brown transition period ($T_{1,2,9,10,11,12}$) representing the model: binary selection ~ ndvi + delta.ndvi + RG*habitat + (1|indiv).

Variable	Coefficient	SE	Wald's Z	p-value		Odds Ratio
Intercept	-2.14337	0.07906	-27.109	<2E-16	***	0.11726
ndvi 2	0.05203	0.07247	0.718	0.472798		1.05341
ndvi 3	-0.36751	0.09369	-3.923	8.75E-05	***	0.69246
ndvi 4	-0.62172	0.19565	-3.178	1.48E-03	**	0.53702
delta.ndvi 2	-0.13378	0.07952	-1.682	9.25E-02	.	0.87478
delta.ndvi 3	-0.30484	0.08724	-3.494	0.000476	***	0.73724
delta.ndvi 4	-0.32608	0.09768	-3.338	8.43E-04	***	0.72175
RG level 2	0.31227	0.07322	4.265	2.00E-05	***	1.36652
RG level 3	0.17372	0.20960	0.829	4.07E-01		1.18972
habitat 1	-0.1473	0.18110	-0.813	4.16E-01		0.86304
RG level 2: habitat 1	-0.10662	0.26723	-0.399	0.689904		0.89887
RG level 3: habitat 1	1.85163	0.39120	4.733	2.21E-06	**	6.37019

ndvi Normalized Difference Vegetation Index, *delta.ndvi* Change in NDVI value between T_n and T_{n-1}, *RG* Relative Greenness

Figures

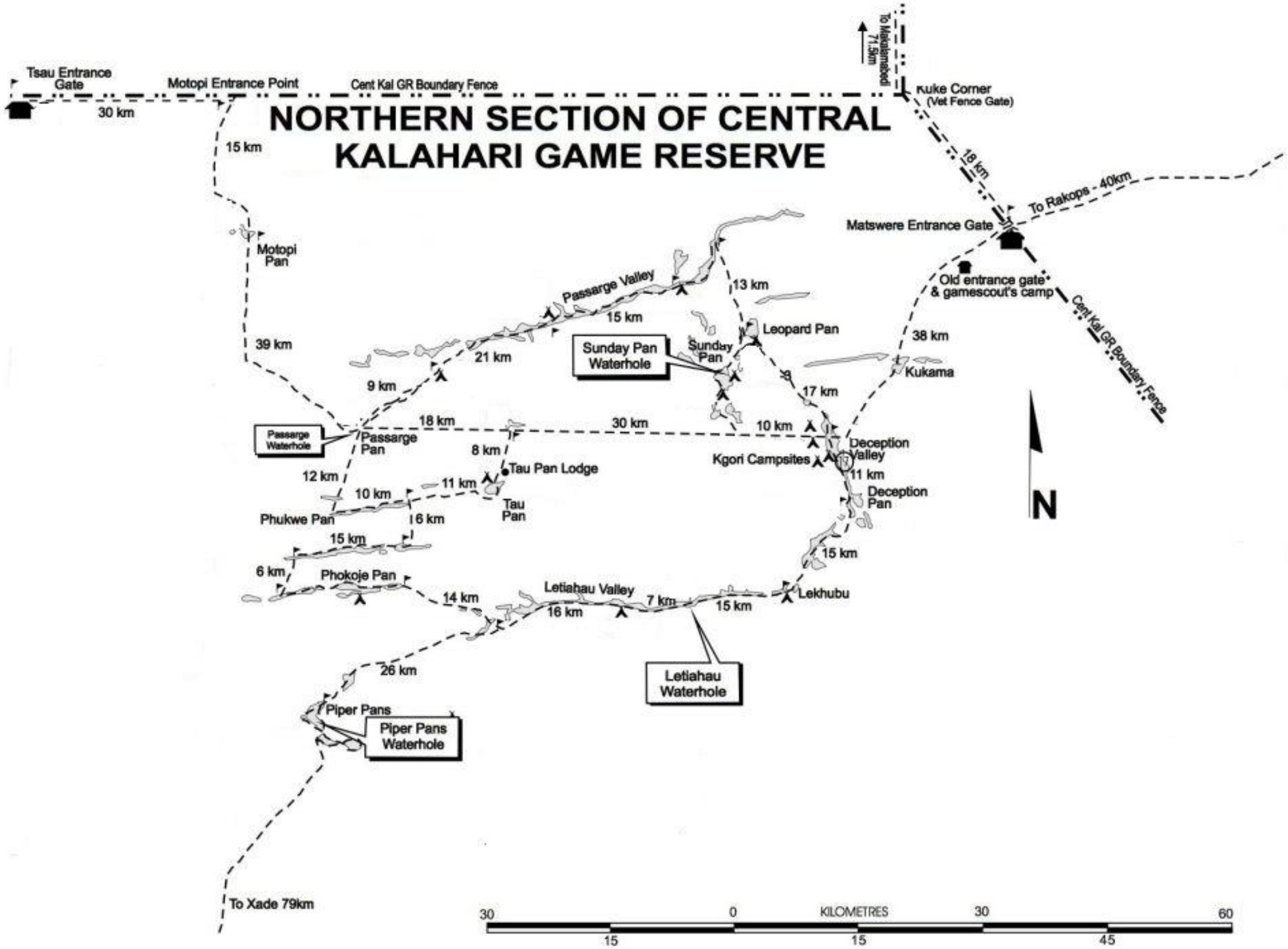


Figure 3.1 Map of the northern region of the Central Kalahari Game Reserve, Central Botswana (Adapted from Copyright © 2010 Bigfoot Tours: www.bigfoottours.co.bw, Delta Quest Photography).

