A COMPARATIVE STUDY OF BEHAVIOURAL AND THERMOREGULATORY RESPONSES OF BLUE WILDEBEEST AND GEMSBOK TO ARIDITY

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DECLARATION

I declare that this thesis is my own, unaided work. It is being submitted for the degree of Doctor of Philosophy at the University of the Witwatersrand, Johannesburg. The work herein has not been submitted before for any degree or examination at any other university.

Moyers

Signed on the 4th day of June 2018, in Johannesburg

ABSTRACT

Future climate change scenarios predict that many arid and semi-arid ecosystems within southern Africa, will get warmer and drier with increased frequency of droughts. Although the effects of climate change may only be apparent over a few decades, understanding the physiological and behavioural flexibility of individuals currently inhabiting hot and dry climates provides an analogue for conditions likely to become prevalent in the future. To enhance our understanding of how a species may respond to future hotter and drier environments, I set out to investigate seasonal variation in behaviour and thermoregulation of two ungulate species with differing water dependency in a semi-arid savanna. I focused on thermoregulatory (body temperature) and behavioural responses (activity and microclimate selection) of the water-dependent blue wildebeest (*Connochaetes taurinus*), and the arid-adapted gemsbok (*Oryx gazella gazella*) free-living in the Kalahari. Both species prioritised behavioural thermoregulation in the form of cool microclimate selection during the heat of the day and reduced both diurnal and 24 h activity, particularly when conditions were hot and dry. Both species experienced high maximum 24 h body temperature when conditions were hot and low minimum 24 h body temperatures when conditions were dry, resulting in a large amplitude of 24 h body temperature rhythm during the hot dry period. Yet, wildebeest appeared to be more sensitive to changes in aridity with a larger amplitude of 24 h body temperature rhythm compared to gemsbok (3.1 ± 0.2 °C vs. 2.1 ± 0.5 °C), during the drought. These seasonal analyses imply that the species behavioural and thermoregulatory responses were influenced by seasonal changes in water and forage availability.

Low minimum 24 h body temperatures may result from an energy deficit during the dry season, but no study to date has explicitly linked changes in body temperature of free-living ungulates, to forage quality within the environment. I therefore investigated the influence of vegetation greenness on body temperature and activity of blue wildebeest and gemsbok inhabiting the same environment. I then investigated if the responses of gemsbok were heightened in a more arid environment. I used Normalized Difference Vegetation Index (NDVI) as a standardized index of vegetation greenness, which can be considered a proxy for vegetation productivity and quality. Both species reduced total 24 h activity and became hypothermic when exposed to brown vegetation but when exposed to brown vegetation minimum 24 h body temperatures were lower for blue wildebeest compared to gemsbok. When exposed to more extreme aridity, gemsbok showed an exaggerated lowering of minimum 24 h body temperatures. Under conditions of low food availability, the cost of thermoregulation may become too demanding. Therefore, when food resources are limited in quality, wildebeest and gemsbok in arid regions appear to prioritize the conservation of energy over the maintenance of a high body temperature.

Within seasonal environments, access to water is often the limiting factor for plants and animals. I therefore investigated how distance to water (i.e., how frequently animals were likely to have accessed drinking water) during the hot season influenced microclimate selection, activity and body temperature of blue wildebeest and gemsbok. Both species selected similarly cool microclimates during the heat of the day, with slight enhancement in the quality of microclimates selected when they were further from water. Both species decreased activity during the heat of the day when they were further from water. Gemsbok were able to compensate for their reduced activity during the heat of the day and showed little change in total 24 h activity, but wildebeest showed a more exaggerated decline in activity during the heat of the day for which they were unable to compensate, i.e. total 24h activity of wildebeest declines when they were further away from water sources. Both species displayed higher maximum 24 h body temperatures when they were further away from water, with the hyperthermia being exaggerated for the wildebeest compared to gemsbok. Hyperthermia in both species resolved following the first rains and likely access to drinking water. Access to water appears to be the primary driver towards hyperthermia in the wildebeest, potentially resulting from dehydration during thermal stress.

In summary, I have investigated behavioural and thermoregulatory flexibility that large African ungulates currently inhabiting hot and dry climates currently employ. I have shown that ungulates in the Kalahari may differ in their use of microclimate selection and activity patterns to buffer thermal, energetic and water stressors. My study is unique in that I have looked at where the animal was in space and time and linked it to their physiological and behavioural responses. I have, therefore, quantified microclimate selection, activity and body temperature responses in relation to NDVI and distance to water and have shown that the driving mechanisms behind the seasonal changes of body temperature and activity patterns is access to energy and water. I have further enhanced our existing knowledge and created the link between body temperature, vegetation quality and distance to surface water for antelope of the Kalahari and effectively assessed a functional trait. With climate change predicted to increase ambient temperatures and have less predictable rainfall in the semi-arid Kalahari, wildebeest will be forced to remain within the Kalahari, because historical migratory paths have been blocked by fences, and they may not have the behavioural and physiological flexibility to survive a hotter and drier future.

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LIST OF ABBREVIATIONS

CKGR	Central Kalahari Game Reserve
GPS	global positioning system
I.M.	intramuscular
IUCN	International Union for Conservation of Nature
KTP	Kgalagadi Transfrontier Park
MODIS	Moderate Resolution Imaging Spectroradiometer
NDVI	Normalised Difference Vegetation Index
NDWI	Normalised Difference Water Index
SCP	Semi-Automatic Classification Plugin
TAMSAT	Tropical Application of Meteorological Satellites
VHF	very high frequency

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CHAPTER 1

Introduction

1.1 Rationale

The effects of climate change are already apparent in both terrestrial and marine ecosystems (Parmesan & Yohe 2003; Pio et al. 2014). The primary challenge to be faced by many animals as climate change progresses will be the increase in ambient temperature (Niang et al. 2014). In the semi-arid areas of southern Africa, however, the threat of reduced water availability adds complexity to the thermal threat, or even exceeds it (Field et al. 2012; van Wilgen et al. 2016). A species has three prospective scenarios when faced with climate change: migrate or shift their current distribution range, adapt to the regional changes, or become extirpated or extinct (Walther et al. 2002; Pearson & Dawson 2003; Fuller et al. 2010). Theoretically, in a constraints-free environment, mammals will move to more suitable areas within the species' tolerance limits. But how far must a large mammal move to find its suitable habitat and what is realistically possible?

Obstacles, such as land transformation, fences and urbanisation, constrain animal movements (Williamson et al. 1988). If a species is unable to track its climatic envelope, then adaptation to changes in the environment becomes vital for a species to survive. As such, adaptation is critical and likely to be a universal aspect of biotic responses to future climate change (Fuller et al. 2010 & 2016; Urban et al. 2016). Animals can adapt either genetically (microevolution) or phenotypically to changes in environmental conditions. The current rate of climate change is predicted to be too fast to allow large-bodied species with long generation times, such as large mammals, to adapt genetically (Berteaux et al. 2004). If long-lived mammals are to survive climate change they will have to show plasticity in the expression of the genes they currently possess, so called "phenotypic flexibility" (Pigliucci et al. 2006; Raubenheimer et al. 2012; Fitzpatrick 2012). Phenotypic flexibility may involve alterations in an animal's behaviour, morphology, or physiology in response to altered environmental conditions. Yet, even the most plastic organisms have limitations on their capacity to compensate for environmental changes (Seebacher & Franklin 2012). Therefore, it is imperative to identify the species that are most vulnerable to climate change (Foden et al. 2013).

Behavioural ecology studies have improved our understanding of how large mammals adjust to changing environmental conditions and resources availability, such as by increasing their diet breadth during the dry seasons (Owen-Smith 2002) or by using shade when conditions are hot (Hetem et al. 2012a). However, behaviour ecology studies alone may not be enough to understand the effects of climate change (Angert et al. 2011; Lenoir & Svenning 2015). Physiological studies are required to improve our understanding of the mechanisms that drive such behaviours (Bozinovic & Pörtner 2015). To integrate this knowledge, studies on large mammal behavioural and physiological responses are required to enhance our understanding of large mammal phenotypic flexibility, which may improve our understanding of how they might cope with future climate change. This introductory chapter contextualises my research within what is currently known and relevant about climate change, identifies key gaps in the research and poses the questions that are addressed in my thesis.

1.2 Background literature

1.2.1 Climate change

The current climate system is warming. Already, the Intergovernmental Panel on Climate Change (IPCC) 2014 synthesis report detected an increase in global temperature of 0.12 °C per decade over the past 60 years from 1951 to 2012, a rise in sea levels of about 3.2 mm per year from 1993 to 2010, and a decline in the expanse of snow and ice by 3.5 – 4.1% since 1979, and predicts global temperatures to increase between 0.3 °C and 4.8 °C by the end of the 21st century with more frequent and longer lasting heat waves (IPCC 2014). Africa, a vulnerable continent, has already experienced an increase in extreme temperatures during the last 50 to 100 years, and most regions in Africa are expected to show an increase in heat waves and warm spell durations more than twice the global rate of temperature increase (Figure 1.1; Niang et al. 2014; Engelbrecht et al. 2015). Southern Africa, a predominantly semi-arid region, is projected to become generally warmer with hot days exceeding 35°C more frequently (Davis 2011; van Wilgen et al. 2016). However, the thermal threat projected for southern Africa is compounded, or even exceeded, by the threat of reduced water availability (Field et al. 2012). Food resources are already diverse in quantity, quality, and in space and time (Senft et al. 1987) and animals that currently live in semi-arid regions have adapted to these seasonal variations of resources. Since spatial and temporal variability in climate will theoretically intensify under future climate change scenarios (Huey et al. 2012), will the adaptations that large mammals currently employ be able to endure future climate change and to what degree will these current adaptations suffice? As such, numerous biological and ecological processes have already been affected by changing climates (Scheffers et al. 2016).

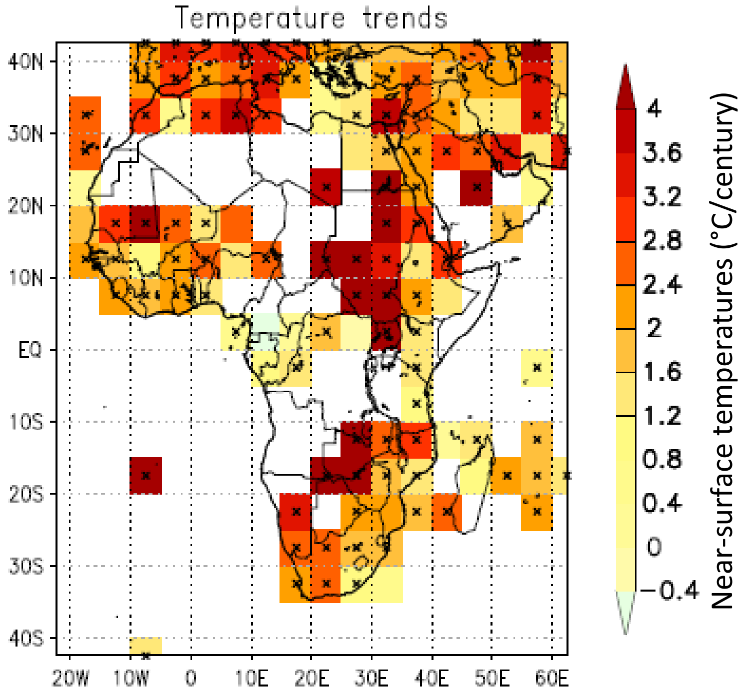

Figure 1.1: Observed trends in annual-average near-surface temperatures (°C/century) over Africa for the period 1961-2010 (adapted from Engelbrecht et al. 2015).

1.2.2 Universal responses to climate change

Three general responses have been reported so frequently that they are now considered 'universal' ecological responses to warming climates (Fenberg et al. 2016), i.e., climate-related range shifts (see Lenoir & Svenning 2015); changes in phenology (see Chambers et al. 2013; Buitenwerf et al. 2015); and changes in morphology (see McCain & King 2014; Gardner et al. 2011). Understanding the influence of environmental temperature on an animal's performance is critically important to predict the species' response to climate change (McCarty 2001; Thuiller et al. 2006; Acevedo-Whitehouse & Duffus 2009; Fuller et al. 2010 & 2016; Huey et al. 2012; Tattersall et al. 2012).

1.2.2.1 Climate-related range shifts

Species may be able to cope with changing climates and avoid extinction, if they are able to track their respective bioclimatic envelope (Lenoir & Svenning 2015). As such species range shifts have been well documented as a response to increased environmental temperatures (Parmesan & Yohe 2003; Root et al. 2003; Chen et al. 2011; Lenoir & Svenning 2015), suggesting that movement may be the initial response to warming conditions (Walther et al. 2002). Despite the high volume of studies documenting species range shifts, simply linking ecological variables to dispersal processes is not enough to predict realistic responses to climate change (Foden et al. 2013; Lenoir & Svenning 2015). For instance, if moving is not a feasible option, species will have to persist and cope with the changing climatic conditions. Species have the capacity to adapt to changing environmental conditions both by phenotypic flexibility within a life span (e.g., changes in behaviour, morphology or physiology) and by genetic plasticity (e.g., microevolution) over a few life spans (Fuller et al. 2010). However, climate change is occurring at a relatively fast rate and some species, such as large bodied species with long generation times (e.g., large mammals), may not be able to adapt fast enough genetically (Berteaux et al. 2004). If long-lived mammal species are to survive climate change they will have to show flexibility in the expression of the genes they currently possess.

1.2.2.2 Changes in phenology

Even for short-lived species phenotypic plasticity has been shown to be the primary driver of phenological changes (Reale et al. 2003). Resulting from climate change, many phenological changes have already been recorded (Chambers et al. 2013; Buitenwerf et al. 2015; Scheefers et al. 2016). Seasonal shifts in ambient temperature in the southern hemisphere are occurring 2.2 days earlier (Chambers et al. 2013). An increase in atmospheric CO_2 levels and ambient temperatures has led to a prolonged growing season of many plant populations (Reyes-Fox et al. 2014), which may result in a positive aspect of climate change. Although most mammals already deal with seasonal and inter-annual variation in climate, alterations in phenology could potentially reduce the risks of species extinction due to climate change (Bradshaw & Holzapfel 2008). But only if they are able to keep pace (e.g., from matching to mismatching the environmental conditions; see Stenseth & Mysterud 2002), such adaptation may not be possible for some species. One large mammal that may have a limited ability to adapt to climate change is the African wild dogs (*Lycaon pictus*). Wild dogs' typically breed during winter, when they rely on cool periods to raise their pups, but with the local climate predicted to become hotter, cooler denning periods may be impossible to achieve just by altering their reproductive timing (Woodroffe et al. 2017). As such, changes in phenology may provide a useful indicator for identifying which species can adapt to the changing climate or identify which species may be limited in their adaptive potential (Chambers et al. 2013).

1.2.2.3 Changes in morphology

Along with range shifts and phenological changes, morphological changes are believed to constitute a first response to climate change (Barnosky et al. 2003). Morphological variation within a species could also potentially increase their survival success under locate climate conditions. Koala's (*Phascolarctos cinereus*) morphological patterns in body size and fur, for example, vary according to heat exchange processes, suggesting that they can change their insulation in response to changing environmental conditions (Briscoe et al. 2015). Warming climates seem to favour a reduction in body size over time, since large surface to volume ratios potentially increase heat loss rates, thus energy and water requirements are reduced (Gardner et al. 2011; Scheffers et al. 2016). Consequently, because of their size and longevity, large mammals' potential responses may be limited making them more vulnerable to extinction (Cardillo 2005). Large mammals are important flagship species for conservation efforts and a change in large mammal populations could have dire consequences on all population dynamics within ecosystems thus affecting biodiversity conservation, ecotourism, societal and economic factors (Berteaux et al. 2006; Urban et al. 2016). Changes in large mammal populations have already been observed globally because of anthropogenic disturbances, with large mammal populations decreasing both inside and outside of protected areas (Caro & Scholte 2007; Craigie et al. 2010), with one-quarter of the world’s carnivore and ungulate species being close to extinction in the past 40 years (Di Marco et al. 2014).

1.2.3 Extinction

If species are unable to move or adapt to changing climatic conditions, the species will become extirpated or extinct (Walther et al. 2002; Pearson & Dawson 2003; Fuller et al. 2010), as has happened in the past. For example, the current climate change event is predicted to be of similar magnitude to that at the end of the Permian where 95% of species on earth went extinct (Benton & Twitchett 2003). The Bramble Cay melomys (*Melomys rubicola*) is the first mammal that has now been declared extinct as a result of anthropogenic climate change (Waller et al. 2017). Up to 69% of South African mammals are predicted to be at risk of extinction by 2050 as a result of climate change, if dispersal is limited (Thomas et al. 2004). Model predictions of extinction risks from anthropogenic climate change are needed, but still overly simplistic (Willis et al. 2015; Urban et al. 2016). The majority of climate change prediction models used very basic correlative models and species distribution models, which ignore the underlying biological mechanisms that play a role in species distribution (Foden et al. 2013; Willis et al. 2015; Urban et al. 2016). There are now many emerging mechanistic models that incorporate fundamental biological mechanisms (e.g., Kearney & Porter 2009; Bocedi et al. 2014), but these models require measurements of physiology and behaviour which are often lacking for many species or systems (Foden et al. 2013; Willis et al. 2015).