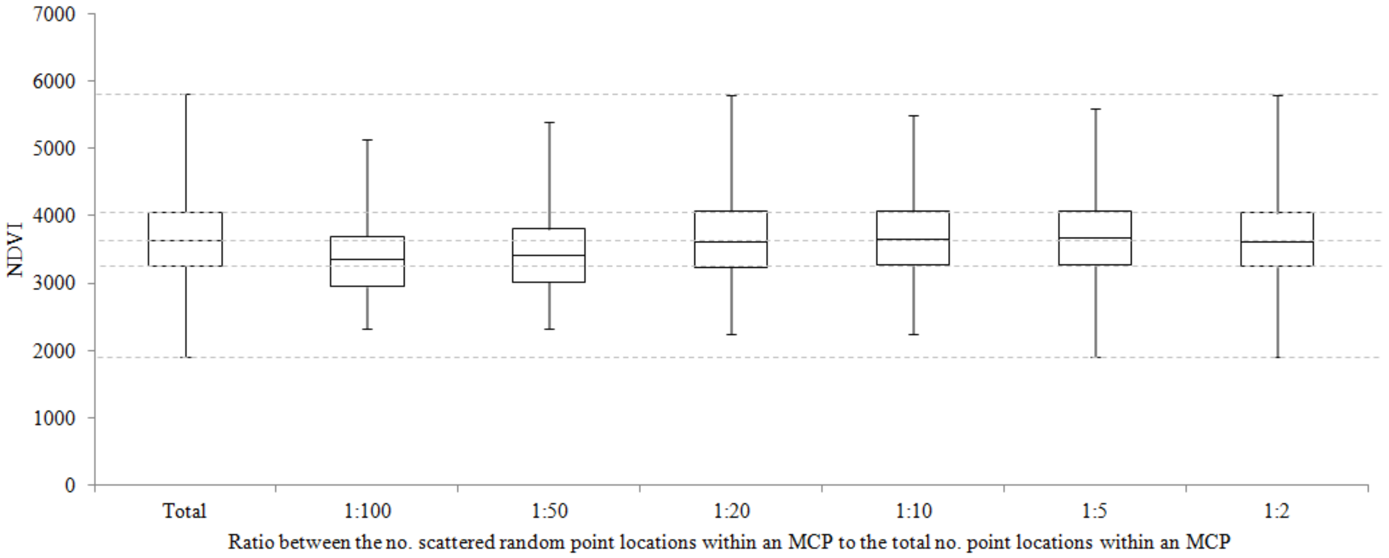


Figure 3.2 Boxplots of the NDVI values across a total Minimum Convex Polygon (MCP), compared to various ratios of scattered random points:total points across the same MCP. This figure was used to indicate that when the ratio of scattered points to total points is 1:20 or larger, the scattered random points should accurately represent the total MCP.

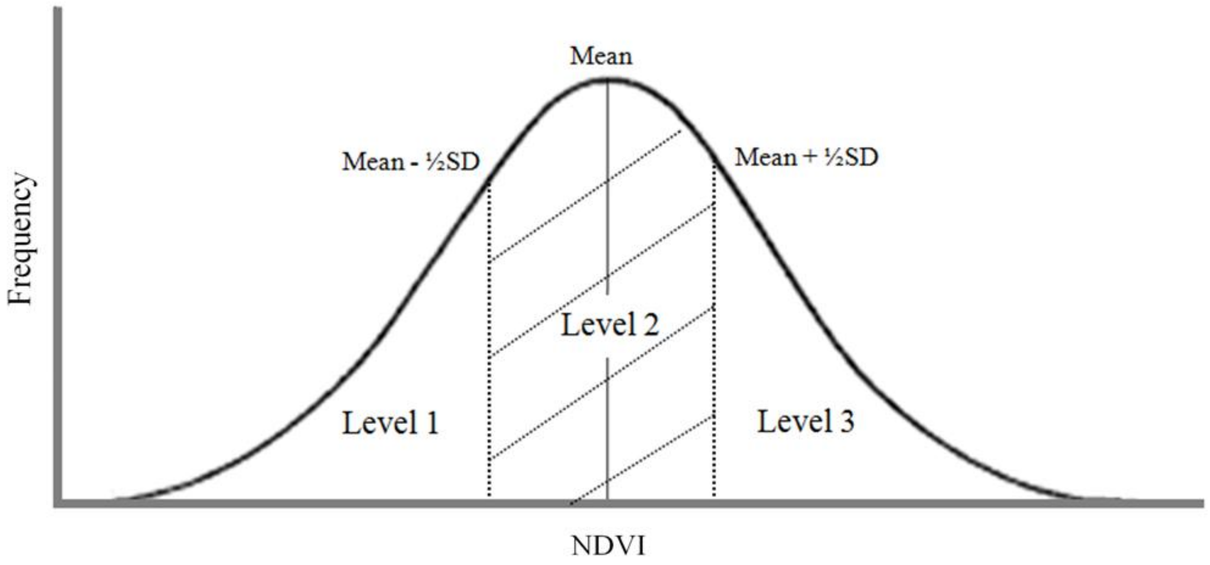


Figure 3.3 Graphical representation of the division of Relative Greenness levels on a pixel-by-pixel basis, where level 1 relative greenness includes time periods when that particular pixel exhibited NDVI values less than the mean - ½ standard deviation, level 3 relative greenness includes time periods when that pixel exhibited NDVI values greater than the mean + ½ standard deviation above the mean and level 2 relative greenness are all the periods when that pixel's NDVI value falls between level 1 and 3. Mean NDVI and standard deviation was calculated for each pixel across the collar period.

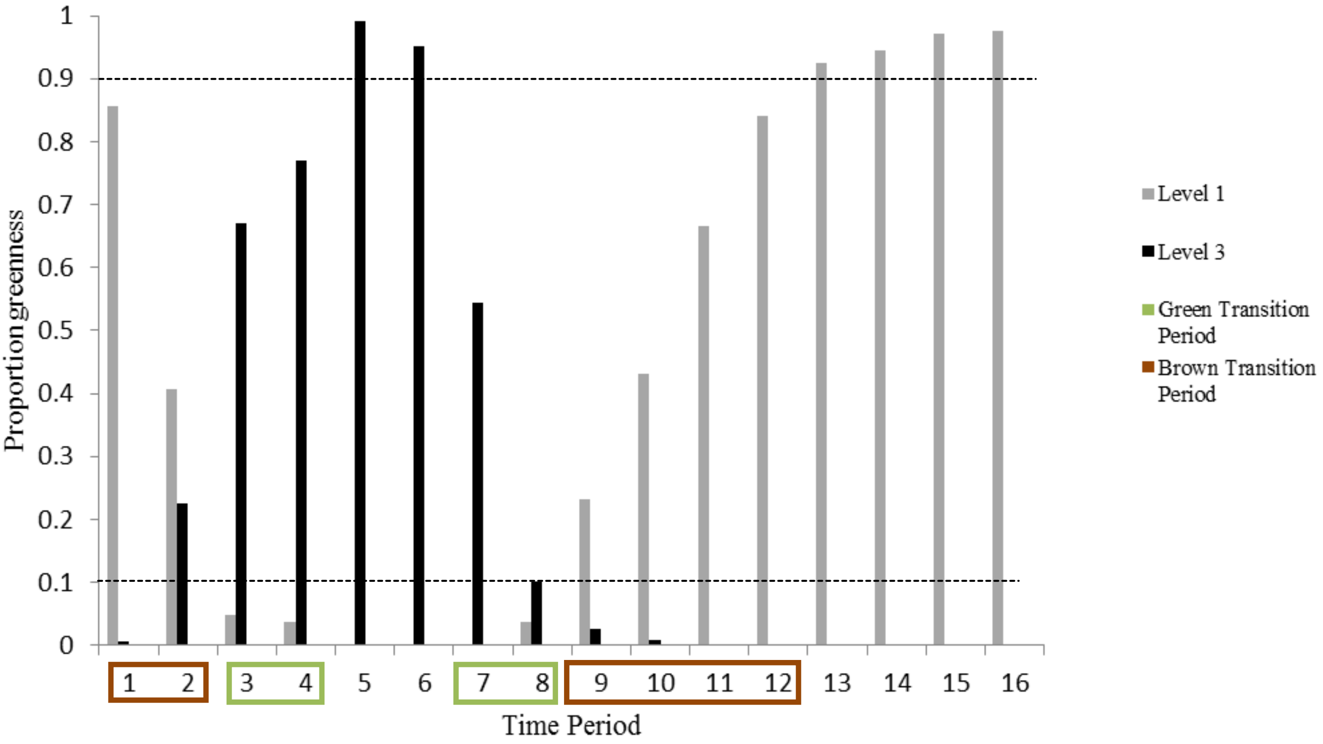


Figure 3.4 Determination of the transition periods used for the logistic regression analysis, where the proportion of level 1 and level 3 relative greenness, within the combined gemsbok ranges, were compared across time periods. When level 1 relative greenness exceeded 90% of the range, the landscape was considered to be homogeneously brown, and similarly for level 3, the range was declared homogeneously green. The transition periods were divided into green and brown and classification was based on whether more of the habitat exhibited level 1 or level 3 relative greenness.