It has been proposed that if species can adapt to local conditions by phenotypic flexibility, realized range shift and extinction risks may be less pronounced than those projected by many studies (Thuiller et al. 2006). As physiological and behavioural responses to environmental changes can be instantaneous (Muñoz et al. 2015), these responses often mediate how climate conditions are influencing a species’ welfare (Urban et al. 2016). Behavioural adjustments, such as flexible activity traits, may buffer the impact of climate change (Mitchell et al. 2008; Kearney et al. 2009; Huey et al. 2012; McCain & King 2014). Even the most plastic organisms have limitations on the capacity to compensate for environmental changes, such as climate change (Seebacher & Franklin 2012) and animals that inhabit extreme environments may already be living at the edge of their plasticity envelope (Hetem et al. 2010). Thus, it is imperative that a comprehensive picture of the species’ responses is built into prediction models to understand its fundamental niche (Kearney & Porter 2004) and the effects that climate change may have on a species (Barnard & Thuiller, 2008; Urban et al. 2016). Yet, the relevant physiological and behavioural responses are often difficult to measure and incorporating these responses into realistic biological models is often time consuming. Despite such limitations, focussing research on species living in hot and dry environments as an analogue to future climate change scenarios, such as large mammals, may help to improve forecasts of the impacts of climate change on biodiversity (Muñoz et al. 2015; Urban et al. 2016).

1.2.4 Fine-scale responses

1.2.4.1 Movement to resources

Theoretically an animal’s first response to changing climatic conditions will be to track their climatic envelope (Parmesan & Yohe 2003). Movement is fundamental to most organisms to survive and is defined as an act of moving the whole individual across space and time (Nathan et al. 2008). Abiotic factors (such as slope and distance to water) are the primary determinants of large-scale movements and act as constraints within which mechanisms involving biotic factors operate (Bailey et al. 1996). Therefore, one should consider the influence of both biotic and abiotic factors in determining the distribution patterns of large mammals (Redfern et al. 2003), particularly in the context of climate change. With the rapidly changing climate, species will be required to move large distances (Lawler et al. 2013), but large mammal distribution patterns are largely dominated by the trade-off between water requirements and nutritional needs (Western 1975). This trade-off that species face between nutritional requirements and surface-water constraints varies according to the species’ water dependence, which may be further heightened by aridity when forage quantity is reduced (Redfern et al. 2003). Despite the relevance of surface water availability for mammals, very few studies have addressed this topic.

In the modern human-dominated landscape, are all species capable of moving to a more suitable environment? Large mammals, such as ungulates, may have the capacity to keep track with changing climate envelopes over the 21st century, as shown in Figure 1.2 (Settele et al. 2014). Yet that capacity may not be realized because of the non-climatic influences that these animals would need to overcome. Over the last two centuries, non-climatic influences, such as biotic interactions (e.g., competition with domestic livestock) and/or anthropogenic habitat fragmentation (e.g., urbanisation and agriculture), have severely disrupted ungulate migrations (Bolger et al. 2008), and in conjunction with climate change may hamper the ability of a species to move (Thuiller et al. 2006; Levinsky et al. 2007). Therefore, the ability of a species to track its bioclimatic envelope at a sufficient rate to keep up with the changing climate will largely be dependent on the dispersal characteristics of individual species (Pearson & Dawson 2003), on anthropogenic and natural restrictions on distributions, such as scarcity of forage and water, competitive interactions with other wildlife or livestock and predation (Groom & Harris 2009). For example, the scimitar-horned oryx (*Oryx dammah*) will have to move thousands of kilometres from its current habitat in the Sahara Desert to the Kalahari Desert in Namibia or Botswana in order to track its bioclimatic envelope by 2050 (Figure 1.3; Thuiller et al. 2006). Such distances are probably not feasible in a modern human-dominated landscape. Not only does a species have to deal with anthropogenic habitat fragmentation, but it will have to endure unprecedented extreme weather that results from climate change, with increases in the frequency, intensity, spatial extent, duration and timing of extreme weather and climatic events reported (IPCC 2014). The IPCC predicts that reduced precipitation and increased evapotranspiration will undoubtedly intensify droughts in southern Africa over the 21st century (IPCC 2014; Field et al. 2012). If a species is unable to track its bioclimatic envelope or escape extreme

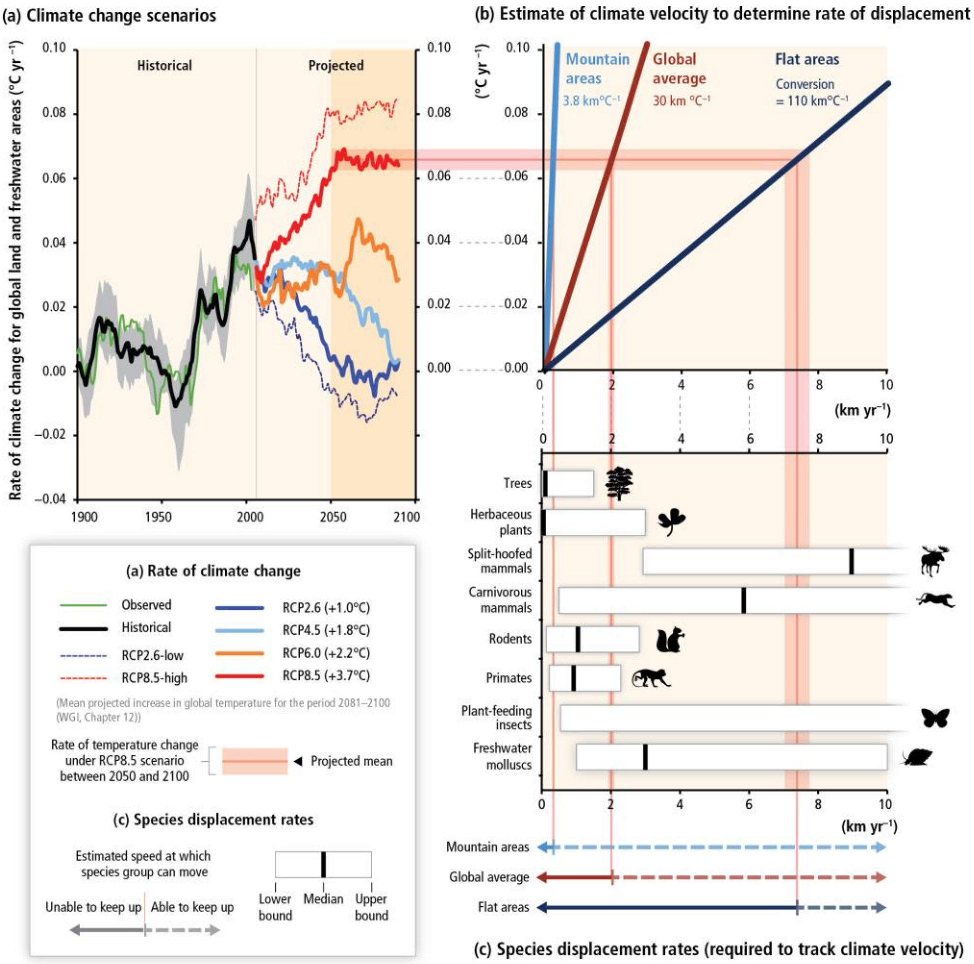

Figure 1.2: | (a) Rates of climate change, (b) corresponding climate velocities, and (c) rates of displacement of several terrestrial and freshwater species groups in the absence of human intervention. Horizontal and vertical pink bands illustrate the interpretation of this figure. Climate velocities for a given range of rates of climate change are determined by tracing a band from the range of rates in (a) to the points of intersection with the three climate velocity scalars in (b). Comparisons with species displacement rates are made by tracing vertical bands from the points of intersection on the climate velocity scalars down to the species displacement rates in (c). Species groups with displacement rates below the band are projected to be unable to track climate in the absence of human intervention. The three scalars are climate velocities that are representative of mountainous areas (left), averaged across global land areas (center), and large flat regions (right). (c) Rates of displacement are given with an estimate of the median (black bars) and range (boxes = approximately 95% of observations or models for herbaceous plants, trees, and plant-feeding insects or median ± 1.5 inter-quartile range for mammals). Displacement rates for mammals were based on modelled dispersal rates of a wide range of mammal species and large herbivore mammal median displacements rate is faster than carnivorous mammals (adapted from Settele et al. 2014).

weather by moving large distances, it may attempt to buffer changing climatic conditions by changing its fine-scale habitat use.

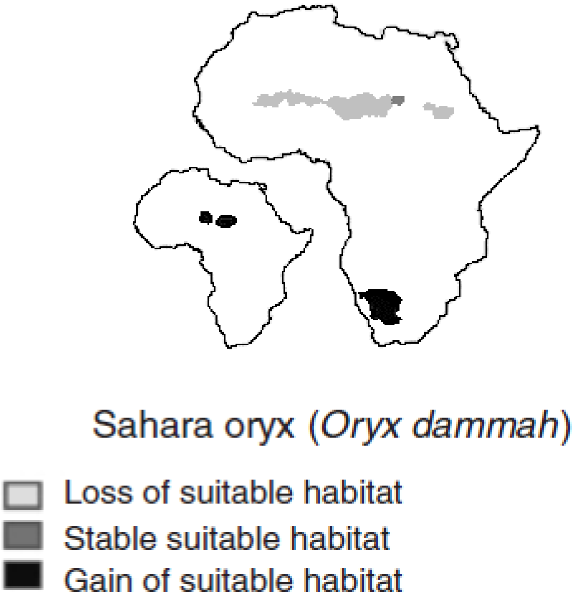

Figure 1.3: Observed current (small map) and predicted (large map) distribution of the scimitar-horned oryx (*Oryx dammah*) for 2050. Light grey areas indicate current climatically suitable habitats predicted to be unsuitable in the future. Moderate grey areas indicate the current climatically suitable habitats which are predicted to stay suitable. Dark grey areas indicate the current climatically unsuitable habitats which are predicted to be suitable by 2050 (adapted from Thuiller et al. 2006).

1.2.4.2 Phenotypic flexibility

If the animal's bioclimatic envelope is inaccessible, an adjustment to their phenotype may occur (i.e., phenotypic flexibility) to buffer the effects of the changing climatic conditions (Fuller et al. 2010; Hetem et al. 2012a & 2014; Valladares et al. 2014). Phenotypic flexibility is broadly defined as 'the ability of individual genotypes to produce different phenotypes when exposed to different environmental conditions' (Pigliucci, et al. 2006; Fitzpatrick 2012; Kelly et al. 2012; Raubenheimer et al. 2012). That is, the ability of the individual animal to modify their behaviour, morphology, or physiology in response to altered environmental conditions. Phenotypic flexibility has been expressed by a wide diversity of organisms in response to biotic and abiotic aspects of their environments (reviewed in Piersma & Drent 2003, Reale et al. 2003; Miner et al. 2005; Williams et al. 2008; Raubenheimer et al. 2012; Merilä & Hendry 2014).

1.2.4.2.1 Fine-scale Behavioural Responses

Several flexible behavioural strategies are used by mammals to avoid high thermal heat load. A reduction in activity, for example, could potentially minimize endogenous heat production (Wang et al. 2006), as well as shade-seeking (cool microclimates) could reduce heat load (Hetem et al. 2012a & 2016; Fuller et al. 2016), and switching to nocturnal activity could potentially compensate for any activity lost to high heat loads during the day (Hetem et al. 2012a). By selecting different microclimates, terrestrial animals are able to maximise heat gain/loss and reduce the need for evaporative cooling by sustaining a favourable temperature gradient between the body and the environment thereby enabling convective heat loss (Cain et al. 2008; Hetem et al. 2012a), thus conserving body water. Desert bighorn sheep (*Ovis Canadensis Mexicana*) (Cain et al. 2008), Arabian oryx (*Oryx leucoryx*) (Hetem et al. 2012a), impala (*Aepyceros melampus*) (Jarman & Jarman 1973), and klipspringer (*Oreotragus oreotragus*) (Dunbar 1979) were all recorded using cool microclimates (shade-seeking) during midday when ambient temperatures were high.

Access to cool microclimates may not be possible for some species. For example, the black wildebeest (*Conochaetes gnou*) inhabits the plains of the temperate grasslands and semi-arid shrubland of South Africa, which are often treeless habitats with very little access to shade (Estes 1991). Thus, the use of shade-seeking behaviour during high ambient temperatures as an adaptation to increasing temperatures is not possible. Therefore, the black wildebeest may orient their body relative to solar radiation to reduce heat loads (Maloney et al. 2005; Lease et al. 2014), reduce diurnal feeding activity at high ambient temperatures and feed mainly at night to compensate for lost diurnal foraging during the warm seasons (Maloney et al. 2005). Becoming more active at night to compensate for reduced diurnal activity during the warm season has been noted in several species. Desert mule deer (*Odocoileus hemionus crooki*; Hayes & Krausman 1993), kudu (*Tragelaphus strepsiceros*; Owen-Smith 1994), and moose

(*Alces alces*; Dussault et al. 2004) showed an increase in nocturnal activity during periods of high thermal stress. In addition, foraging at night could potentially increase water and energy intake by foraging on higher water content plants (Nagy & Knight 1994) or through preformed water (Cain et al. 2006). However, the cool nocturnal period may be too short to allow complete compensation, particularly if the hot period coincides with a dry period when forage quality and quantity is limited (Hetem et al. 2012a; Fuller et al. 2016). Yet, being active at night may cause a trade-off with predator avoidance (Godvik et al. 2009; Hebblewhite & Merrill 2009; Valeix et al. 2009). Kudu increased their nocturnal activity when predation pressure was low but completely avoided being active at night when reintroduction of lions and hyenas resulted in high predation pressure (Tambling et al. 2015). The exact trade-offs experienced by large mammals in relation to climate change is largely unknown and the costs of phenotypic flexibility remains to be discovered.

Gaining knowledge about how a large mammal’s activity and microclimate selection changes according to environmental stresses is critically important in understanding the major drivers behind such behaviours. Behavioural adjustments such as seeking cooler microclimates and change in activity patterns may buffer the impact of climate change (Mitchell et al. 2008; Kearney et al. 2009; Huey et al. 2012), but for endotherms such behavioural adjustments may involve trade-offs between thermoregulation, osmoregulation, and acquisition of energy (Hetem et al. 2016). To predict the extent to which species are resilient to these environmental changes requires some measure of these functional traits (i.e., behavioural and physiological responses) and whether such behavioural adjustments are actually occurring in free-living species needs to be investigated further. Therefore, quantifying thermoregulatory behaviour is a necessary first step to evaluate climate-induced effects on population dynamics of large herbivores effectively (Grosbois et al. 2008; Mysterud & Saether 2011).

1.2.4.2.2 Physiological Responses

Adjusting to changing conditions through behavioural responses are generally less costly than using autonomic processes, but behavioural responses may be insufficient to curb climate change (Fuller et al. 2016; Hetem et al. 2016). Changes in physiological processes could identify the causative effect of climate change resulting in the change of behaviour (Seebacher & Franklin 2012). Understanding of the thermal physiological sensitivity of a species is required to predict the direct effects of climate change. Body temperature, a variable likely to be affected by changing temperature and resources, is relatively easy to measure in free-ranging individuals. Endotherms actively control their body temperature independently of environmental temperature through a combination of autonomic and behavioural processes, defined as thermoregulation (Tattersall et al. 2012). For endotherms, when ambient temperature ebbs lower than body temperature, heat is passively lost by means of radiation, convection and conduction to the environment (Cain et al. 2006). However, when ambient temperature exceeds body temperature or the gradient between the endotherm and the environment becomes too small, an endotherm must either use evaporative cooling to dissipate heat or tolerate an increase in body temperature (Cain et al. 2006; Tattersall et al. 2012).

Evaporative cooling, better known as evaporative heat loss, can occur through evaporation of water from either the skin (sweating/licking) or respiratory tract (panting; Hetem et al. 2016). When water is accessible, large mammals, such as ungulates, increase their sweating and panting with an increase in ambient temperatures (Taylor 1970a,b). However, when access to water is limited, ungulates must “trade off” osmoregulation (control of body water) with thermoregulation (control of body temperature). It appears that desert ungulates prioritise osmoregulation above thermoregulation when access to water is limited and some species (e.g., Grant's gazelle (*Nanger granti*), Thomson's gazelle (*Eudorcas thomsonii*), oryx (*Oryx beisa*), eland (*Tragelaphus oryx*), and camel (*Camelus dromedarius*)) can reduce evaporative cooling (sweating) by as much as 89% by allowing body temperature to fluctuate over a wide range (Schmidt-Nielsen et al. 1957; Taylor 1970b). Some desert-adapted endotherms potentially conserve body water by tolerating high body temperatures and reducing the need to evaporative water that is initially required for thermoregulation (Schmidt-Nielsen et al. 1957, Mitchell et al. 2002), for example, the dromedary camel can store up to 6 °C when it’s dehydrated (Schmidt-Nielsen et al. 1957), and Arabian oryx stored up to 7.7 °C (Hetem et al. 2010). Theoretically, large mammals can withstand an increase in body temperature to reduce the gradient between ambient temperature and body temperature (Taylor 1970a,b), provided the extra heat load can be lost during the night (Abere & Oguzor 2011). Therefore, a combination of water deprivation and an increase in ambient temperatures often leads to a process called dehydration-induced hyperthermia in which ungulates allow their body temperatures to rise along with ambient temperature, thereby decreasing the thermal differential with the environment and conserving body water (Mitchell et al. 2002). However, this increase in body temperature does not come without costs as such hyperthermia is likely to occur with dehydration and may reflect a stress rather than adaptive strategy (Hetem et al. 2016). It was originally thought to be adaptive (Schmidt-Nielsen et al. 1957; Grigg et al. 2009), but the adaptive value has recently been questioned since hyperthermia has not been demonstrated in hydrated individuals (Fuller et al. 2010 & 2016, Hetem et al. 2016). Hetem et al. (2016) have recently raised concerns about whether such hyperthermia is a programmed active process, or whether it is incidental, resulting from failure of thermoregulation (Figure 1.4). A recent study on wild rabbits (*Oryctolagus cuniculus*) showed that a failure of thermoregulation (an increase in heterothermy) resulted in reduced fitness (Maloney et al. 2017).

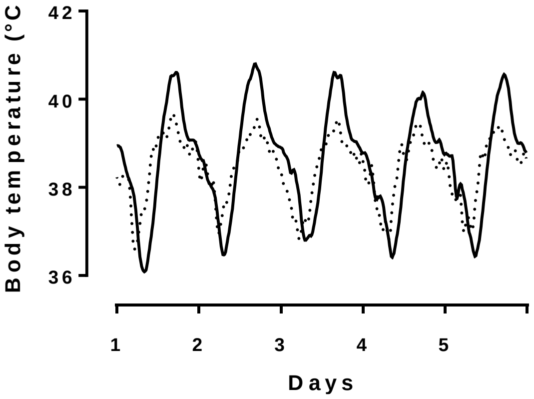

Figure 1.4: Free-living male oryx displaying dehydration-induced hyperthermia (solid line) over a 5-day period after ephemeral pools of water had dried up following the last rain two months prior and captive male oryx (dotted line) with free access to water, despite ambient temperatures being similar between the periods (adapted from Hetem et al. 2016 with permission).

It is not only high temperatures and low water availability that affect thermoregulation. The maintenance of a constant body temperature within a narrow range (homeothermy) requires an endotherm to use energy in the form of metabolism which requires adequate energy intake (Maloney et al. 2002). Food availability, especially in seasonal environments, varies across space and time (Senft et al. 1987). If food is limited, endotherms may not be able to gain sufficient energy to maintain the high metabolic rate required for homeothermy and may be incapable of maintaining their body temperature within a narrow range. Under conditions of low food availability, the cost of thermoregulation may become exorbitantly expensive (Geiser 2004). For instance, low prey availability because of drought conditions compromised aardvarks' (*Orycteropus afer*) wellbeing (Rey et al. 2017). Limited food and water resources may lead to a "trade off" between the use of energy to search for food and water, and achieving optimal management of body water and thermoregulation. Therefore, energy availability is expected to be the primary constraint on the abundance and distribution of endotherms (Buckley et al. 2012) and ungulates that live in semi-arid ecosystems may be more sensitive to reduced vegetation than increased temperatures, which may become more erratic as a secondary effect of climate change.

Animals can decrease energy expenditure by reducing locomotor activity (Wang et al. 2006). However, if an endotherm cannot source adequate food or use behavioural adaptations to reduce energy expenditure, it may become hypothermic. Hypothermia is a process whereby an endotherm reduces its body temperature below the required temperature for normal metabolism (Tattersall et al. 2012). Such hypothermia may be a form of torpor (i.e., controlled down regulation of body temperature) under a continuum of thermoregulatory strategies (Heldmaier & Ruf 1992). In fact, it has also been suggested that a low metabolic rate and the resulting low body temperature may be a vital adaptive response to starvation in mammals (McCue 2010). Many temperate species, such as red deer (*Cervus elaphus*; Arnold et al. 2004; Turbill et al. 2011), Przewalski horse (*Equus ferus przewalskii*; Arnold et al. 2006), and Alpine ibex (*Capra ibex ibex*; Signer et al. 2011) could reduce their energy expenditure during the late winter by reducing their locomotive activity, by allowing their body periphery to cool considerably and by reducing their basal metabolic rate (i.e., hypometabolism). This hypometabolism is suggested to be an endogenously controlled adjustment in metabolism similar to torpor displayed by small mammals (Turbill et al. 2011), ultimately reducing body temperature.

Alternatively, hypothermia may be a result of starvation (low energy reserves), in which animals are simply unable to sustain the high metabolic cost of maintaining body temperature within narrow limit, as observed in kangaroos (*Macropus fuliginosus*), dromedary camel (*Camelus dromedaries*; Grigg et al. 2009), and Arabian oryx (Figure 1.5; Hetem et al. 2016). Blue wildebeest (*Connochaetes taurinus*), in Mapungubwe Game Reserve in South Africa, were unable to maintain homeothermy during the dry season and displayed 24 h amplitude of body temperature of 3.5 °C and low minimum body temperatures of 36 °C (Shrestha et al. 2011). However, the low morning body temperatures recorded, not only occurred at a time of low energy availability but also of low ambient temperatures, therefore, it cannot be concluded for certain if it was ambient temperature or insufficient forage to drive the lower minimum body temperatures. Yet, several large ungulates who were deprived of adequate energy during warm periods, were unable to rewarm after progressively depleting the energy stores necessary to maintain homeothermy and succumbed to death in the early morning, as seen for blue wildebeest, and Arabian sand gazelle (*Gazella subgutturosa marica*; Figure 1.6; Hetem et al. 2016). Even medium sized mammals, such as aardvark (Rey et al. 2017), did not recover when body temperatures dropped critically low as a result from inadequate energy acquisition. Heterothermy associated with a drop in minimum body temperature in large mammals therefore appears to reflect thermoregulatory failure resulting from undernutrition (Hetem et al. 2016), rather than under active physiological control as suggested for torpor (Schmidt-Nielsen et al. 1957; Ostrowski et al. 2003; Maloney et al. 2004). Unless normal body temperature is restored, this kind of hypothermia is lethal.

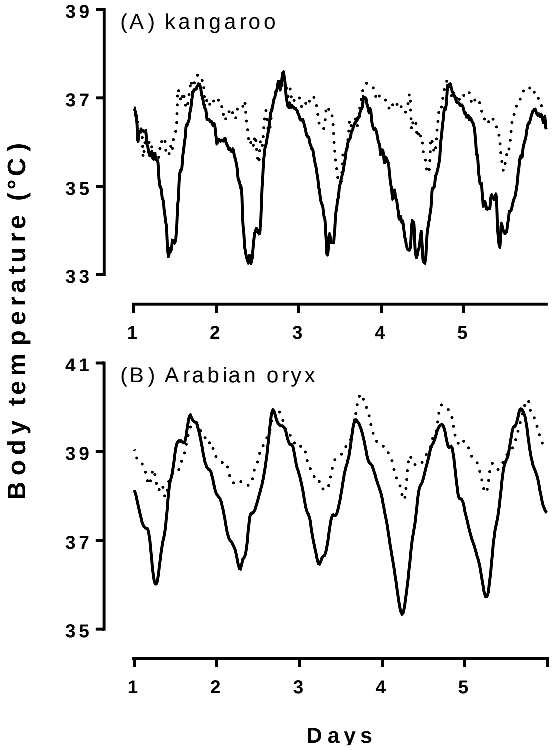

Figure 1.5: Body core temperature rhythms of a kangaroo (*Macropus fuliginosus*; A) and an Arabian oryx (*Oryx leucoryx*; B) over a 5-day period when forage was lacking (solid line) and in the same individual over a 5-day period when forage was abundant (dotted line) during a hot season. Ambient temperatures were similar during these two periods (adapted from Hetem et al. 2016 with permission).

Large mammals that live in hot and dry environments tend to have limited thermal shelters and because they spend a large amount of time inactive as a result of high ambient temperatures, they may allow their body temperature to fluctuate rather widely on a daily basis. This fluctuation of body temperature, a process called adaptive heterothermy (i.e., with lower than normal minimum body temperature and higher than normal maximum body temperature), has been suggested to be an important physiological adaptation (Mitchell et al. 2002). Through adaptive heterothermy, within a 24 hours cycle, large mammals allow their body to store heat during the day with a constant rise in body temperature until a bearable maximum is reached, and then slowly dissipate that heat during the night until a tolerable minimum body temperature has been reached (Mitchell et al. 2002).

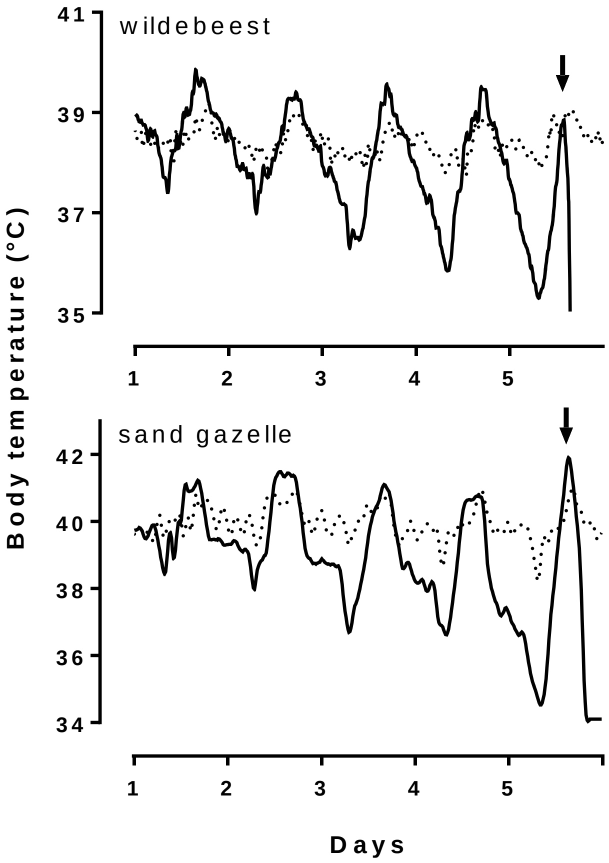

Figure 1.6: Body core temperature rhythms of free-living Arabian sand gazelle (*Gazella subgutturosa marica*; A) and blue wildebeest (*Connochaetes taurinus*; B) over a 5-day period when the animals were healthy (dotted line) and in the same individual over a 5-day period prior to their deaths (solid line). Estimated time of death is indicated by the arrow. A progressive lowering of minimum body temperature resulted prior to death (adapted from Hetem et al. 2016 with permission)

Adaptive heterothermy has therefore been proposed to be an effective water-saving mechanism and it has been suggested that gemsbok use adaptive heterothermy as a physiological strategy to cope with heat and aridity (Taylor 1969). Only one previous study has looked at body temperature of free-living gemsbok over a short two month period (Maloney et al. 2002). In a mild climate with free access to water, gemsbok maintained 24 h amplitude of body temperature ~2.2 °C at the beginning of the hot wet season, showing no signs of adaptive heterothermy. In fact, these animals were not dehydrated nor starved as they had free access to food and water in a 62 ha enclosure. Only two large mammalian herbivores have been known to show adaptive heterothermy in semi-arid/arid environments: Arabian oryx (*Oryx leucoryx*; Ostrowski et al. 2003;

Hetem et al. 2012b) and sand gazelle (*Gazella subgutturosa marica*; Ostrowski et al. 2006, Hetem et al. 2012b). However, the low morning body temperatures recorded for free-ranging Arabian oryx and sand gazelle in an extreme desert environment, occurred at a time of low energy availability and lack of water which may result in the combined effect of starvation hypothermia and dehydration hyperthermia, therefore, it is not possible to say for certain that the animals were deploying adaptive heterothermy (Hetem et al. 2012b). Whether such heterothermy is “adaptive” or indicative of a stressful environment has thus been debated (see Hetem et al. 2016).

1.2.4.3 Functional traits

To enhance our understanding of how a species may respond to their environment, we need to understand the threats and vulnerability of that species and to do that we will need an understanding of the ‘response mediating’ traits (i.e., functional traits), as proposed by Foden et al. (2013) and Garcia et al. (2014). Phenotypic flexibility, such as behavioural or physiological traits, are considered functional traits as they affect the potential of individuals to tolerate changing climates (Garcia et al. 2014; Nock et al. 2016). Different physiological and behavioural variables, such as body temperature, activity and energetic expenditure of free-living large mammals can now be measured by biologging devices or biotelemetry, without human bias (Wilmers et al. 2015). For instance, continuous recordings of body temperature could potentially allow the monitoring of responses of individual animals to environmental stressors (Maloney et al. 2017). Although advances in biologging technology now make such measurements feasible (Wilmers et al. 2015), the implementation of such measurements may be costly which has resulted in limited application.

Initial research has shown the dry period as a stressor and majority of the studies to date have inferred relationships between the lack of forage and water availability that occur during the dry season and the animal's physiology (e.g., Hetem et al. 2010; Shrestha et al. 2011). But we need to explicitly link the drivers behind the functional traits observed. Remote sensing data combined with biologging of individual species responses may enable us to quantify the link between seasonal variability in resources, such as vegetation quality and distance to water, and thermoregulatory behaviours of long-lived endotherms, such as ungulates. Integrating knowledge of physiological stresses and environmental data will ultimately enhance our understanding of large mammal phenotypic flexibility. For example, an integrative conceptual framework for movement ecology of animals was developed by Nathan et al. (2008). The authors suggested that there are potentially three components to movement: an internal state (i.e., why move?), a motion capacity (i.e., how to move?), and a navigation capacity (i.e., where to move?), with externals factors (i.e., biotic and abiotic environmental factors) as a fourth component influencing the movement and all four components may affect movement interchangeably (Figure 1.7; Nathan et al. 2008). Body temperature may provide an indicator of the internal state of the individual animal and may potentially highlight and explain the decisions that mammals are forced to make when external factors come into play. As an example, a recent study used the pattern of 24 h body temperatures rhythm to indicate the fitness of wild rabbits (Maloney et al. 2017). If we combined movement trajectories with simultaneous physiological and behavioural measurements, it may help us to better understand the mechanisms underlying the movements of a species. Such knowledge will increase our understanding of how climate change will affect natural populations. To do so, we first need to understand physiological and behavioural flexibility of individuals currently living in hot and dry climates.