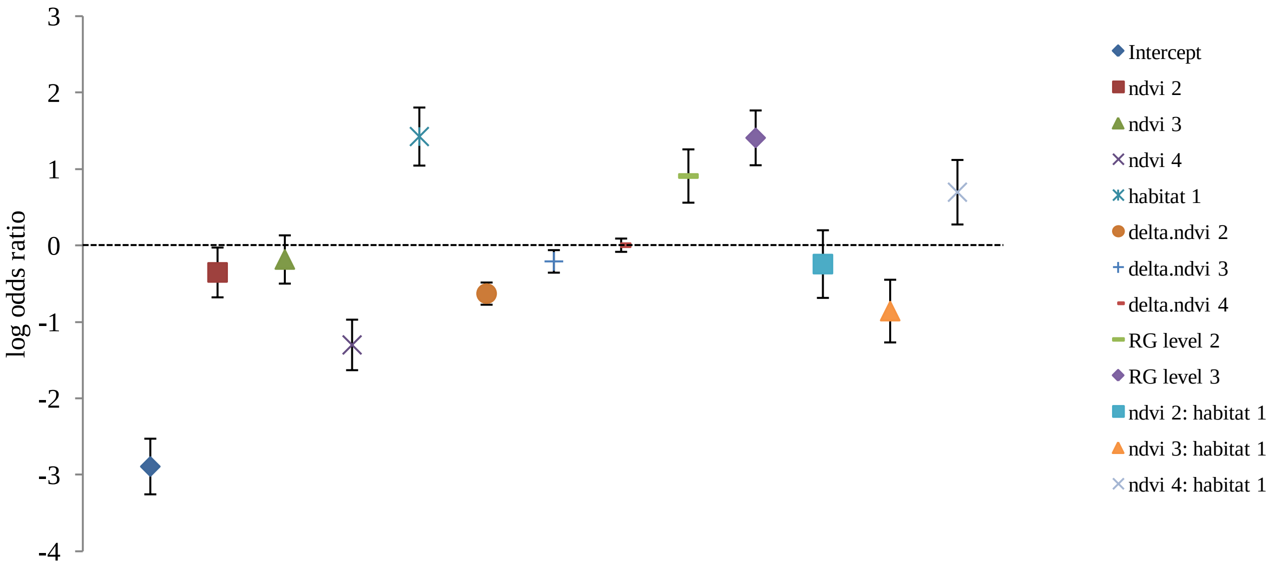


Figure 3.5 Greenness and habitat selection estimates for the model: binary selection ~ ndvi*habitat + delta.ndvi + RG + (1|indiv) for eight gemsbok herds, during the green transition period, in the northern region of the Central Kalahari Game Reserve, Botswana.

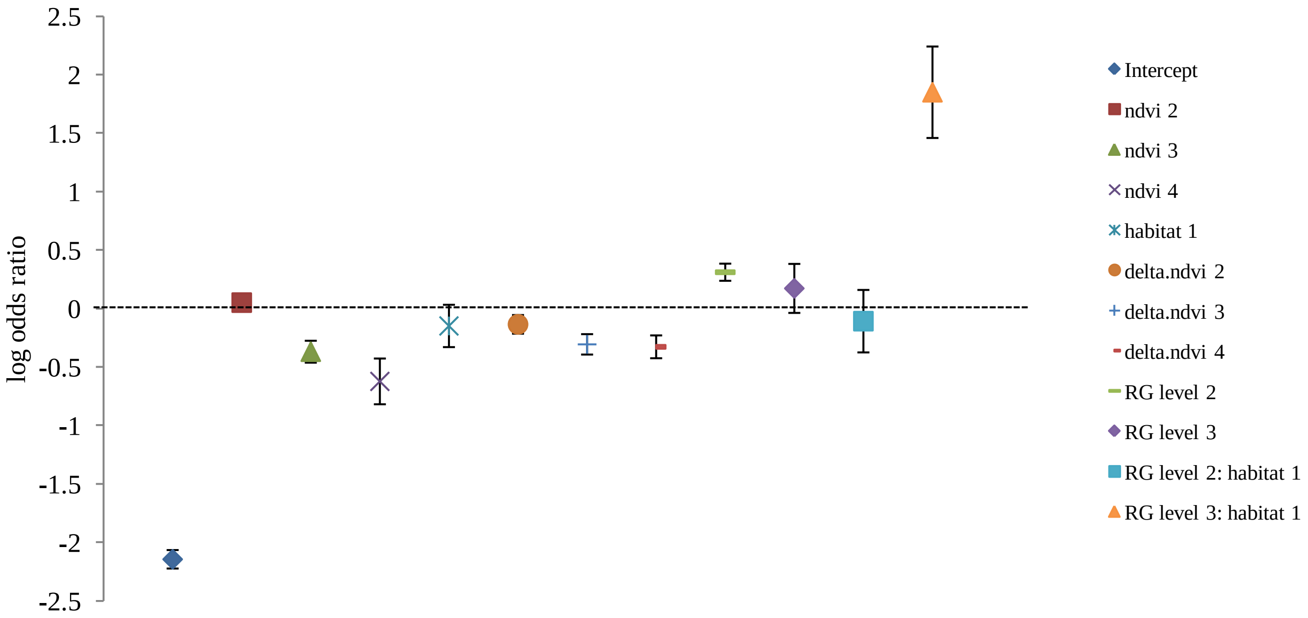


Figure 3.6 Greenness and habitat selection estimates for the model: binary selection ~ ndvi + delta.ndvi + RG*habitat + (1|indiv) for eight gemsbok herds, during the brown transition period, in the northern region of the Central Kalahari Game Reserve, Botswana.

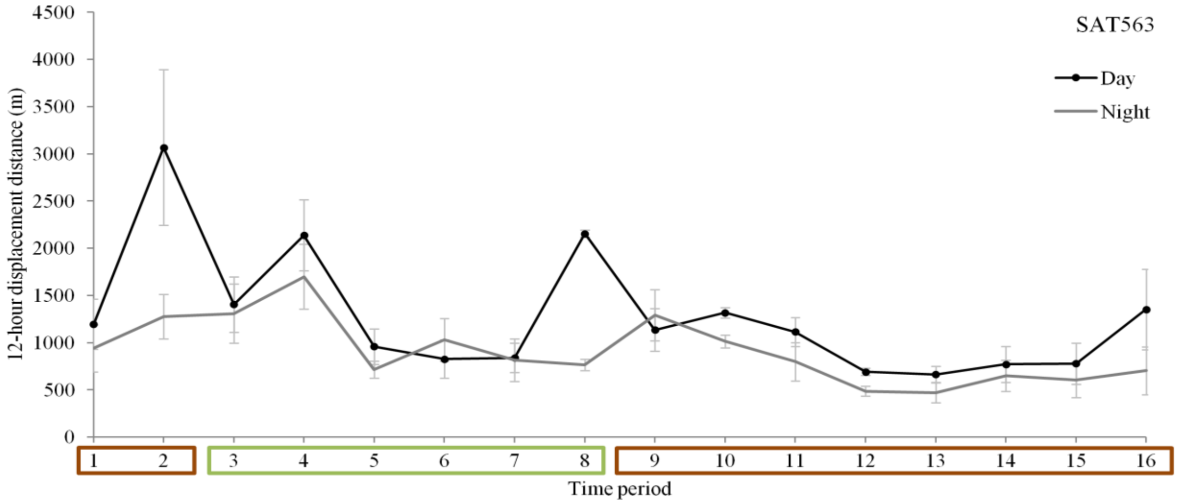


Figure 3.7 Average twelve-hour displacement distance for day (07h00 – 19h00) and night (19h00-07h00 of the following day) across the duration of the study period for the individual SAT563. Green borders around the time periods represents those periods falling within the green season, while brown borders around the time periods represents the brown season.

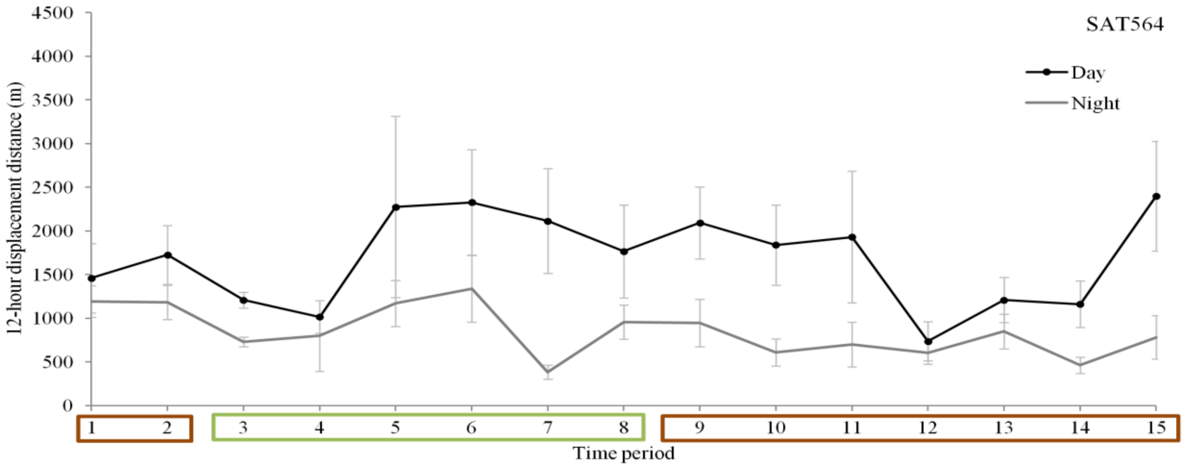


Figure 3.8 Average twelve-hour displacement distance for day (07h00 – 19h00) and night (19h00-07h00 of the following day) across the duration of the study period for the individual SAT564. Green borders around the time periods represents those periods falling within the green season, while brown borders around the time periods represents the brown season.

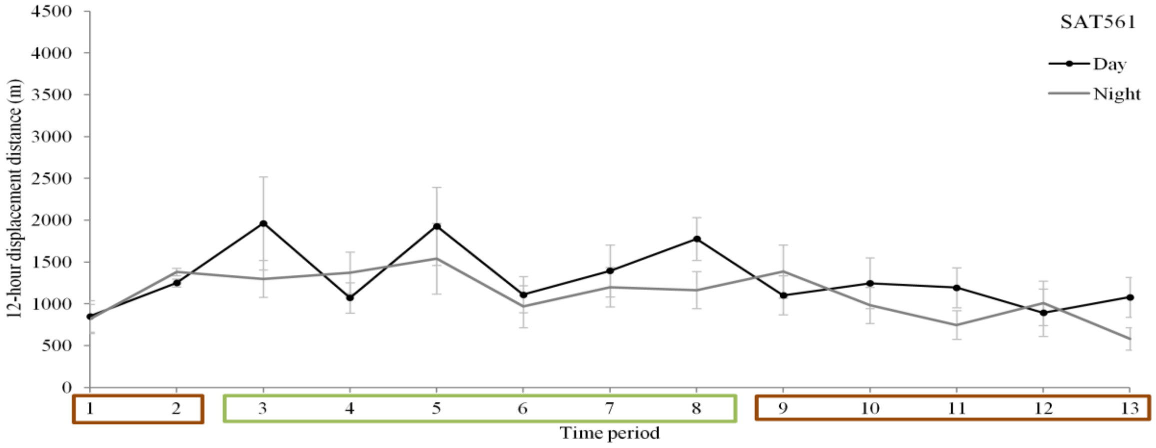


Figure 3.9 Average twelve-hour displacement distance for day (07h00 – 19h00) and night (19h00-07h00 of the following day) across the duration of the study period for the individual SAT561. Green borders around the time periods represents those periods falling within the green season, while brown borders around the time periods represents the brown season.