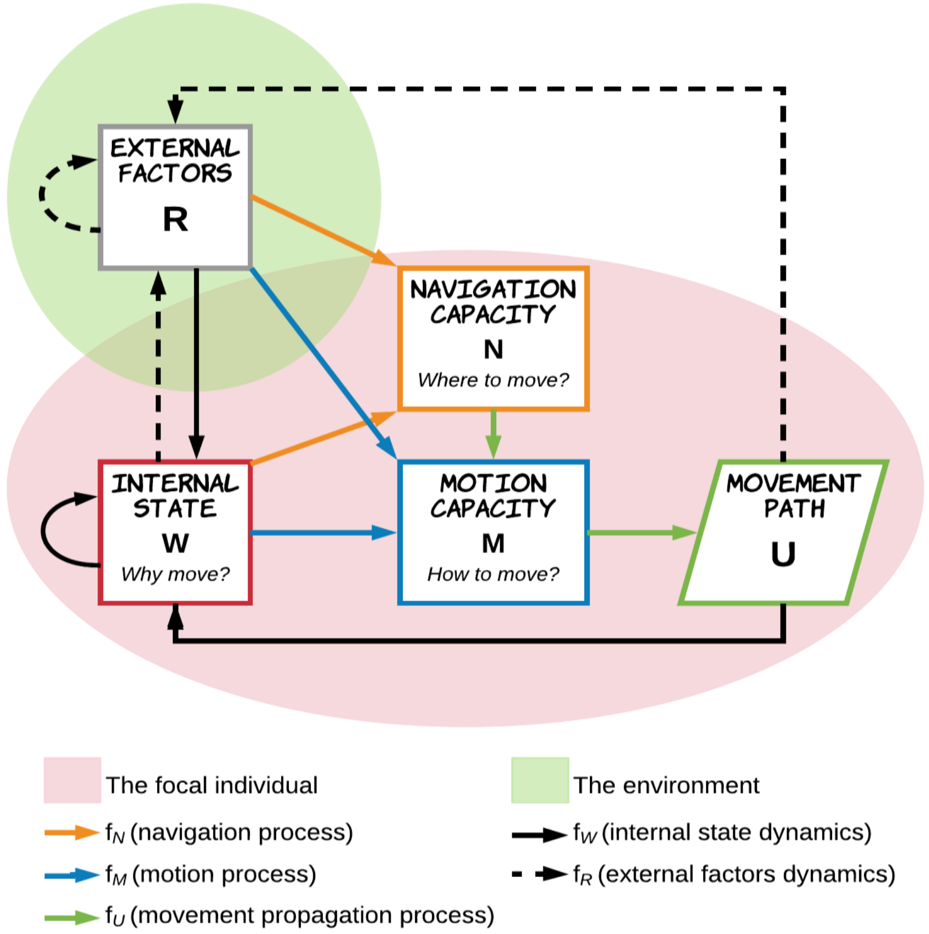

Figure 1.7: General conceptual framework for movement ecology, composed of three basic components (pink background) related to the focal individual (internal state (physiology and neurology), motion capacity (biomechanical or morphological machineries), and navigation capacity (cognitive or sensory machineries to obtain and use information)) and a fourth basic component (green background) referring to external factors (biotic and abiotic environmental factors) affecting its movement. Relationships among components related to the processes by which they affect each other, with arrows indicating the direction of impact. The resulting movement path feeds back to the internal and external components (Adapted from Nathan et al. 2008; Copyright (2008) National Academy of Sciences).

1.3 Thesis aim, objectives and thesis outline

Long-lived terrestrial mammals do not have access to microevolution as an adaptation strategy for climate change because many of the projected changes will occur within their lifespans. Since warming trends are predicted to be accompanied by reduced precipitation and increased frequency of droughts in arid and semi-arid ecosystems, projected increases in temperature will be confounded by secondary effects of reduced food and water availability. Ungulates will therefore become reliant on behavioural thermoregulatory strategies during arid conditions, like seeking shade and shifting activity to cooler periods, which may further compromise diurnal foraging. In the Kalahari, the long dry season typically begins in May and continues throughout August when ambient temperatures start to rise. Dry conditions continue to prevail as conditions heat up, until the first good rains sometime in mid-November. However, climate change is likely to increase the variability in the timing of those first rains and shift the rains even later in January, which may result in the period of resource scarcity and heat being extended to really test the limits of endurance of herbivore populations. Therefore, what are the current implications of this seasonal climate on the species which live there? How might they cope in terms of microclimate selection, activity, and thermoregulation? What trade-offs are required to survive during this late dry season? Even though the realised effects of climate change will only be apparent over a period of decades, understanding the plasticity of individuals currently inhabiting hot and dry climates is crucial to making predictions about the conditions that will become dominant in the future. I set out to investigate aspects of behaviour and thermoregulation of two ungulate species with differing water dependency in a semi-arid savanna region where annual rainfall is variable and access to surface water is restricted. I focused on the thermoregulatory and behavioural responses (activity and microclimate selection) of the water-dependent blue wildebeest, which in recent years have undergone a substantial population decline in southern Botswana, and the arid-adapted gemsbok, which continue to thrive in the Kalahari region. Understanding the physiological and behavioural strategies that enable animals to survive in current hot and dry conditions will provide an analogue for the kind of flexibility required for species to survive future climate change.

Three broad objectives were assessed:

- Objective 1: To investigate the seasonal changes in behaviour (microclimate selection and timing of activity) and thermoregulation (temperature rhythm) of sympatric gemsbok and blue wildebeest (addressed in chapter 3).
- Objective 2: To investigate how changes in vegetation greenness (as assessed from NDVI) influence variability in activity and thermoregulation (minimum body temperature) responses of these two ungulate species (addressed in chapter 4).
- Objectives 3: To investigate if access to surface water (indexed as proximity to surface water) influences variability in behavioural (microclimate selection and timing of activity) and thermoregulatory (maximum body temperature) responses of gemsbok and blue wildebeest during hot periods (addressed in chapter 5).

This thesis has been separated into an introductory chapter (Chapter 1), a general methodology chapter (Chapter 2), three research chapters (Chapters 3 – 5), and a concluding chapter in which I place my main findings within a larger conceptual framework and highlight potential avenues for future research (Chapter 6).

To avoid repetitions in the references, I have listed the references for all chapters at the end of the thesis. Some of my results have been presented at international conferences listed below:

Boyers, M., Parrini, F., Erasmus, B.F.N., Owen-Smith, N., & Hetem, R.S. Inanition hypothermia in gemsbok in the arid Kalahari. Presented at the 5th International Symposium on the Physiology and Pharmacology of Temperature Regulation (PPTR), Kruger National Park, South Africa 7-12 September 2014 (poster presentation)

Boyers, M., Parrini, F., Erasmus, B.F.N., Owen-Smith, N., & Hetem, R.S. Inanition hypothermia in gemsbok in the arid Kalahari. Presented at the 13th Annual Savanna Science Network Meeting, Kruger National Park, South Africa 9-12 March 2015 (oral presentation)

Boyers, M., Parrini, F., Owen-Smith, N., Erasmus, B.F.N., & Hetem, R.S. Water-dependent wildebeest display enhanced heterothermy compared to arid-adapted gemsbok. Presented at the Australian and New Zealand Society for Comparative Physiology and Biochemistry, New South Wales, Australia 3 – 6 December 2015 (oral presentation)

CHAPTER 2

General materials and methods

2.1 Study areas

With species losses predicted to be highest in the western part of southern Africa (Erasmus et al. 2002), the Kalahari is an ecosystem under threat from future climate change. This area is predicted to get both hotter and drier with more severe droughts compared to today’s climate (van Wilgen et al. 2016). The Kalahari stretches from the Orange River to tropical Africa and forms part of the South West Arid Biome (Eloff 1984). This study focusses on the Kalahari ecosystem in Botswana, which features various conservation areas, in particular, the Kgalagadi Transfrontier Park (KTP) in the south west extending northwards to the Central Kalahari Game Reserve (CKGR), with the Bakgalagadi Schwelle (a nutrient rich hot spot) situated in between (Figure 2.1; Fynn & Bonyongo 2011). Before the erection of veterinary fences, ungulates from the Bakgalagadi Schwelle historically moved north to the Okavango system, south to the Orange River, or southeast to the Limpopo River during the dry seasons, as depicted in Map 1 (Figure 2.2a; Child 1972; Williamson 2002). However, the dry season movement to the north is now restricted by the erection of the veterinary fences, which has drastically curtailed access to surface water and to higher-rainfall refuges beyond the fence during severe droughts (Map 2; Figure 2.2b; Williamson 2002). The CKGR exhibits no barriers to animal movement south-west through the Bakgalagadi Schwelle towards the KTP extending into South Africa (Figure 2.1 & Figure 2.2b). These days there are very strong barriers to movement between CKGR and the Bakgalagadi Schwelle. Remaining corridors are now almost closed by fences, ranches, cattle posts, towns (Selebatso 2017). Species inhabiting this semi-arid region may already be pushed to the limit of their ability to cope with hot and dry conditions, making the Kalahari an ecosystem particularly under threat from climate change. Thus, the Kalahari ecosystem provides an ideal location to explore species responses to the current climatic conditions, to gain a better understanding of the behavioural and thermoregulatory mechanisms which might allow ungulates to cope with future climate change.

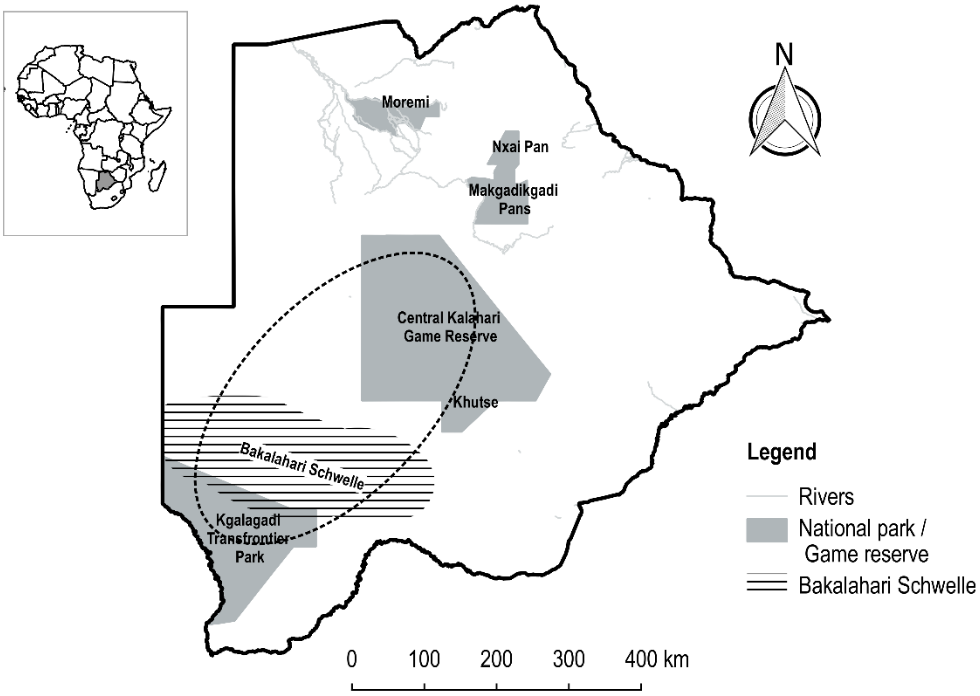

Figure 2.1: Map of Botswana, including continental position (map inset), showing the national parks and game reserves. The Central Kalahari Game Reserve (CKGR) is fenced on the northern and eastern boundary of the reserve allowing animal movement south-west towards the Kgalagadi Transfrontier Park (KTP) extending into South Africa. The eastern boundary of KTP is unfenced leaving this border open to animals that migrate from east to west. The Bakgalagadi Schwelle is the watershed situated between CKGR and KTP reserves. The ellipsoid represents the extent of the study areas within this thesis.

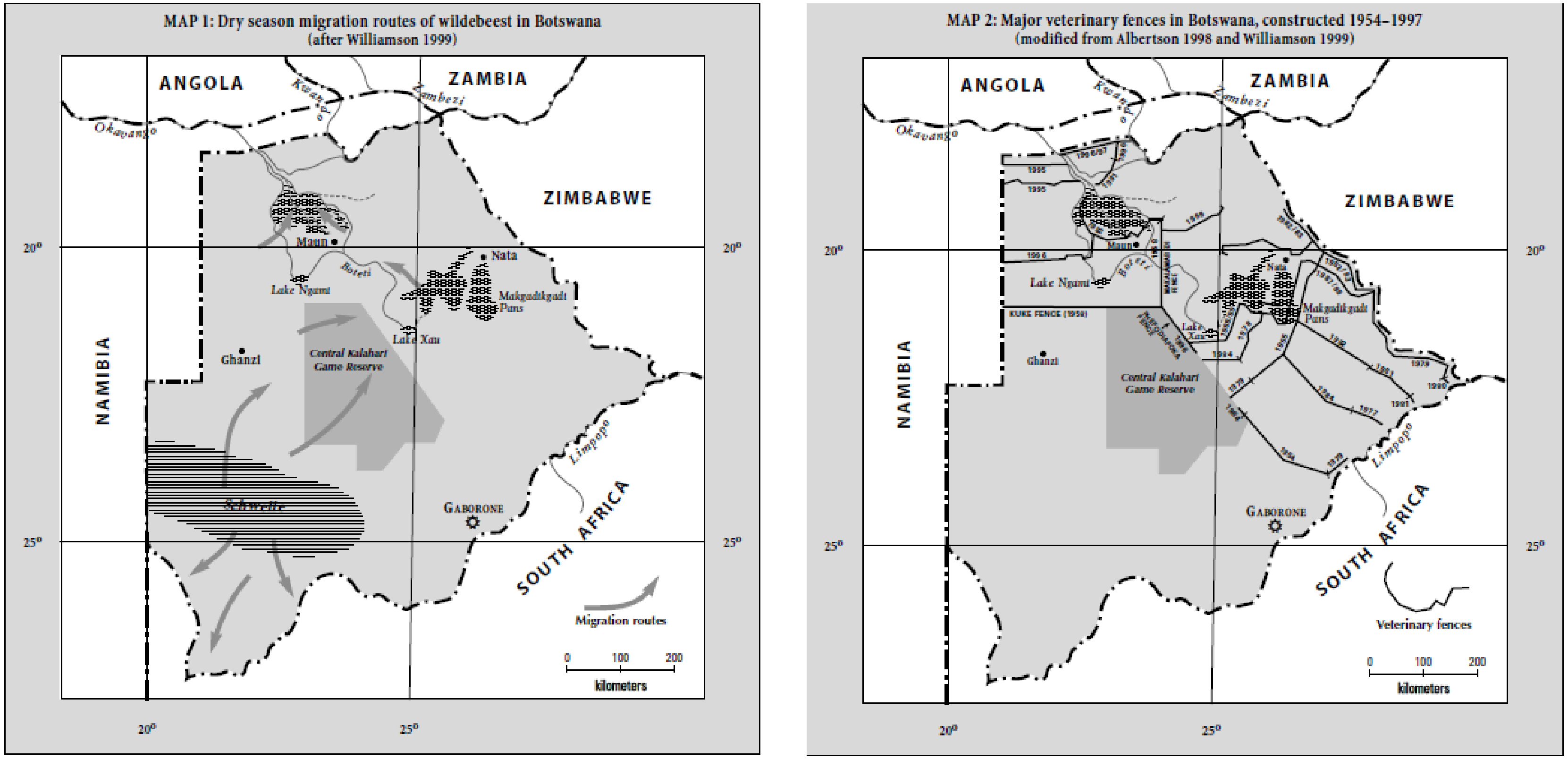

Figure 2.2: Maps of a) dry season nomadic movement routes of wildebeest (*Connochaetes taurinus*) in Botswana (Map 1) and b) major veterinary fences in Botswana, constructed 1954-1997 (Map 2). The hatched areas represent the salt pans. The dates represent year of construction of the fences and the arrows indicate historical migratory routes (adapted from Williamson 2002).

The Kalahari exhibits a south-westerly aridity gradient, with the CKGR experiencing rainfall below 400 mm (Letlhakane rain station; 24°4´S 25°2´E; long-term annual mean 383 ± 130 mm; year 1962-2001; Parida & Moalafhi 2008), and the KTP rainfall below 300 mm (Tsabong rain station; 26°0´S 22°24´E; long-term annual mean 296 ± 128 mm; year 1961-2003; Parida & Moalafhi 2008). The Kalahari has very little free-standing naturally occurring water yet provides considerable scope for animals to exploit spatial heterogeneity in vegetation. It supports a variety of large mammals, such as red hartebeest (*Alcelaphus buselaphus caama*), eland (*Tragelaphus oryx*), springbok (*Antidorcas marsupialis*), blue wildebeest (*Connochaetes taurinus*), gemsbok (*Oryx gazella gazella*), and predators such as lion (*Panthera leo*), leopard (*Panthera pardus*), spotted hyaena (*Crocuta crocuta*) and brown hyaena (*Hyaena brunnea*) mostly within the conservation areas.

2.1.1 Central Kalahari Game Reserve

The Central Kalahari Game Reserve (CKGR) is located in central Botswana and covers an area of 52000 km^2 (Figure 2.3). The CKGR is bordered to the north by the Kuke veterinary cordon fence and to the south by the Khutse Game Reserve. The air temperatures in CKGR range between a maximum of 43 °C in November to a minimum of -6 °C in June (Selebatso et al. 2017a). The climate of CKGR is semi-arid, with between 350 and 400 mm of rainfall per annum (Makhabu et al. 2002; Selebatso et al. 2017a).

The CKGR is a flat land with immobile sand dunes. There are three fossil river systems running across CKGR, namely Deception valley and the adjoining Passage Valley in the north; and Okwa Valley in the centre (Owens & Owens 1978). The soils of the pans are primarily calcrete and clay soils, while the soils outside the pans are predominantly sandy (Makhabu et al. 2002). Artificial water points are randomly located along the fossil river. These water points are supplied by 13 boreholes which were constructed between 1986 and 1990 (Makhabu et al. 2002; Selebatso et al. 2017a). Not all are functional at the same time due to break downs.

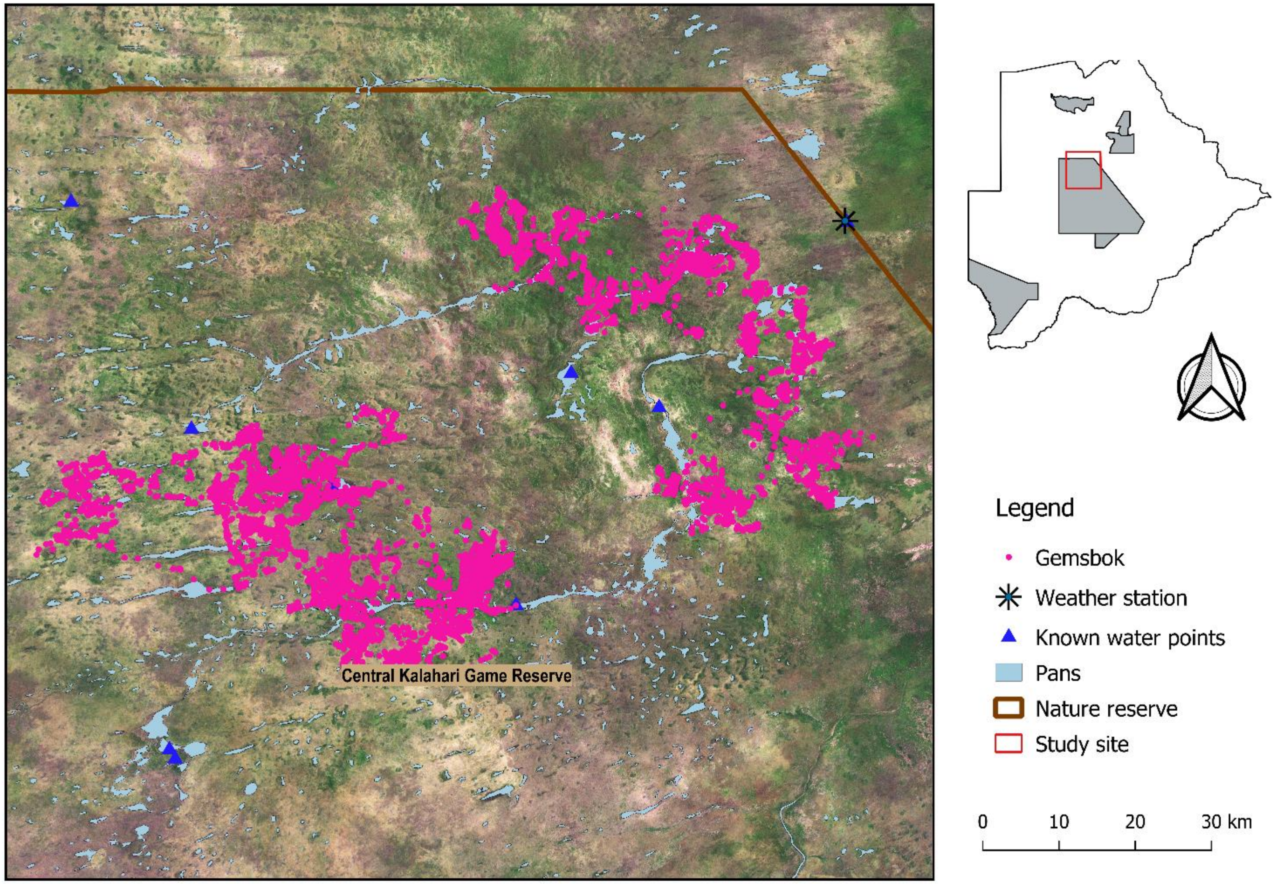

Figure 2.3: Map of the Central Kalahari Game Reserve study area, including regional position (map inset), showing waterholes and pan systems and GPS locations of all eight collared gemsbok herds between November 2012 and July 2013.

The four predominant habitat types are the fossil river valley/pans, dune, interdunal and plain habitats (Makhabu et al. 2002). The vegetation in the river valley/pans is mainly grassland scattered with occasional clumps of trees (Makhabu et al. 2002). The vegetation in the dunes and interdunal habitat consists of woodland, shrub and grassland, while the plains are characterised by mixed shrub and grassland (Makhabu et al. 2002). The dominant woody species are *Lonchocarpus nelsii*, *Vachellia* spp., *Terminalia sericea* with clumps of *Rhigozium* spp. and *Catophractes alexandrii* on pan edges, while dominant grass species include *Stipagrostis* spp., *Aristida* spp., *Eragrostis* spp. and *Schmidtia* spp. (Makhabu et al. 2002).

2.1.2 Bakgalagadi Schwelle

The Bakgalagadi Schwelle region (here after called Schwelle) is the watershed between the Orange River system and channels draining to the north (Thomas & Shaw 1991). It encompasses part of the KTP (Botswana side) and surrounding wildlife management areas, in south-western Botswana (S 24.35°, E 20.62°; Figure 2.4). Air temperature in the Schwelle range between a maximum of 40 °C in November and a minimum of -11 °C in June (Knight 1995). The Schwelle receives most of its rain during summer months and has a rainfall gradient from around 250 mm per annum in the southwest to 350 mm per annum in the northeast, decreasing gradually towards the south (Stapelberg et al. 2007; Fynn & Bonyongo 2011). The relative humidity is low and annual evaporation rate is high (Parris 1984).

One landscape feature, which adds noticeably to the heterogeneity of the area, is the clay-bottomed depressions known as pans. These pans have high mineral levels that attract ungulates and other wildlife (Parris & Child 1973). There is a higher density of saline pans in the Schwelle than in the KTP or CKGR. Owing to the sandy substrate and the high evapotranspiration rates, little free-standing water occurs naturally within this area (Knight 1995). Several artificial waterholes were constructed since 1936 throughout the nature reserve (KTP) with many being placed around the riverbeds. Water in the boreholes is often highly mineralized

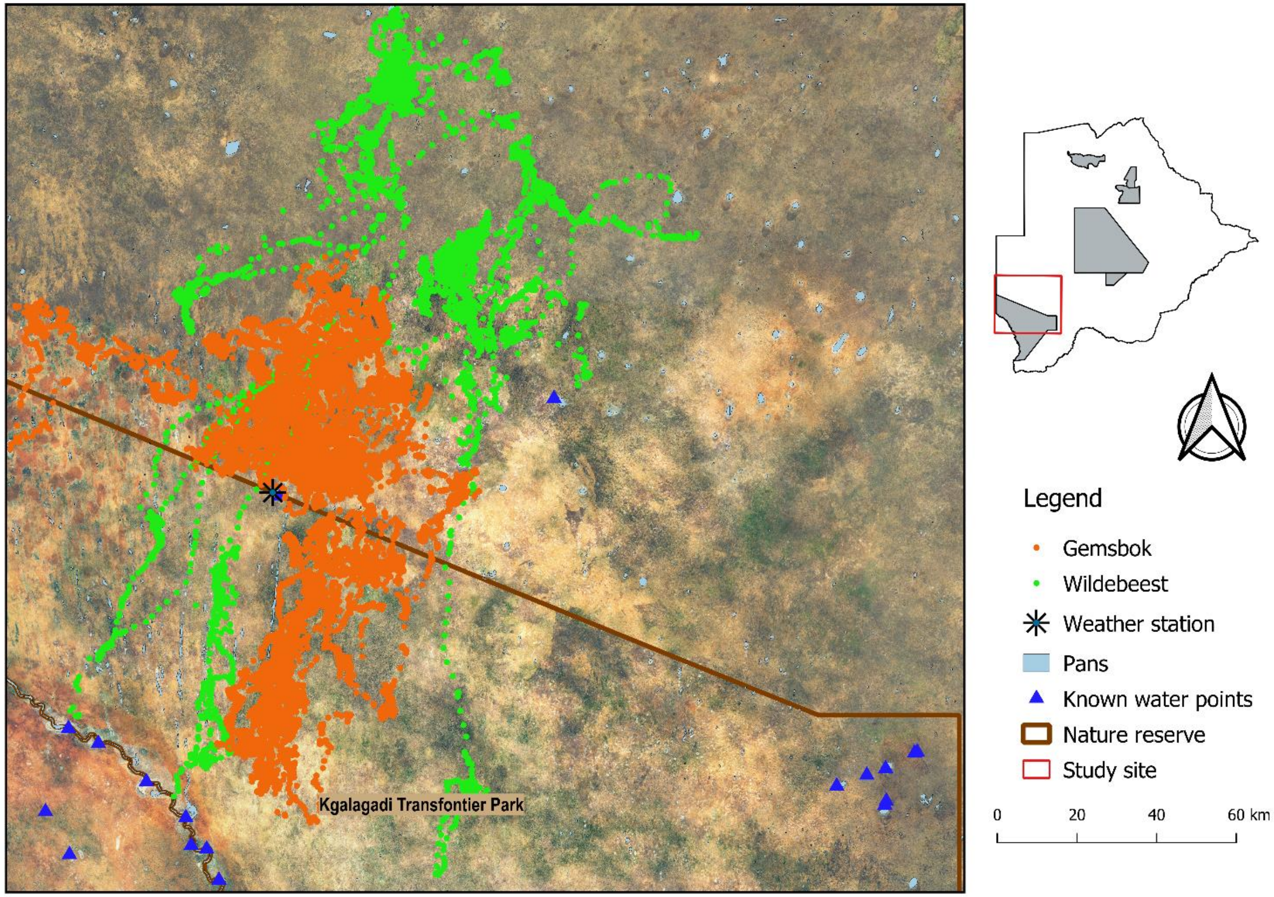

Figure 2.4: Map of the Bakgalagadi Schwelle study area, including regional position (map inset), showing waterholes and pan systems and movement locations of all eight collared gemsbok herds (orange dots) and all eight collared wildebeest herds (green dots) between October 2013 and February 2015.

and the quality of the borehole water varies greatly which may affect its potability (Parris 1984).

The vegetation is mostly an open shrub savanna with scattered trees (Acocks 1979), becoming increasingly more open down the rainfall gradient towards the south-western section of the park (Knight 1995). More specifically the vegetation differs between sand types. The incipient pans, salt pan fringes and riverine habitats have short steppe-like grasslands with large *Vachellia erioloba* and *V. haematoxylon* trees (Knight 1995). The dunes are more open with smaller *V. erioloba,* Tsama melons (*Citrullus lanatus*)*, V. haematoxylon* and *Boscia albitrunca* trees, and tall perennial grasses. Further north-east, some broad leafed mainly deciduous woody species such as *Terminalia sericea* and *Lonchocarpus nelsii* occur, but deciduous, microphyllous species generally dominate (Skarpe 1986). Dominant species throughout the study site included trees: *Vachellia erioloba*, *Vachellia luederitzii*, *Boscia albitrunca* and *Terminalia sericea*; shrubs: *Grewia flava* and *Senegalia mellifera*; and grasses: *Schmidtia kalahariensis* and *Stipagrostis uniplumis* (van Rooyen et al. 2008; Keeping 2014).

2.2 Study animals

The focal ungulate species are two grazers that are dependent on similar food resources but with differing water dependencies: (1) gemsbok, a water-independent species; and (2) blue wildebeest, a less water-independent species (Estes 2013).

2.2.1 Gemsbok

Gemsbok (*Oryx gazella gazella*; Linnaeus 1758) primarily occupy desert and semi-desert habitats, with their distribution range extending into open savanna and bush savanna (Figure 2.5; IUCN 2008). The gemsbok is often cited in scientific literature as the epitome of large mammal arid adaptation (Maloney et al. 2002). Hypothetically, gemsbok are able to survive independently of drinking water because of their specialized adaptations, i.e., reduced metabolism, low evaporation rates, a flexible body temperature and the use of water rich underground tubers (Knight 1991). However, metabolic rates and evaporation rates have not been measured in free-ranging gemsbok. Only one previous study has looked at body temperature of free-living gemsbok (Maloney et al. 2002) and it was limited to a two month period. The gemsbok were placed in a 62-ha enclosure and had free access to food and water. The dry-bulb air temperature varied from an average of 15 °C at night to 25–30 °C during the day. Gemsbok peak body temperatures did not coincide with peak environmental heat load, but in general body temperatures increased during the day and decreased during the night with amplitude that did not exceed 2.2 °C. In contrast to the 6 °C amplitude in body temperature rhythm reported for captive dehydrated gemsbok (Taylor 1969), free-living gemsbok did not display heterothermy (i.e., a large fluctuation in body temperature rhythm). Gemsbok select succulent plant parts because of their narrow muzzle and obtain majority of their water requirements by eating water rich melons and tubers and by feeding predominantly in the cooler mornings and evenings during the dry season (Knight 1991, 1995; Knight 2013). Also, gemsbok spend about 50% of their time resting and 40% of their time stationed under shade, thus reducing their heat loads by seeking shade and reducing their diurnal locomotor activity during the hot season (Knight 1991; Knight 2013).

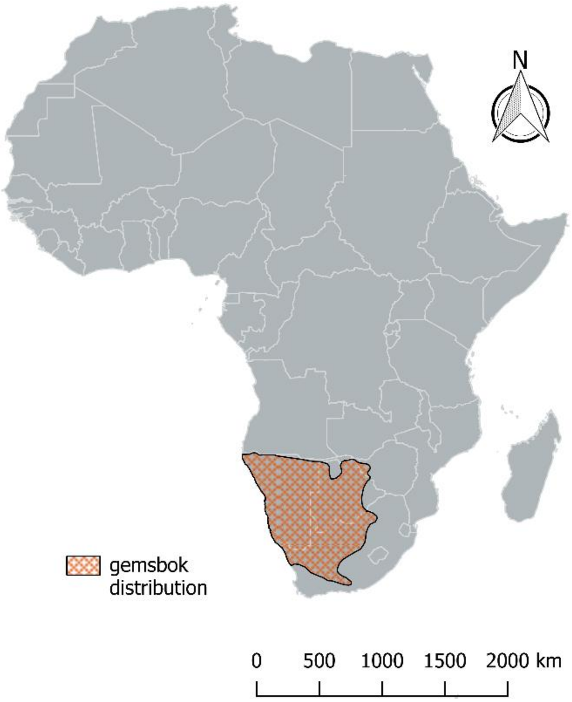

Figure 2.5: Current distribution map of gemsbok (*Oryx gazelle gazella*; adapted from IUCN 2008)

2.2.2 Blue wildebeest

Blue wildebeest (*Connochaetes taurinus*; Burchell 1823) constitute a pivotal species because they are considered as one of Africa’s most abundant game species at present and are widely distributed throughout southern and eastern Africa (Figure 2.6; Estes 2013). As one of the more water-dependent ungulates in the Kalahari, wildebeest can go without drinking water for several days if they can gain enough water from green forage or high-water content plants (e.g., tsamma melons (*Citrullus lanatus*)), but they need to drink every other day when grass becomes dry during the dry season (Berry 1980; Estes 2013). This dependence on water and high-quality mineral rich grass has lead wildebeest to move between wet and dry season ranges, as observed in the great migration of wildebeest in the Serengeti ecosystem (Murray 1995; Wilmshurst et al. 1999). Consequently, because the erection of fences has restricted historical movement routes between wet and dry season ranges (Figure 2.2), wildebeest of the Kalahari have declined drastically since 1983, because of restrictions on movements between wet and dry season ranges (Fynn & Bonyongo 2011; Owen-Smith & Ogutu 2012). Since the erection of fences (Figure 2.2b), wildebeest have been prone to periodic large-scale die-offs during severe droughts, whereby many carcasses were found along the fences (Child 1972; Parry 1987). For example, the 1983 drought led to a population collapse of more than 52 000 animals (Figure 2.2b; Williamson & Mbano 1988; Owen-Smith & Ogutu 2012).

Blue wildebeest prefer open grassland and bush savanna, but also inhabit sparse woodland (Estes 2013). Blue wildebeest are primarily diurnal with crepuscular peaks in activity during the morning and late afternoon (Knight 1991). However, they do exhibit seasonal differences in the times and duration of activities which correlate with daytime temperatures, spending more time feeding and less time resting in the cool dry season than in the hot dry season (Knight 1991). Blue wildebeest, like gemsbok, are primarily grazers however they have a higher component of grass in their diet compared to other grazers so are considered as hypergrazers (Estes 2013).