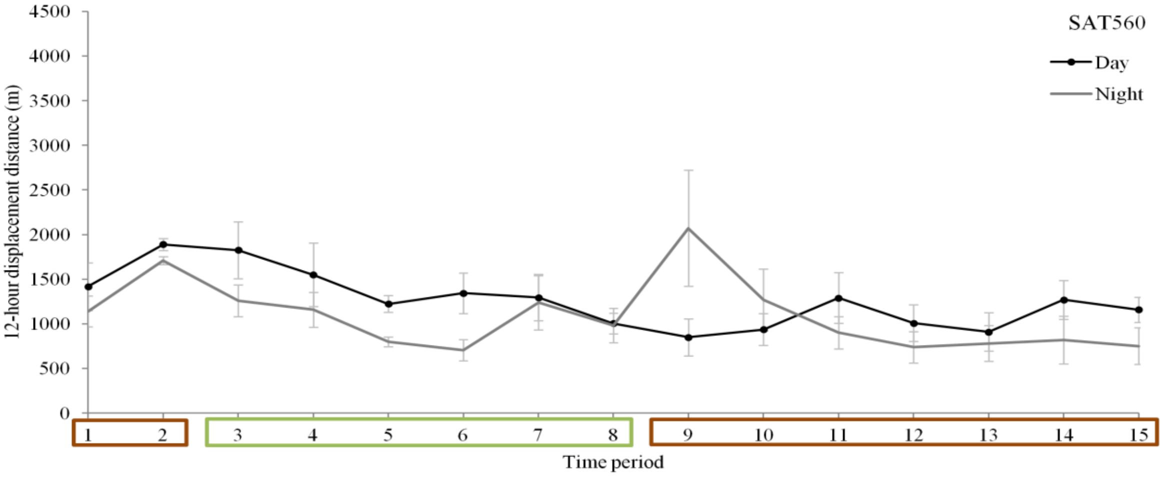


Figure 3.10 Average twelve-hour displacement distance for day (07h00 – 19h00) and night (19h00-07h00 of the following day) across the duration of the study period for the individual SAT560. Green borders around the time periods represents those periods falling within the green season, while brown borders around the time periods represents the brown season.

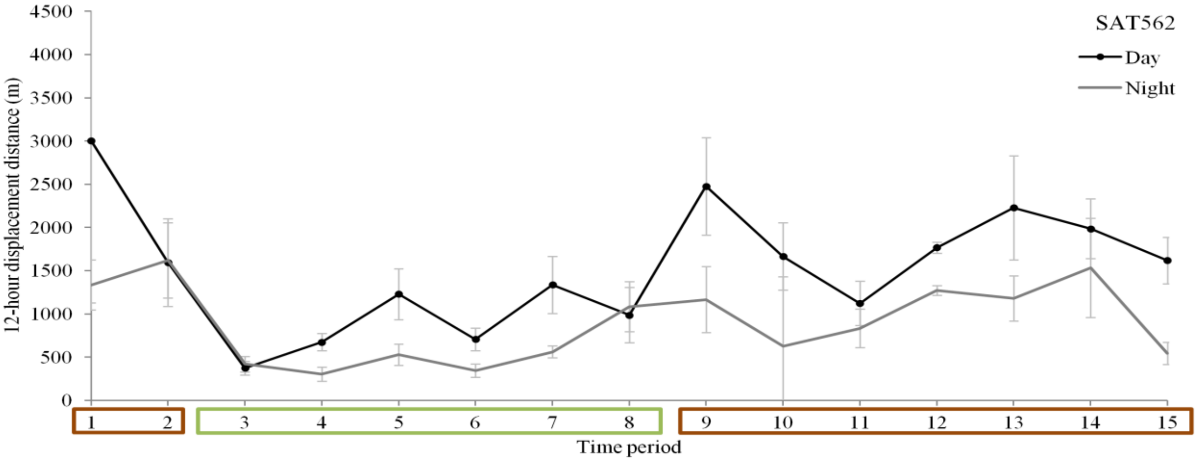


Figure 3.11 Average twelve-hour displacement distance for day (07h00 – 19h00) and night (19h00-07h00 of the following day) across the duration of the study period for the individual SAT562. Green borders around the time periods represents those periods falling within the green season, while brown borders around the time periods represents the brown season.

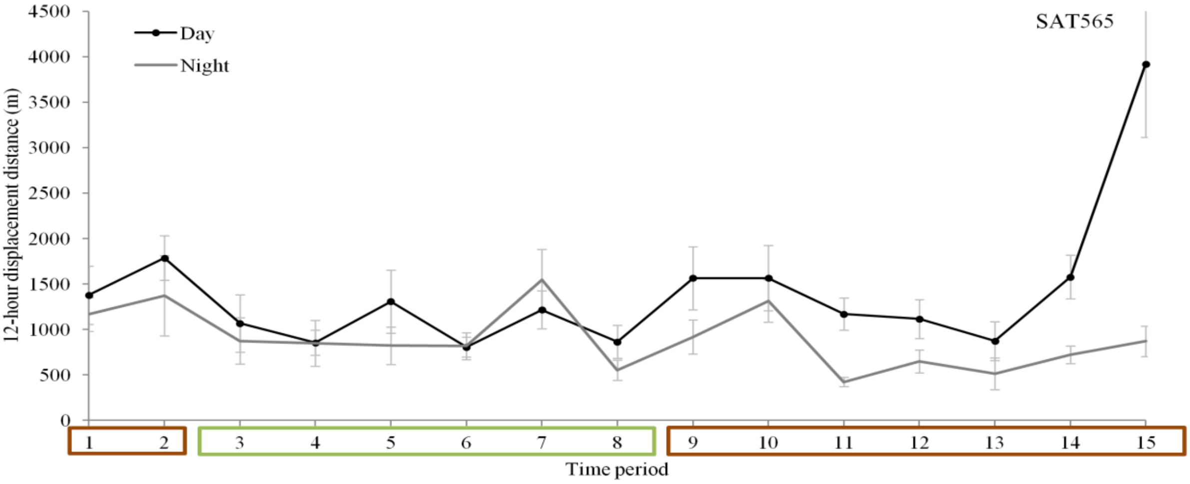


Figure 3.12 Average twelve-hour displacement distance for day (07h00 – 19h00) and night (19h00-07h00 of the following day) across the duration of the study period for the individual SAT565. Green borders around the time periods represents those periods falling within the green season, while brown borders around the time periods represents the brown season.

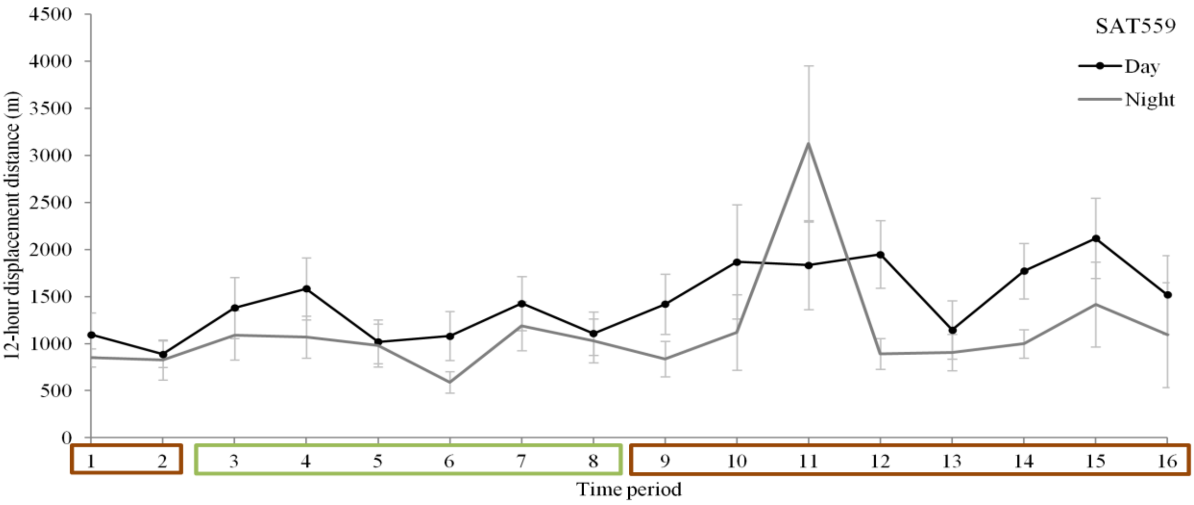


Figure 3.13 Average twelve-hour displacement distance for day (07h00 – 19h00) and night (19h00-07h00 of the following day) across the duration of the study period for the individual SAT559. Green borders around the time periods represents those periods falling within the green season, while brown borders around the time periods represents the brown season.