Figure 2.6: Current distribution map of blue wildebeest (*Connochaetes taurinus*; adapted from IUCN 2016)

Behavioural mechanisms such as reduced diurnal activity and shade-seeking behaviour may help large mammals to conserve water during summer. Blue wildebeest reduce their activity when it gets hot (Knight 1991). In addition, blue wildebeest are believed to exhibit a higher degree of shade-seeking behaviour compared to other ungulate species, as they are thought to have a low thermal tolerance (Berry et al. 1984). When ambient temperatures exceeded 35ºC, blue wildebeest spent more than half the day in the shade, potentially sacrificing valuable foraging time (Berry et al. 1984; Estes 2013). Although the blue wildebeest shade use increased when temperatures exceeded 35°C in the southern Kalahari, they did not venture far from the available drinking water which may have enabled them to use evaporative cooling to easily dissipate environmental heat load (Knight 1991). Yet, water is generally lacking in the Kalahari and it has been proposed that blue wildebeest inhabiting this environment go for years without drinking if they had access to tsamma melons (Estes 2013; Selebatso 2017).

One previous study in Mapungubwe National Park and Asante Sana Game Reserve in South Africa recorded body temperatures of free-living blue wildebeest (Shrestha et al. 2011). During the dry season when forage was assumed to have been limited, 24 h body temperature amplitudes of 3.5 °C were recorded for blue wildebeest, with low minimum body temperatures of 36 °C, resulting in starvation-induced hypothermia (Shrestha et al. 2011). However, the authors argued that the low morning body temperatures occurred at a time when low energy availability and low ambient temperatures coincided, therefore, they cannot say for certain that it was the ambient temperatures or the insufficient forage that drove the low minimum body temperatures (Shrestha et al. 2011). This response suggests that blue wildebeest may be incapable of tolerating the periods of poor forage quality which occurs during the Kalahari dry season.

2.3 Data collection

Data collection spanned 30 months (November 2012 to April 2015), split into two data collection periods based on the field site, namely CKGR data collection

(November 2012 to July 2013) and Schwelle data collection (August 2013 to April 2015).

2.3.1 Weather measurements

I collected weather data from two portable weather stations (HOBO Weather Logger [H21-001], Onset Computer Corporation, USA) erected at Kalahari Plains Camp, CKGR (S 21.49°, E 24.01°) and at Kaa gate, KTP (S 24.3°, E 20.6°) for the duration of the study periods. The weather stations recorded wind speed (m s^{-1}), solar radiation (W m^{-2}), and black globe temperature (°C) every hour. Free-standing miniglobes were placed in direct sun, 1 m above ground, which recorded miniglobe temperature (°C) every hour by a temperature data logger (Hobo, Onset Computer Corporation, Pocasset, MA, USA) for the duration of the study periods (Schwelle: S 24.35 °, E 20.62 °; CKGR: S 21.61 ° E 24.04 °). Other climatic data (including dry-bulb air temperature (°C) and rainfall (mm)) were obtained from the Agricultural Research Council weather station located at the Nossob campsite (S 25.4°, E 20.6°) for Schwelle and from the Central Kalahari Game Reserve Office at Matswere gate for CKGR (S 21.26 °, E 24.12 °).

2.3.2 Animals

Eight female gemsbok in the northern section of CKGR and eight female gemsbok and eight female blue wildebeest in the Schwelle region were collared with GPS collars in November 2012 and August 2013 respectively (Figure 2.7). The individuals were all from different herds. Each collared individual underwent surgery to implant temperature-sensitive and motion-sensitive data loggers. I selected females as representatives of both species because they tend to travel together in herds which may give a better representation of the population.

Figure 2.7: Photo of gemsbok (a) and blue wildebeest (b) taken on site once animals were collared before release.

2.3.3 Surgical procedures

A veterinarian experienced in game capture darted all 24 individuals from a helicopter and surgery was performed where the animal fell. Each dart had a combination of thiafentanil (gemsbok: 7-8 mg, wildebeest: 4-6 mg, Thianil, Kyron Laboratories, Johannesburg, South Africa), medetomidine hydrochloride (gemsbok: 3-6 mg, wildebeest: 2-4 mg, Medetomidine, Kyron Laboratories, Johannesburg, South Africa) and ketamine (gemsbok: 75-150 mg, wildebeest: 50-150 mg Pfizer Animal Health, Sandton, South Africa). Once immobile, the animals were placed in sternal recumbency, supported by sandbags, with their heads elevated. They were intubated, and anaesthesia was maintained with 2–5% isoflurane (Aerrane, Astra Zeneca, Johannesburg, South Africa), administered in 100% oxygen. Respiratory rate, heart rate, arterial oxygen saturation, and rectal temperature were monitored throughout the surgery which lasted approximately 30 - 45 mins.

For measurement of body temperature and activity, miniature temperature-sensitive data loggers were inserted in the retroperitoneal space and motion-sensitive data loggers were tethered to the abdominal muscle wall. The data loggers were covered with biologically and chemically inert wax (Sasol, Johannesburg, South Africa) and sterilised with instant sterilant (F10 Sterilant with rust inhibitor, Health and Hygiene (Pty) Ltd., Roodepoort, South Africa) before implantation. Incision sites were shaved and sterilised with chlorhexidine gluconate (Hibitane, Zeneca, Johannesburg, South Africa). A local anaesthetic (3 ml 2% subcutaneously (S.C.); lignocaine hydrochloride, Bayer Animal Health (Pty) Ltd., Isando, South Africa) was administered to the incision site. Once the loggers were in place, the incision was sutured closed.

Wounds were treated with a topical antiseptic spray (Necrospray, Bayer (Pty) Ltd., Isando, South Africa) and covered in tick grease (SWAVET tick grease, SWAVET RSA (Pty) Ltd., Northriding, South Africa). The animals received a long-acting antibiotic (~0.04 ml kg^{-1}, intra muscular (I.M.), penicillin, Duplocillin La, Schering-Plough Animal Health Ltd., New Zealand), and a non-steroidal anti-inflammatory analgesic (~0.5 mg kg^{-1} I.M., Metacam, Meloxicam injectable solution, Boehringer Ingelheim Vetmedica, Inc, St. Joseph, U.S.A.). After the surgical procedure, but while the animals were still anaesthetized, an external collar containing 1) a miniglobe thermometer (Hetem et al. 2007; 30 mm diameter hollow copper sphere painted matt black), 2) a satellite-enabled GPS data logger, and 3) a VHF radiotelemetry tracking device was placed around the neck of each animal (see details below). Following surgery and termination of inhalation anaesthesia, the anaesthesia originally administered by the dart was completely reversed by a combination of naltrexone (gemsbok: 75-120 mg, wildebeest: 60-100 mg, I.M. Naltrexone, Kyron Laboratories, Johannesburg, South Africa) and atipamezole (gemsbok: 10-20 mg; wildebeest: 10-15 mg, I.M. Antisedan, Atipamezole hydrochloride, Orion Corporation, Orion Pharma, Finland). Once awake and mobile, the animals were allowed to roam freely as they had previously done and were left undisturbed, apart from the occasional opportunistic visual contact by tourists, rangers and locals, for the entire study period at both sites.

2.3.4 Temperature and activity measurements

Each individual animal was fitted with a satellite-based GPS collar (African Wildlife Tracking, Pretoria, South Africa) with a 12 h on/off VHF radiotelemetry device. In addition, each collar supported a miniature black globe thermometer (“miniglobe”; Figure 2.8), identical to the free-standing miniglobe. A miniglobe thermometer is a small hollow copper sphere that has been painted matt black with a temperature sensor inside. This miniglobe thermometer, attached to the top of the collar, allowed for quantification of the microclimate that the ungulates choose to occupy (Hetem et al. 2007). The miniglobe temperature provides a better index of heat stress than air or collar on the animal as it integrates the effects of air temperature, radiation, and wind speed. Miniglobe temperature and GPS positions were recorded hourly. These miniglobes temperature sensors had a resolution of 0.5 °C and a measurement range from -10 °C to 85 °C and a calibrated accuracy better than 0.5 °C. The total mass of the collar was ~1.2 kg which was ~0.6% of the animal's body mass.

Figure 2.8: A satellite-based GPS collar (African Wildlife Tracking, Pretoria, South Africa) with a 12 h on/off VHF radiotelemetry device, supported a miniature black globe thermometer on top.

The miniature temperature-sensitive data loggers (DST centi-T, Star-Oddi, Iceland) used to measure body temperature had outside dimensions of ~15 x 46 mm (Diameter x Length) and a mass of 20 g when covered with wax (Figure 2.9a). Recorded data was stored on its internal memory with a real-time clock reference for each measurement and had a resolution of 0.032 °C and measurement range from 5 °C to 45 °C and calibrated accuracy better than 0.1 °C. The scan interval of the temperature-sensitive loggers was 10 min. All temperature sensors and loggers were calibrated against a high-accuracy thermometer (Quat 100, Heraeus, Hanau, Germany) in an insulated water bath.

The motion-sensitive loggers (ADXL345, Sigma Delta Technologies, Australia) recorded at 5 min intervals, had dimensions of 35 mm x 35 mm x 10 mm, and weighed 20 g when covered in wax (Figure 2.9b). The motion-sensitive logger had a triaxial accelerometer with equal sensitivity across three planes (resolution ¼ 4 mg/least significant bit) and motion changes were recorded as activity counts within the first 10 seconds of each 5-min interval, similar intervals of 10 seconds at the start of every minute were validated against behavioural observations of vervet monkeys (McFarland et al. 2013). The total mass of equipment implanted and attached to the animals was less than 1% of their body mass and is unlikely to have adversely affected their behaviour.

Figure 2.9: Two different data loggers were implanted into the animals: a) miniature temperature-sensitive data loggers (DST centi-T, Star-Oddi, Iceland) covered in wax (top); (b) motion-sensitive loggers (ADXL345, Sigma Delta Technologies, Australia) covered in wax (bottom) and were tethered to the abdominal muscle wall. A measuring tape is added to indicate relative size. The motion-sensitive loggers were inserted into the retroperitoneal space and the motion-sensitive data loggers were tethered to the abdominal muscle wall.

2.3.5 Data retrieval

In CKGR, of the eight gemsbok initially collared, three individuals died from natural causes (most likely as a result of predation). Using the VHF beacon I was able to locate their remains and recover all three collars, but I was only able to salvage one of the implanted temperature data loggers as the other loggers were not with the remains anymore. Three of the surviving gemsbok were located and redarted from a helicopter in May 2014, following the same procedures as the original capture. The animals were anaesthetized, and the data loggers were removed under a surgical procedure similar to that used for the original implantation. The original wounds had healed and all individuals were infection free from the initial surgery. The animals were released after all the monitoring equipment was removed. The remaining two gemsbok could not be found as a result of the VHF radio telemetry on the collars stopping prematurely. Hence, of the eight gemsbok originally collared in the CKGR, I recovered nine months of GPS data for seven gemsbok, nine months of activity data for three individuals, and 18 months of body temperature data for three individuals and nine months of body temperature data for one individual (see Appendix 1).

In the Schwelle, a technical glitch stopped all the collars in the last week of August 2013, but we were able to replace the collars in the last week of September 2013. Of the eight gemsbok initially collared, three died in October 2013 due to possible predation and their remains were located but no loggers were found. Of the eight original wildebeest two were also never relocated due to failed VHF radio telemetry and/or possible predation. The remaining 11 animals were tracked and redarted from a helicopter in May 2015, as per the original capture. Once again, the animals were anaesthetized, and the data loggers were removed under a surgical procedure similar to that used for the original implantation. The animals' wounds had healed and there were no signs of infection from the initial surgery. After removal of all monitoring equipment, the animals were released. Out of 11 (five gemsbok and six wildebeest) individuals recaptured in Schwelle, all of the loggers were explanted. Eleven internal body temperature loggers (gemsbok: five, wildebeest: six); seven internal motion-sensitive loggers (gemsbok: four; wildebeest: three); and seven miniglobe temperature sensors from the external collars (gemsbok: five; wildebeest: two) had recorded data for all 15 months (see Appendix 2). I excluded two wildebeest that only recorded body temperature from the analysis. GPS data from the collars (five gemsbok and two wildebeest) was retrieved via satellite that had recorded continuous data for all 15 months (see Appendix 2).

2.4 Permits and ethics

The Government of Botswana via the Ministry of Environment, Wildlife and Tourism and Department of Wildlife and National Parks granted approvals and permits (numbers EWT 8/36/4 XX (32), EWT 8/36/4 XXVII (15), EWT 8/36/4

XXIV (102)) to conduct the study within this publicly owned, partially protected area. The Animal Ethics Screening Committee of the University of the Witwatersrand (protocol no. 2012/24/04) approved all experimental procedures (Appendix 3).

CHAPTER 3

Seasonal variation in behavioural and thermoregulatory responses of two sympatric free-ranging ungulates with differing water dependencies in the semi-arid Kalahari.

3.1 Abstract

Large herbivores that live in semi-arid ecosystems respond to seasonal changes in temperature and precipitation by phenotypic flexibility in behavioural and physiological responses, such as shade seeking, reduction in diurnal activity and foraging at night. Such behavioural changes may not be sufficient to buffer seasonality and may result in seasonal changes in body temperature. To test whether behavioural responses and body temperature differed between two sympatric ungulate species living in a semi-arid system, I used biologgers to assess microclimate selection, activity and body temperature of the arid-adapted gemsbok (*Oryx gazella gazella*) and water dependent blue wildebeest (*Connochaetes taurinus*), free-living in the Kalahari. Both species prioritised behavioural thermoregulation during the hot periods by selecting cool microclimates during the heat of the day and sought shade at low air temperatures when conditions were dry. In addition, both species reduced diurnal activity and increased nocturnal activity when conditions where hot, but seemingly were unable to compensate for reduced diurnal activity i.e., both species showed a decreased 24 h activity when conditions were hot and dry compared to when conditions were hot and wet. Both species experienced high maximum 24 h body temperature when conditions were hot and low minimum 24 h body temperatures when conditions were dry, resulting in a large amplitude of 24 h body temperature rhythm during the hot dry period. Yet, wildebeest appeared to be more sensitive to changes in aridity, with a larger amplitude of 24 h body temperature rhythm compared to gemsbok (3.14 ± 0.23 °C vs. 2.11 ± 0.55 °C), during the drought. The heterothermy employed by ungulates in the Kalahari suggest that water and forage availability may be driving those responses.

3.2 Introduction

Seasonal environments show fluctuations in weather conditions, such as ambient temperature and precipitation, on an annual basis. These fluctuations in weather conditions impact the vegetation phenology and quality (Skarpe & Bergström 1986; van der Wal et al. 2000, Gedir et al. 2016). The population success of large mammalian herbivores is strongly linked to the seasonal changes in food quality

(Pettorelli et al. 2005a) and substantial inter-annual variability in the timing of vegetation growth (Owen-Smith 2008a). The complexity of these seasonal ecosystems is exacerbated by the unpredictability of rainfall on an intra and inter-annual basis (Batisani & Yarnal 2010). Since rainfall is mostly constrained to summer months, semi-arid savannas of southern Africa represent a highly stressful environment with limited water resources and extreme temperatures (Makhabu et al. 2002; Bergström & Skarpe 1999). Winters are generally characterized by low ambient temperatures and poor food quality (Knight 1991), leading to increased energetic demands at a time when resources are diminished (Owen-Smith 2008b). Climate change may result in less predictable rainfall and if the first rains of the wet season are delayed then species are likely to be concurrently exposed to high ambient temperatures, poor forage quality and limited access to water during the late dry season (Owen-Smith 2008b; Fynn 2012). Species have already shown phenotypic flexibility to exploit these environments, but additional flexibility will be required to survive changing climates in the future (Hetem et al. 2014; Fuller et al. 2016).

Flexible behaviours such as shade-seeking reduces radiant heat loads (Cain et al. 2008; Hetem et al. 2007) but seeking shade may be traded against diurnal foraging (Fuller et al. 2016). Some (but not all) species may compensate for a decline in diurnal foraging by foraging at night (Green & Bear 1990; Hetem et al. 2012a). Foraging at night could potentially increase preformed water in their diet as the plants have a higher water content at that time (Taylor 1968a; Nagy & Knight 1994; Cain et al. 2006). However, being active at night may increase the risk of predation (Godvik et al. 2009; Hebblewhite & Merrill 2009; Hetem et al. 2012a) or the duration of cool nocturnal periods may not be sufficiently long to compensate for reduced diurnal foraging, resulting in a reduction in the animal's total 24 h activity (Hetem et al. 2012a; Fuller et al. 2016). If species are unable to compensate for a reduced diurnal foraging, a negative energy balance may result in a drop in minimum body temperature (Maloney et al. 2011; Tattersall et al. 2012). If species are unable to maintain a positive water balance an increase in maximum body temperatures may result (Hetem et al. 2010; Tattersall et al. 2012). Low minimum and high maximum body temperatures may conserve body water by reducing evaporative water loss during the day and storing heat, that heat can then be dumped non-evaporatively during the night when ambient temperatures fall below body temperature (Tattersall et al. 2012), a concept of adaptive heterothermy (Mitchell et al. 2002; Grigg et al. 2009). Whether these changes in body temperature are adaptive or a response to environmental stress has been debated (Hetem et al. 2016).