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Appendices

Appendix A: Summary of Wilcoxon rank sum tests for nonparametric data assessing the difference between green and brown season 12-hour displacement distances for 7 individual gemsbok in the northern Central Kalahari Game Reserve.

		Green Season		Brown Season		Shapiro-Wilk normality test		Wilcoxon rank sum test	
Indiv		Mean	SE	Mean	SE	W	p	W	p
SAT563	day	1392.08	124.02	1229.15	120.32	0.697	<2.2E-16	6469.0	1.54E-01
	night	1052.01	106.33	824.77	70.42	0.776	<2.2E-16	5451.0	7.07E-02
SAT564	day	1785.51	246.63	1594.45	146.18	0.696	<2.2E-16	6390.0	9.94E-01
	night	892.51	115.11	814.89	67.02	0.762	<2.2E-16	5692.0	8.97E-01
SAT561	day	1534.18	143.60	1089.40	93.31	0.806	3.49E-15	3873.0	**0.0028**
	night	1257.12	112.40	990.62	90.54	0.824	7.26E-14	3542.0	**0.0130**
SAT560	day	1367.43	112.16	1194.65	81.96	0.847	1.98E-14	5746.0	0.1549
	night	1026.99	83.47	1126.32	106.17	0.724	<2.2E-16	5354.0	0.5126
SAT562	day	901.03	101.67	1929.97	244.55	0.444	<2.2E-16	9025.0	**7.65E-07**
	night	544.82	65.46	1240.02	143.33	0.574	<2.2E-16	7700.0	**2.11E-05**
SAT565	day	1017.82	93.39	1660.59	139.93	0.711	<2.2E-16	8329.0	**2.78E-04**
	night	904.98	95.07	879.46	72.30	0.767	<2.2E-16	5755.5	8.96E-01
SAT559	day	1269.00	113.76	1563.65	120.57	0.821	4.03E-16	7617.0	0.2677
	night	985.56	90.63	1196.47	128.81	0.650	<2.2E-16	5999.0	0.7215

Appendix B: Summary of Wilcoxon rank sum tests for nonparametric data assessing the difference between day and night 12-hour displacement distances for 7 individual gemsbok in the northern Central Kalahari Game Reserve.

	Day		Night		Shapiro-Wilk normality test		Wilcoxon rank sum test	
Indiv	Mean	SE	Mean	SE	W	p	W	p
SAT563	1274.79	164.82	910.15	85.19	0.7047	< 2.2E-16	31139.0	3.03E-05
SAT564	1683.86	135.12	847.51	73.05	0.6563	< 2.2E-16	32735.5	2.12E-08
SAT561	1493.74	217.91	1107.16	73.97	0.7151	< 2.2E-16	21696.0	**0.1366**
SAT560	1264.70	80.82	1087.73	100.51	0.7916	< 2.2E-16	28931.0	0.0105
SAT562	1518.00	184.86	890.13	115.16	0.4693	< 2.2E-16	32707.5	9.98E-07
SAT565	1404.77	196.20	894.03	84.22	0.7013	< 2.2E-16	33856.0	8.39E-07
SAT559	1450.12	94.15	1125.26	140.99	0.7479	< 2.2E-16	33679.0	0.0004

CHAPTER 4: CONCLUSION & SYNOPSIS

Rainfall in the Kalahari is notably unpredictable in its distribution and volume (Fensholt et al., 2012), and is known to be the most important contributing factor to vegetation phenology and the spatial production of plant biomass (Nicholson & Farrar, 1994). Data collected from Matswere gate (north-eastern boundary of Central Kalahari Game Reserve (CKGR)) between 2006 and 2013 revealed an average seasonal rainfall (October – April) of 396 mm, which is in accordance with a study by Nicholson & Farrar (1994), which described the annual rainfall in the northern Kalahari to be approximately 400 mm. However, the rainfall between November 2012 and February 2013 was only 163 mm. As a direct result of limited rainfall, the mean and maximum NDVI over the northern CKGR produced lowest values compared to the previous nine years. Considering that NDVI relates directly to vegetation biomass (Shippert et al., 1995) and can be used as a proxy for above-ground net primary productivity (Paruelo et al., 1997), it is evident that during the collar period (November 2012 – July 2013), the availability of grazing forage was reduced compared to previous years. The drought conditions prevailing during the time of this study provided insight into the behavioural responses of gemsbok (*Oryx gazella*) to exceptionally water-stressed conditions. Initially, I investigated the landscape-level features that could have influenced gemsbok movements, analysing both the long- and short-term greenness trends to which gemsbok could have been responding. In particular, I assessed changes between habitat types that had different vegetation compositions and could have been influenced differently by rainfall. Subsequently, I assessed the degree of selection by gemsbok for greenness and habitat types, and examined the seasonal displacement distances of gemsbok in the northern CKGR.

Greenness

Inter-annual:

NDVI measures were investigated from 2000 until 2012, and the findings confirmed that the northern CKGR experiences high inter-annual variability in NDVI greenness. Two years (2007 and 2012) received lower than average rainfall, thus experienced notably low spatially-averaged annual NDVI measures as well. Clusters of consistently high NDVI from 2000 to 2013 most likely depicted areas of substantial woody cover; while clusters of persistently low NDVI were evident within valley and pan habitats. Grass greenness is highly seasonal in savannas systems, while evergreen/semi-evergreen trees and shrubs exhibit much higher and more consistent NDVI values (Nicholson & Farrar, 1994). This means that persistently high NDVI is often not an indication of favourable forage material for a grazing herbivore, but rather a signal of high shrub cover (Verlinden & Masogo, 1997). I therefore used another metric, seasonal greenness, calculated on a pixel-by-pixel basis by subtracting the sum of the brown season NDVI rasters from the sum of the green season NDVI rasters for that year, which largely removed the effect of vegetation structure. This revealed that the distribution of seasonal green patches were not spatially-persistent from year to year, but were most fundamentally related to spatially-isolated convective rainfall events, which differed across space and time (Porporato et al., 2003). The results indicated that the duration of the green season also varied between years, most likely as a result of the availability of rainfall during that year's rainy season.

Seasonality:

Most rain falls between October and April (Porporato et al., 2003), resulting in a high degree of seasonal variance in NDVI. The results obtained in this study supported those of Nicholson and Farrar (1994), who found that the start of the green season occurred between November and December, and persisted until June/July. Nicholson and Farrar (1994) discerned that in the Kalahari, green vegetation seems to follow the trends in rainfall with a lag period of about two months. NDVI seasonality was assessed bimonthly for the collar period, i.e. from November 2012 until July 2013. During this period, the landscape was mostly brown, until late December, when a transition into green conditions commenced. Peak greenness was reached towards the end of January 2013 and persisted into February 2013, when the landscape was considered to be more or less homogeneously green. NDVI greenness decreased until late March, when brown conditions became more prevalent, and the landscape was deemed homogeneously brown at the end of May 2013.

Considering that selectivity is not possible when resources are homogeneously distributed, gemsbok selection was only assessed during two time periods, referred to as transition periods, when the landscape was neither homogeneously green nor brown. These transition periods were defined as green, when the majority of the landscape was composed of the highest relative greenness level; and brown, when most of the landscape was composed of the lowest relative greenness level (as calculated in Chapter 3). During the green transition period gemsbok selected for high and intermediate relative greenness levels, rather than low relative greenness. Subsequently, however, during the brown transition period when green vegetation was less available, gemsbok showed a preference for intermediate greenness, over both low and high greenness. Considering that high greenness was exceedingly less available during this period, selection for intermediate greenness over low greenness demonstrated that gemsbok preferred grazing forage with a higher chlorophyll content.

Habitats

Pans and valleys:

Pan and valley habitats (grouped as pan-valley habitats) showed no deviation from dune regions in their rate of *greenup*, nor in the duration of green season conditions. It is important to mention, however, that a coarse temporal scale (16-day) would have been inadequate for revealing phenological variations between habitat types at a scale smaller than 16 days. Nevertheless, at this 16-day temporal scale, it is conceivable that vegetation phenology was influenced more by the distribution and availability of precipitation than by soil and vegetation structure. Pan and valley habitats did, however, show a lower degree of greenness than dunes. The degree of greenness is believed to be controlled largely by the spatial composition of soil and vegetation. Pans and valleys held considerably more clusters of low than high NDVI, and showed inter-annual variability in green clusters. Since many pan and valley regions alternate periodically between short grasslands during the green season and bare soils during brown conditions, clusters of low NDVI were expected, due to the low vegetation biomass prevailing in these regions. Gemsbok showed pronounced positive selection for pan and valley habitats over dunes during the green transition period. However, during the brown transition period, no significant difference was found in the preference for one habitat over another. High quality vegetation plays a valuable role in herbivore habitat preference and selection (Grant & Scholes, 2006). As a result, pan and valleys are regarded as valuable, resource hot-spots for grazing herbivores in the Kalahari, particularly, but not exclusively, during the green season. Because of the preference gemsbok have for these habitats, it is likely that they are more vulnerable to factors such as degradation, trampling and over-use, and these should be carefully monitored and considered within conservation policies.

The results of the logistic regression analysis revealed a high selection by gemsbok for high NDVI values within pan-valley habitats, compared to low NDVI in dune regions, which possibly indicates selection for tree islands. Tree islands (of usually *Vachellia* spp.) form shady micro-habitats, within or on the fringes of pans and valleys, and have been known to support the growth of short, nutritious shade grasses (Knight, 1991; pers. obs). *In situ* observations did confirm the use of tree islands by gemsbok (Figure 4.1); however, more thorough field work is necessary to confirm the hypothesis that tree islands are represented by high NDVI values in pans and valleys. Similarly, during the brown transition period, gemsbok selected for high relative greenness within pan and valley regions, suggesting that they probably selected the greenest grasses, which were available in the mineral-rich pan and valley habitats.

Dunes:

The immense dune regions cover the vast majority (>99%) of the northern Kalahari study area. Dune regions showed minimal deviation in the inter-annual availability of green and brown patches. The ratio of clustered to non-clustered pixels in dune regions remained consistently less than 0.2, indicating that there are always more non-clustered pixels compared to both high and low clusters. A high percentage of non-clustered pixels indicated a state of fine spatial deviation in NDVI amplitude between adjacent pixels. Having a spatial resolution of 250 m, deviations in NDVI at this spatial resolution were probably a result of heterogeneous vegetation and soil structure. Dune habitats also appeared to support equal clusters of low and high greenness, suggesting that the northern Kalahari displayed complex vegetation patterns. Dunes in the wet season are characterised by a continuous grass layer, patchily deviating in its degree of greenness as a result of the distribution of rainfall, and scattered green trees and shrubs varying spatially in their level of cover (Campbell, 1981) During the dry season, dune regions consist of tall, mostly brown, grasses, with intermittent evergreen, unpalatable trees and shrubs providing the majority of greenness. High biomass, low quality dune grasses make up the bulk of gemsbok diets during brown conditions (Knight, 1991). Fruits and tubers, strewn throughout dune regions, form a valuable supplementary food resource to gemsbok diets, particularly during adverse conditions (Knight, 1995a; Williamson, 1987).

Movement of gemsbok

Population success can be severely jeopardized by a high degree of temporal variability in food resources (Fryxell et al., 2005), especially in harsh environments like the Kalahari, where high quality forage is limited. This was made evident during the 1980s when substantial numbers of eland (*Taurotragus oryx*), wildebeest (*Connochaetes taurinus*), red hartebeest (*Alcelaphus buselaphus*) and ostrich (*Struthio camelus*) perished as a result of starvation during drought conditions (Knight, 1995b). In comparison to these species, gemsbok populations suffered to a lesser extent (Knight, 1995b). It is only through large-scale spatial heterogeneity in forage resources that large, mobile herbivores are able to compensate for temporally limited resources at smaller spatial scales (Fryxell, et al., 2005; Illius & O' Connor, 2000). Gembok movements appeared to be adaptive, in response to dynamic variation in the availability of resources. Gemsbok did not show marked seasonal differences in their 12-hour displacement distances, and were thus considered to move opportunistically, so as to capitalise on the prevailing conditions. Nomadic movements (Kreulen, 1985), use of alternate water resources (Knight, 1995a), physiological adaptations (Cain et al., 2006) and the lack of a constant dependence for surface water (Knight, 1991) ensure the survival and population success of indigenous gemsbok within the Kalahari environment.

Study complications

Premature battery failure of the satellite collars proved to be an unfortunate and unexpected setback in this study. Of the eight collars, originally intended to last two years, one failed after only three months. The remaining seven functioned successfully for at least 8 months from the time of dispatch, providing an adequate seasonal comparison in movements during a low rainfall, thus environmentally stressful year. Regrettably, the collars did not persist into the critical period at the end of the dry season of 2013, thus preventing the analysis of movement and selection during a crucial time of year, when herbivores are at their most vulnerable to starvation and/or dehydration (Fryxell, 1987; Sinclair, 1975). Fortunately, however, data from enough of the brown season in 2013, combined with the previous year's (2012) brown season, were available to effectively interpret gemsbok selection for greenness during the transition brown period.