These responses are unlikely to be identical across species inhabiting the same environment; responses may even be more exaggerated for water dependent species. Compared to the famously water independent gemsbok (*Oryx gazella gazella*), the water dependent blue wildebeest (*Connochaetes taurinus*) seeks shade more frequently (Berry et al. 1984) and is more reliant on green grass (Knight 1991), which may explain recent population declines in wildebeest populations during a drought in the Kalahari (Ogutu et al. 2011; Owen-Smith & Ogutu 2012). Yet, the arid-adapted gemsbok is often reported to display heterothermy (i.e., a large fluctuation in 24 h body temperature) and survive high body temperatures, but that idea stems from a single laboratory study (Taylor 1969). The only study to look at body temperature (and selective brain cooling) in free-living gemsbok (Maloney et al. 2002) found no evidence for heterothermy when animals had free access to water. I therefore set out to measure microclimate selection, activity and body temperature in a water dependent and independent species inhabiting the same semi-arid environment.

More specifically, I set out to (1) determine if there are seasonal differences in microclimate selection, activity, and body temperature between the arid adapted gemsbok and the similarly-sized water dependent blue wildebeest within a typical year in the Kalahari; and (2) determine the inter-annual variability in microclimate selection, activity, and body temperature of gemsbok and blue wildebeest during two hot dry periods in which ambient temperatures were similar but rainfall patterns varied. In respect to the first objective, regarding microclimate selection, I expect that (a) when ambient temperatures are high, both species will reduce heat loads by actively seeking cool microclimates more frequently than during the cooler seasons; the response may be exaggerated when it’s dry, in an attempt to conserve water and reduce evaporative cooling. I expect that (b) during the hot periods, both species will decrease their diurnal activity with a compensatory increase in nocturnal and/or crepuscular activity without compromising total 24 h activity. Regarding body temperature, I expect that (c) during dry periods both species would decrease their minimum 24h body temperature as a response to low forage compared to wet periods; (d) during the hot and dry periods both species would increase maximum 24h body temperature as a response to a lack of water compared to hot and wet periods when species could employ evaporative cooling to maintain homeothermy. For the second objective I expect that during the drought, the response will be more exaggerated for wildebeest than gemsbok, with wildebeest selecting cooler microclimates more efficiently (i.e., select cooler microclimates at lower ambient temperatures and more frequently) and will show a larger fluctuation in their body temperature compared to gemsbok.

3.3 Materials and methods

3.3.1 Study area

The study took place within a region of south-western Botswana, encompassing the Kgalagadi Transfrontier Park (Botswana side) and surrounding wildlife management areas commonly known as the Bakgalagadi Schwelle region (S 24.35°, E 20.62°). This area primarily consists of open semiarid savanna, overlying a sandy substrate with hardly any free-standing water except momentary after rains. One landscape feature, which adds noticeably to the heterogeneity of the area, is the clay-bottomed depressions known as pans. Vegetation of the pans is completely different to the off-pan savannas. There are no trees on the pans and grasses are short saline tolerant species such as *Sporobolus ioclados* (Selebatso 2017). These pans have high mineral levels that attract ungulates and other wildlife (Parris & Child 1973). This area boasts a number of large mammal species (refer to chapter 2). Dominant vegetation species include trees: *Vachellia erioloba*, *Vachellia luederitzii*, *Boscia albitrunca* and *Terminalia sericea*; shrubs: *Grewia flava* and *Senegalia mellifera*; and grasses: *Schmidtia kalahariensis* and *Stipagrostis uniplumis* (van Rooyen et al. 2008; Keeping 2014). Air temperatures fluctuate seasonally, with temperatures over and above 40 °C in summer, and cool, generally frost-free winters reaching below 1 °C in winter (Knight 1991). Rainfall is irregular, falling primarily during short-duration, high-intensity thunderstorms between November and May. The average annual rainfall for the Bakgalagadi Schwelle region is 250 mm – 350 mm (Fynn & Bonyongo 2011), decreasing gradually towards the south. Humidity is low, and evaporation is high (Parris 1984), the latter resulting in the characteristic large deficit in the annual water budget of the environment (Van Rooyen 1984).

3.3.2 Data collection

Eight individual female gemsbok and eight individual female blue wildebeest, each from separate herds, were captured within the study area in August 2013 and fitted with GPS collars (African Wildlife Tracking, Pretoria, South Africa). Each collar supported a miniature black globe ("miniglobe") thermometer. A miniglobe thermometer is a small (30 mm diameter) hollow copper sphere that has been painted matt black with a temperature sensor inside it. This miniglobe thermometer, attached to the top of the collar, allowed for quantification of the microclimate that the ungulates choose to occupy (Hetem et al. 2007). Miniglobe temperatures were recorded hourly. In addition, each individual underwent surgery to implant miniature temperature-sensitive data loggers in the retroperitoneal space and motion-sensitive data loggers tethered to the abdominal muscle wall, following the procedures outlined in chapter 2. The miniature temperature-sensitive data loggers (DST centi-T, Star-Oddi, Iceland) recorded body temperature at 10 min intervals and the motion-sensitive data logger (ADXL345, Sigma Delta Technologies, Australia) recorded at 5 min intervals. Locomotion was recorded as activity counts within the first 10 seconds of each 5-min interval. For more details on calibrations and accuracy of temperature-sensitive and motion-sensitive data loggers refer to chapter 2.

3.3.3 Weather data measurements

I collected weather data from a portable weather station (HOBO Weather Logger [H21-001], Onset Computer Corporation, USA) erected at Kaa gate, Kgalagadi Transfrontier Park (S 24.3 °, E 20.6 °). The weather station recorded wind speed (m s^{-1}), solar radiation (W m^{-2}), and black globe temperature (°C) every hour. A free-standing miniglobe was placed in direct sun and recorded temperature (°C) every hour (reference globe). Dry-bulb air temperature (°C) and rainfall (mm) data were obtained from Agricultural Research Council (ARC) weather station located at the Nossob campsite (S 25.4 °, E 20.6 °).

3.3.4 Data analysis

Based on animal deaths and inability to relocate animals, I analysed data from nine (five gemsboks and four wildebeest) internal body temperature loggers; six (three gemsboks and three wildebeest) internal motion sensitive loggers; and seven (five gemsboks and two wildebeest) miniglobe temperature sensors from the external collars (see Appendix 2 for details). The data collected expanded 21 months, from August 2013 until May 2015. August and September 2013 were not included in my analysis to allow for post-surgical recovery. I did not include data from December 2014 onwards as many of the activity data loggers and collars stopped recording prematurely because of technical failure. Fifteen months (September 2013 to November 2014) of data were used in the analyses.

For analysis of seasonal patterns, I subdivided data from the 15-month study period into five seasonal periods consisting of three months each, namely ‘first hot dry’ (September to November 2013), ‘hot wet’ (December 2013 to February 2014), ‘transitional wet’ (March to May 2014), ‘cold dry’ (June to August 2014), and ‘hot dry’ (September to November 2014). Because the ‘first hot dry’ period occurred at the end of a prolonged dry period, I termed this period ‘drought’. I therefore omitting this drought period in the initial seasonal analysis and compared ambient conditions across one full year of data beginning from December 2013 till November 2014. I averaged mean, maximum and minimum black globe temperature, maximum and minimum air temperature, mean solar radiation and mean wind speed over successive 24 h periods and compared seasonal periods using a one-way analysis of variance (ANOVA) and Tukey’s multiple comparisons tests to identify sources of differences. I then assessed inter-annual variability by using an unpaired t-test to compare the ambient conditions during the drought (September to November 2013) and hot dry (September to November 2014) periods.

To quantify microclimate selection, I calculated the difference between miniglobe temperature on the collar and an identical miniglobe located on the weather station in the sun per hour per individual animal. I calculated the mean temperature differences per hour across each seasonal period and averaged these per species to get the 24h rhythm of microclimate selection. To test whether there was a species and seasonal difference in quality of shade sought, I compared the minimum 24 h difference between the collar and weather station miniglobe (reference globe) temperature (i.e., the coolest microclimate sought) between species and across periods with two-way repeated measures ANOVA and identified any sources of differences with Tukey's multiple comparisons tests. To assess the efficacy of shade seeking, I correlated collar miniglobe temperatures against weather station miniglobe temperatures per individual animal using linear Pearson procedures and tested whether the slope of the regression equation was significantly different from the slope of line of identity (slope = 1). A slope of one implies no thermoregulatory behaviour (no selection of microclimates i.e., consistent exposure to sun) whereas a slope of zero implies that the microclimates experienced were independent of ambient temperatures in the sun (Hetem et al. 2007). In addition, I tested whether the slopes of the regression equations were significantly different between the gemsbok and wildebeest across the seasonal periods, using two-way repeated measures ANOVA. Tukey's multiple comparisons posthoc test was used to identify sources of differences. The temperature at which each individual began seeking shade was calculated as the temperature at which the regression line intersected with the line of identity. This temperature threshold was compared between species and across seasonal periods with two-way repeated measures ANOVA and Tukey's multiple comparisons posthoc test.

To assess the 24h rhythm of activity, I calculated hourly activity per individual and averaged these across each seasonal period per species. For consecutive 24 h periods, I calculated the total 24 h activity per individual and averaged these for each individual per season. I compared the species across seasonal periods with a two-way repeated measures ANOVA with Tukey’s multiple comparison posthoc test. To assess the diel activity patterns of each individual animal, I portioned the total 24 h activity into three-time periods and defined them as ‘proportion of diurnal activity’ from 07:00 to 17:00, ‘proportion of crepuscular activity’ from 05:00 to 07:00 and from 17:00 to 19:00, and ‘proportion of nocturnal activity’ from 19:00 to 05:00 the following day. These three time periods were expressed as a proportion of total 24 h activity. I kept the time periods consistent across seasons to avoid bias in changing time periods and sunrise/sunset occurred within the crepuscular periods throughout all seasons. To test whether the proportion of diurnal activity differed between species and across seasonal periods, I averaged the proportion of diurnal activity per individual per seasonal periods and compared it between species across seasonal periods with a two-way repeated measures ANOVA with Tukey’s multiple comparison posthoc test. I repeated the same analysis with proportion of crepuscular activity and proportion of nocturnal activity.

For the 24 h rhythm of body temperature, I averaged body temperature per 10 minutes of the day per individual per seasonal periods and averaged across species. For successive 24 h periods, I calculated mean, minimum, maximum and amplitude (maximum minus minimum) of the 24 h rhythm of body temperature for each individual animal. I averaged the body temperature parameters for each individual, for each period and compared species across seasonal periods with a two-way repeated measure ANOVA and Tukey’s multiple comparisons posthoc tests.

To compare the inter-annual variability in species responses I ran a series of two-way repeated measures ANOVAs with Tukey’s multiple comparisons posthoc tests across the two hot dry periods. Statistical analyses were performed using GraphPad Prism (version 6.00 for Windows, GraphPad Software, San Diego, CA, USA). Values are expressed as mean and standard deviation and $p < 0.05$ was considered significant.

3.4 Results

3.4.1 Weather

The wet season from November 2012 till March 2013, five months before the study commenced, accumulated a total of 202 mm of rain within 31 days over a five-month period, lower than the long term mean which is usually between 250 mm – 350 mm (Fynn & Bonyongo 2011). Most of that rain (57% or 115 mm) fell on seven consecutive days at the end of March 2013 (Figure 3.1). This rainy season was then followed by a long dry period of roughly seven months (April till October 2013) wherein less than 5 mm of rain fell. My study was initiated during this prolonged dry season. The following wet season commenced in November 2013 and ended in May 2014. This seven-month wet season accumulated a similar amount of rain to the previous year (total of 203 mm of rain) but the rainfall events were more evenly distributed across the 7 months with 42 days of rain, wherein 65% (132 mm) of that rain was spread over 25 days within three months (December, January, and February) of that year. The following dry season was roughly five months (June till October 2014) with a few rainfall events totalling 5 mm during August and September 2014. Therefore, the first hot dry season of my study period occurred at the end of a seven month (April till October 2013) dry spell (drought) whereas the second hot dry season occurred following a more typical dry spell expanding across five months (June till October 2014). Rainfall totalled 223 mm over the entire study period, from September 2013 till November 2014.

Monthly air temperatures show similar seasonal fluctuations in 2013 and 2014 (Figure 3.1). During the study period, air temperature at Nossob campsite reached a maximum of 49 °C in November 2013 and November 2014 and dropped to as low as −9 °C in July 2014 giving a range of air temperatures of 58 °C across the year. The minimum air temperatures usually occurred before dawn (04:00– 07:00) and the maximum air temperatures usually occurred in the afternoon (14:00–17:00). The mean ($F_{3,361}$ = 10.8, p = 0.008), maximum ($F_{3,361}$ = 8.6, p = 0.014) and minimum ($F_{3,361}$ = 16.6, p = 0.003) 24 h black globe temperature in the hot periods (hot wet and hot dry) was significantly hotter than the cold dry period and the minimum 24 h black globe temperature in the transitional wet period was significantly hotter than the cold dry period. On average, during the two hot seasons' (hot wet and hot dry) ambient temperatures were ~ 10 °C hotter than during the cold dry period. Minimum ($F_{3,361}$ = 12.6, p = 0.005) and maximum ($F_{3,361}$ = 13.4, p = 0.004) air temperature show similar seasonal differences where the hot periods were significantly higher than the cold dry period but the transitional wet period did not differ compared to the other three seasons (Table 3.1). The mean 24 h solar radiation ($F_{3,361}$ = 6.8, p = 0.023) was higher in the hot wet period compared to the cold dry period. Mean 24 h wind speed ($F_{3,361}$ = 3.7, p = 0.083) did not differ across seasons (Table 3.1). When comparing inter-annual variability in weather conditions during the two hot dry periods, mean (t_{180} = 0.07, p = 0.94), minimum (t_{180} = 1.67, p = 0.10) and maximum (t_{180} = 0.75, p = 0.46) 24 h black globe temperatures, minimum (t_{180} = 1.05, p = 0.29) and maximum (t_{180} = 0.42, p = 0.67) 24 h air temperature, solar radiation (t_{180} = 0.83, p = 0.45) , and wind speed (t_{180} = 1.21, p = 0.23) did not differ (Table 3.1), however, the two periods differed in the amount of rain received and the number of days of rain doubled from drought to hot dry period. Even though the inter-annual hot dry periods did not differ in ambient temperatures, the drought period followed a particularly long dry season compared to the hot dry period.

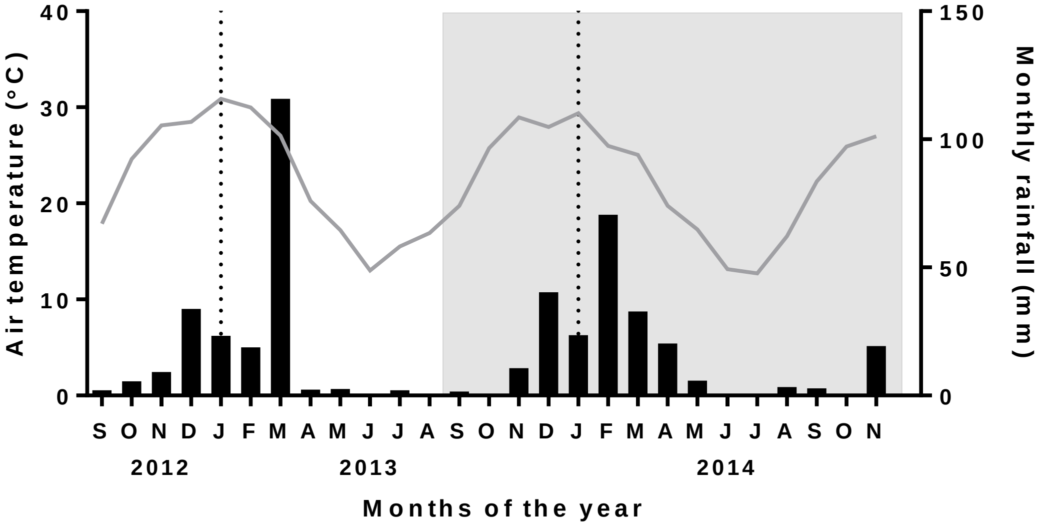

Figure 3.1: Monthly average air temperature (solid grey line) and total rainfall (black bars) obtained from Agricultural Research Council (ARC) weather station located at the Nossob campsite (S 25.4, E 20.6) from September 2012 to November 2014. The light grey box represents the 15-month study period (September 2013 to November 2014).

Table 3.1: Environmental conditions (mean± SD) prevalent across four seasonal periods and between the inter-annual hot dry periods, separated by the dotted line. There were no differences in environmental conditions experienced during the inter-annual hot dry periods (hot dry and drought), but the hot dry period termed ‘drought’ followed a prolonged dry spell.