Three greenness variables acquired from MODIS (MODerate resolution Imaging Spectroradiometer) satellite imagery were used to test the degree of selection by gemsbok. Gemsbok did not appear to select for categorical NDVI or ΔNDVI (the change in NDVI between T_n and T_{n-1}). This was attributed to a common problem found with the use of NDVI imagery, principally within savannas. Heterogeneous vegetation structures give off contrasting degrees of greenness, and resultantly high NDVI values may have been a representation of unpalatable and unsuitable forage for gemsbok, such as areas of high tree or shrub cover. Being predominantly grazers, gemsbok were more likely to make use of open grassland areas, which give off a significantly lower NDVI signal than woodland areas (Verlinden & Masogo, 1997). Relative greenness (as calculated in Chapter 3) and seasonal greenness (used in Chapter 2) are useful greenness measures, in that they largely omit the effect of spatial variability in vegetation structure. Relative greenness provides a comparative measure of greenness calculated pixel-by-pixel through time. Selection for relative greenness was displayed by gemsbok in the northern central Kalahari during both the green and brown transition periods. It was likely that areas depicting high relative greenness values had recently experienced a rainfall event, and therefore showed some degree of *green-up* (or increase in greenness). Knight (1991) found that gemsbok responded to increased grass greenness. Considering that Knight (1991) measured grass greenness visually, the effect of variability in vegetation composition was inconsequential. The use of seasonal greenness and relative greenness, as calculated in this study, are thought to be beneficial measures with which to assess greenness dynamics without thorough fieldwork or the timely development of vegetation composition maps.

Another notable constraint involved the temporal and spatial scale of the satellite imagery utilised in this study. The 16-day temporal scale was too broad to investigate any deviation in the duration of greenness or rate of *greening* between habitat types at a temporal scale less than 16 days. However, no change in phenology between habitats was established with the use of 16-day NDVI composites. In addition, 250 m x 250 m pixels are considered to be very large for a precise investigation of gemsbok selection for NDVI greenness. However, despite this large spatial scale, the use of the relative greenness measure did show selection by gemsbok for high and intermediate greenness. Finally, during the dry season, when the pan and valleys were primarily devoid of grass cover, the effect of soil brightness might have negatively affected the degree of NDVI greenness calculated via MODIS NDVI.

Future directions and conclusions

Habitat selection models are widely used to quantify the intricate relationships that animals have with their environments. When enough variables are considered, they can be useful in the prediction of future space use by animals (Beyer et al., 2010). Future research into supplementary factors influencing gemsbok movements and habitat selection, such as the availability of water resources, soil composition, inter- and intra-species competition and predation, could be valuable additions to these habitat use-availability models. Additionally, a more detailed investigation of the prevailing environmental conditions, habitat type, and vegetation structure within each herd's home range would be a valuable means with which to justify the movement strategies at a particular point in space and time. Although future predictions of gemsbok movement was beyond the scope of this study, the use-availability generalized linear mixed models developed in this study were a valuable means of identifying important resource hot-spots within the landscape, such as pans and valleys. Additionally, a positive selection by gemsbok for high and intermediate relative greenness was demonstrated in the northern CKGR. Relative greenness may be a valuable means with which to investigate habitat selection of grazing herbivores in savanna regions.

Although this study did not directly investigate the availability of water resources for gemsbok, it would be inappropriate to overlook water supply, as a key component of gemsbok survival and fitness within the arid Kalahari. Gemsbok are able to obtain much of their overall water requirements from their food (Knight, 1991), however previous research stresses the importance of alternate water sources for the survival of many animals in the Kalahari, and in particular the substantial use of tsamma melons (*Citrullus lanatus*), by gemsbok (Knight, 1995a). Fruit and underground tubers are believed to form a valuable component of gemsbok diets, possibly for their added nutrients, but most essentially, for their high water content (Knight, 1995a; Williamson, 1987). It is likely that the use of these moisture-rich resources enables gemsbok to survive and reproduce successfully within the Kalahari, without the need for large-scale migratory movements, particularly during unfavourably dry conditions.

This study contributes towards an ongoing extensive research project aimed at assessing herbivore adaptations and activities in extreme conditions of aridity in the central and southern Kalahari. Satellite-derived environmental indices form a valuable component of the overall project, and can be used to assess landscape dynamics at broad spatial and temporal scales. Both MODIS and Landsat imagery will be utilised to investigate the responses of large herbivores to environmental variability in the Kalahari. In addition to the eight gemsbok collared in the CKGR, another five gemsbok and eight blue wildebeest were collared in the Schwelle region, located between the CKGR and the Kgalagadi Transfrontier Park (KTP). The collaborative research study aims at comparing the thermoregulatory and movement responses of the highly water-dependent blue wildebeest with the more arid-adapted gemsbok within the Kalahari environment. In light of recent climate change predictions, southern

African savannas are vulnerable to significant average temperature increases, more frequent droughts and exacerbated fluctuations in rainfall (Hulme et al., 2001). Large herbivores require bulk forage material (Illius & Gordon, 1987), therefore in the Kalahari, these ungulates are at risk of a substantial decline in food and water resources. These combined studies aim to develop on the understanding of the physiological and behavioural mechanisms of large herbivores in an arid savanna system, such as the Kalahari, and thus assist in mitigation and management strategies for the protection of ecosystem and species dynamics.

In summary, the outcomes of this research provide affirmation of the high inter-annual, seasonal and spatial variability in rainfall and vegetation greenness across the northern CKGR. In reaction to this variability, gemsbok responded by adapting their movements, as well as habitat and resource selection, so as to acquire greener grazing forage. Gemsbok revealed no obvious seasonal patterns in their movements, and appeared to display nomadic behaviour. Prolonged drought conditions in the Central Kalahari could potentially drive increasing numbers of herbivores out of the CKGR and into unprotected regions, where they face enhanced anthropogenic threats, such as poaching and habitat degradation (Campbell, 1981). Pan and valley habitats were identified as resource hot-spots for gemsbok, thus pans outside of protected areas could also provide suitable habitats for gemsbok. However, based on previous literature, it is noted that much of the more suitable grazing environments in unprotected regions of the Kalahari are utilised by local people for livestock grazing (Darkoh, 2003; Verlinden, 1998), and are becoming more and more overgrazed and exploited, occasionally leading to bush encroachment (Verlinden et al., 1998). As a result of the presence of livestock and the over-exploitation of high-quality grazing environments, gemsbok and other herbivore populations are forced to avoid these regions (Verlinden et al., 1998). This could constrict the ranges of local wild herbivores to within the confines of protected areas, thus leading to enhanced competition for resources and preventing their natural movements in response to rainfall.

Figures

Figure 4.1 Gembsok (*Oryx gazella*) in the northern region of the Central Kalahari Game Reserve utilizing shaded tree island microhabitats in a pan habitat and grazing on short green grasses. This photograph was taken in February 2013.

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