	Hot Wet (Dec – Feb 2014)	Transitional Wet (Mar – May 2014)	Cold Dry (Jun – Aug 2014)	Hot Dry (Sep – Nov 2014)	Drought (Sep – Nov 2013)
Black globe temperature (°C)					
Mean 24 hour	27.8 ± 1.7^{a}	$20.7 \pm 4.0^{a, b}$	14.1 ± 2.1^{b}	25.1 ± 2.5^{a}	24.8 ± 4.7
Maximum 24 hour	42.7 ± 2.7^{a}	$36.2 \pm 3.4^{a, b}$	31.6 ± 1.6^{b}	42.1 ± 2.8^{a}	40.2 ± 5.5
Minimum 24 hour	16.9 ± 0.6^{a}	9.4 ± 4.5^{a}	0.8 ± 1.4^{b}	9.8 ± 1.9^{a}	10.6 ± 4.0
Air temperature (°C)					
Maximum	37.0 ± 2.0^{a}	$32.4 \pm 2.4^{a, b}$	26.3 ± 1.6^{b}	35.2 ± 1.6^{a}	34.9 ± 3.8
Minimum	19.1 ± 0.7^{a}	$10.9 \pm 4.6^{a, b}$	1.8 ± 2.4^{b}	11.7 ± 3.2^{a}	10.8 ± 4.7
Mean 24h solar radiation (W/m)	26.1 ± 3.2^{a}	$19 \pm 2.9^{a, b}$	16.2 ± 1.6^{b}	$24.4 \pm 2.8^{a, b}$	26.8 ± 4.1
Mean 24 h wind speed (m/s)	1.6 ± 0.2	1.2 ± 0.1	1.3 ± 0.2	1.7 ± 0.2	1.6 ± 0.1
Total rainfall (mm)	43	56	2	20	10
Number of rainy days	18	12	2	6	3

Note: Values with the different superscript letters differed significantly ($P < 0.05$). One-way ANOVA with Tukey’s multiple comparisons test.

3.4.2 Microclimate selection

The quality of microclimates selected by gemsbok and wildebeest, assessed by the minimum 24 h difference between collar and weather station miniglobe temperature, did not differ significantly between species ($F_{1,5} = 0.41$, $p = 0.55$; Table 3.2). There was a significant difference in the quality of microclimates selected across the seasonal periods ($F_{3,15} = 403$, $p < 0.0001$; Table 3.2). During the hot wet and hot dry, both species selected microclimates that were more than 10°C cooler than those experienced in the sun on occasion. During these hot periods, both species selected cool microclimates during the heat of the day, whereas this pattern was less pronounced during the transition wet and cool dry periods (Figure 3.2). Both species responded similarly to seasonal changes in ambient conditions as there was no interaction between species and season ($F_{3,15} = 3.1$, $p = 0.06$; Table 3.2). Despite the inter-annual variability of rainfall in the two hot dry periods, both species selected similar quality microclimates ($F_{1,5} = 0.20$, $p = 0.67$; Table 3.2). There was no difference in the quality of microclimate selected between the inter-annual hot dry periods ($F_{1,5} = 4.3$, $p = 0.09$; Table 3.2) and there was no interaction between species and inter annual hot dry periods ($F_{1,5} = 0.1$, $p = 0.76$; Table 3.2).

To assess the efficacy of microclimate selection, I correlated collar miniglobe temperatures against weather station miniglobe temperatures (Figure 3.3) for all the individuals. Across all seasons, the slopes of the regression lines were significantly less than one (Figure 3.3, ANCOVA, $P < 0.0001$). The regression lines of both species had similar slopes ($F_{1, 5} = 0.36$, $p = 0. 58$; Table 3.2). The slopes of the regression lines differed significantly across the seasonal periods ($F_{3, 15} = 153$, $p < 0.0001$; Table 3.2) with both hot periods showing the flattest slope (most efficient microclimate selection) and the slopes increased in steepness during the cooler periods (Table 3.2; Figure 3.3). There was no interaction between species and seasonal period ($F_{3, 15} = 0.63$, $p = 0.60$; Table 3.2). Slopes of regression lines were flatter for the drought period compared to the hot dry period when comparing inter-annual hot dry periods ($F_{1,5} = 15$, $p = 0.01$; Table 3.2). There was no difference in the regression slopes between species ($F_{1,5} = 1.3$, p =

0.31; Table 3.2) and no interaction was found between species and the inter-annual hot dry periods ($F_{1,5}$ = 2.3, p = 0.19; Table 3.2).

The regression lines intersected the line of identity, implying that animals selected microclimates cooler than the exposed miniglobe at high environmental heat loads, across all four seasonal periods and both hot dry periods. There was no significant difference between species when comparing the threshold temperature at which the regression lines intersected the line of identity ($F_{1,5}$ = 0.1, p = 0.81; Table 3.2), meaning that both species sought shade at similar temperatures. These threshold temperatures differed significantly across the seasonal periods ($F_{3,15}$ = 8.5, p = 0.002; Table 3.2). Threshold temperatures were lowest during the hot dry periods, implying that the animals started to seek shade at a lower ambient temperature (about 24°C) when conditions were hot and dry compared to the other periods (Table 3.2). There was no interaction between species and seasonal periods ($F_{3,15}$ = 1.6, p = 0.22; Table 3.2). When comparing the inter-annual hot dry periods, threshold temperatures didn’t differ between species ($F_{1,5}$ = 1.7, p = 0.25; Table 3.2), nor years ($F_{1,5}$ = 0.77, p = 0.42; Table 3.2) and there was no interaction between species and inter-annual hot dry periods ($F_{1,5}$ = 1.5, p = 0.27; Table 3.2).

Table 3.2: The quality (minimum 24 h difference between collar miniglobe and weather station miniglobe temperature), efficacy (slope of regression line between collar miniglobe temperatures and weather station miniglobe temperatures) and threshold (temperature at which each individual began to seeking shade, i.e., the point at which the regression line intersected with the line of identity) of shade seeking (mean ± SD) for five gemsbok and two wildebeest across four seasonal periods and between the inter-annual hot dry periods, separated by the dotted line.

		Hot wet	Transitional wet	Cold dry	Hot dry	Drought
Quality	Gemsbok	-9.1 ± 0.4^{a}	-5.3 ± 0.7^{b}	-3.7 ± 1.0^{c}	-9.2 ± 0.7^{a}	-9.7 ± 0.3
	Wildebeest	-10.1 ± 0.1^{a}	-5.7 ± 0.1^{b}	-3.7 ± 0.5^{c}	-9.1 ± 0.3^{a}	-9.5 ± 0.02
Efficacy	Gemsbok	0.6 ± 0.01^{a}	0.8 ± 0.03^{b}	0.8 ± 0.03^{b}	0.7 ± 0.02$^{c\ \phi}$	0.6 ±0.01$^{\phi}$
	Wildebeest	0.6 ± 0.04^{a}	0.7 ± 0.04^{b}	0.8 ± 0.00^{b}	0.6 ± 0.00^{a}	0.6 ± 0.00
Threshold (°C)	Gemsbok	27.1 ± 0.5^{a}	28.8 ± 1.4^{a}	27.0 ± 3.5^{a}	23.4 ± 0.9^{b}	23.6 ± 0.3
	Wildebeest	25.8 ± 0.7^{a}	26.9 ± 0.5^{a}	28.2 ± 2.4^{a}	24.4 ± 0.3^{b}	23.6 ± 0.3

Note: Values with the different superscript letters differed significantly between seasons ($p < 0.05$) and values with symbols $^{\phi}$ differed significantly between inter-annual hot dry periods as revealed by two-way repeated measures ANOVAs with Tukey's multiple comparisons tests.

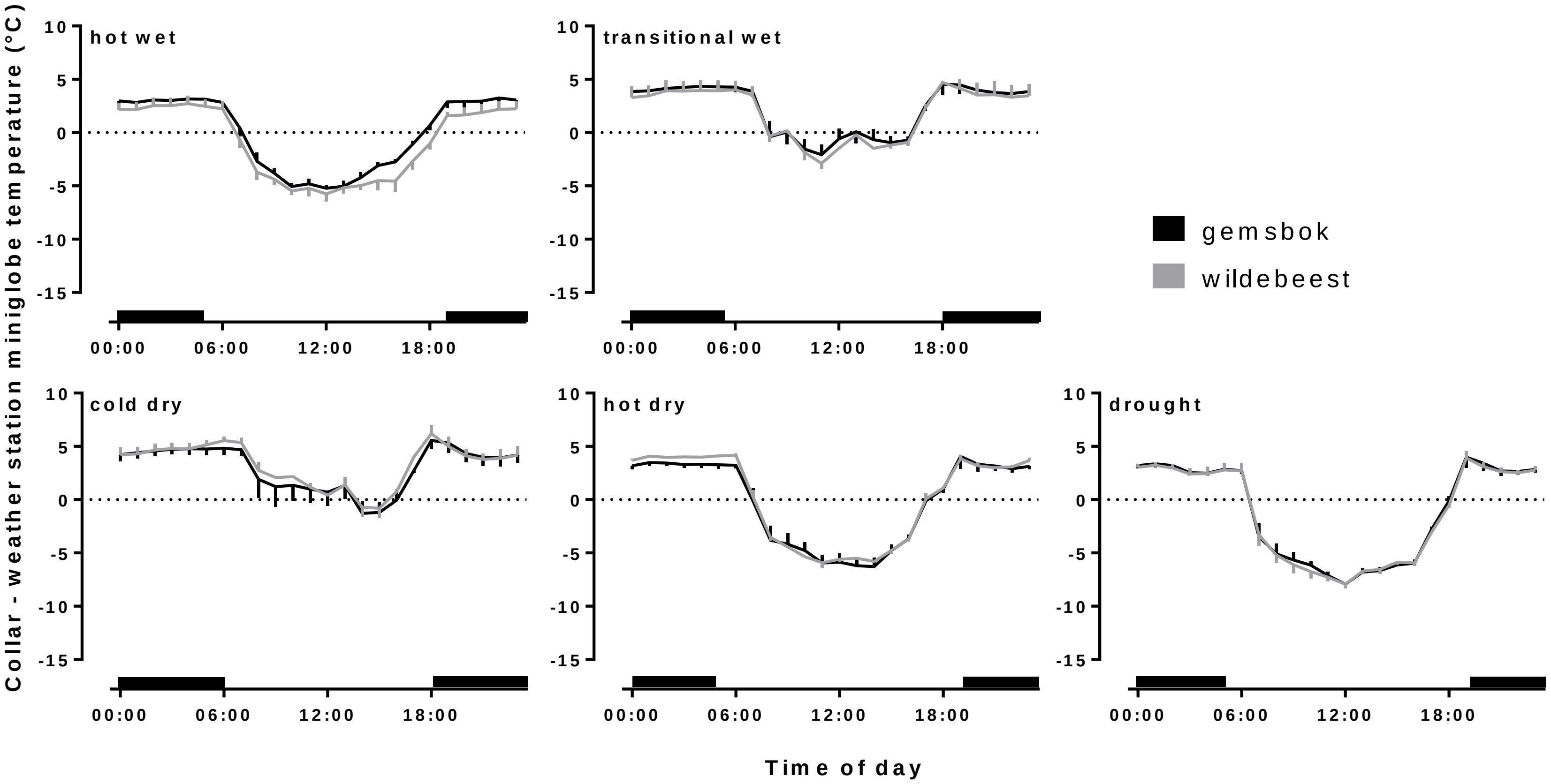

Figure 3.2: 24 h rhythm (mean ± SD) of microclimate selection for five gemsbok and two wildebeest free living in the Kalahari. Microclimate selection is expressed as the difference between miniglobe temperature on the collar i.e., at the site chosen by each individual and the temperature of an identical miniglobe exposed to the sun at a nearby weather station, over the five seasonal periods. Horizontal black bars represent night.

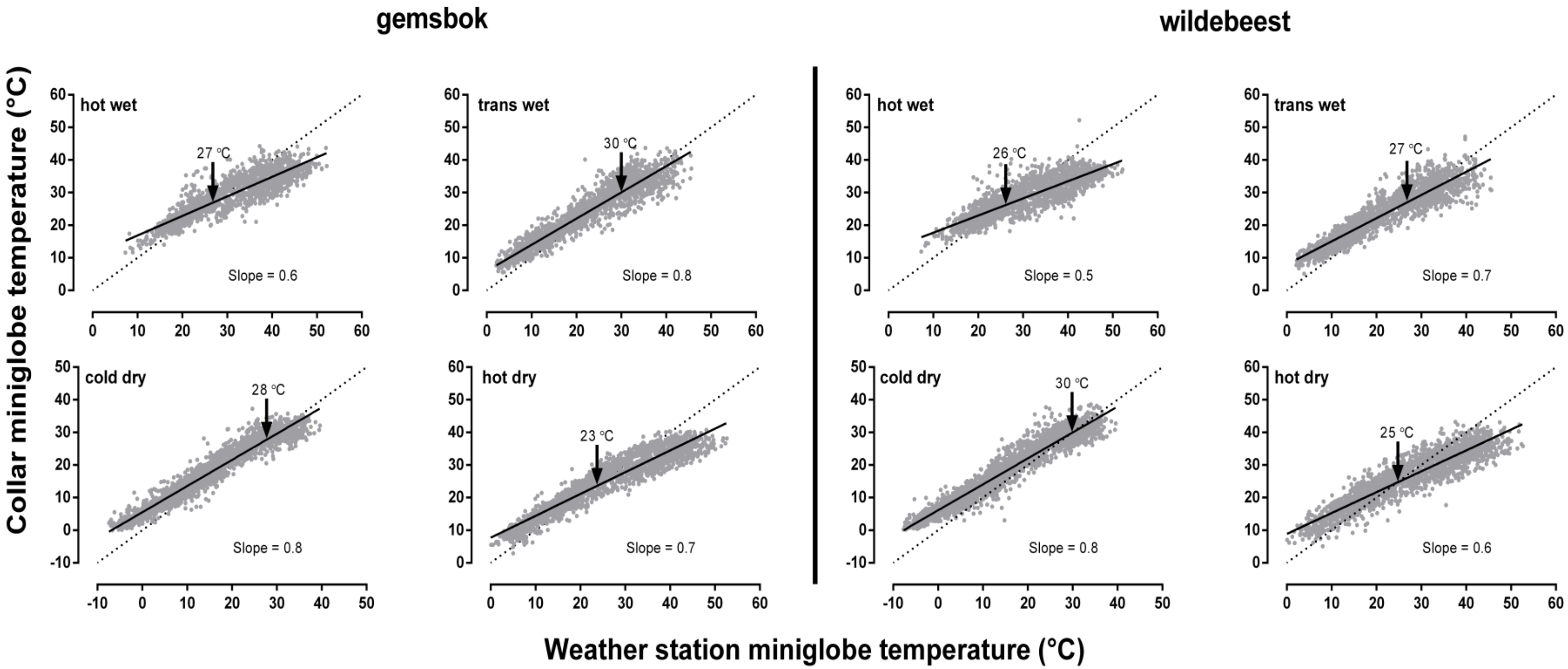

Figure 3.3: Relationship between miniglobe temperatures at the site chosen by a representative female gemsbok (left four panels) and a representative female wildebeest (right four panels) and the miniglobe temperatures recorded at a nearby weather station across the four seasonal periods. The representative individuals were chosen at random. Measurements were made at hourly intervals. The dashed line is the line of identity (y = x), the solid black line is the linear regression. The arrow indicates the threshold at which the representative individual started to seek shade. The slope value indicates how efficient the individual was at selecting cooler microclimates, with a flatter the slope implying more efficient shade seeking.

3.4.3 Activity

Both species generally showed crepuscular peaks of activity but lowering of activity during the heat of the day was less pronounced in the transitional wet and cold periods, particularly for gemsbok (Figure 3.4). Total 24 h activity did not differ between species ($F_{1,4} = 0.31$, $p = 0.61$), but it did differ across seasonal periods ($F_{3,12} = 16$, $p = 0.0002$; Figure 3.5). The two species responded differently to changing climatic conditions ($F_{3,12} = 5.2$, $p = 0.02$), with gemsbok showing a progressive decline in total 24h activity across the seasonal periods so that individuals were significantly less active during the hot dry period compared to the hot wet period, whereas wildebeest showed a substantial decline in total 24h activity following the hot wet period so that activity during hot wet period was significantly higher than that in all other periods (Figure 3.5). However, when comparing the inter-annual hot dry periods, no difference was found in total 24 h activity between the species ($F_{1,4} = 1.1$, $p = 0.35$; Figure 3.5), nor between the two hot dry periods ($F_{1,4} = 3.1$, $p = 0.14$; Figure 3.5) and there was no interaction between species and inter-annual hot dry periods ($F_{1,4} = 1.8$, $p = 0.25$; Figure 3.5).

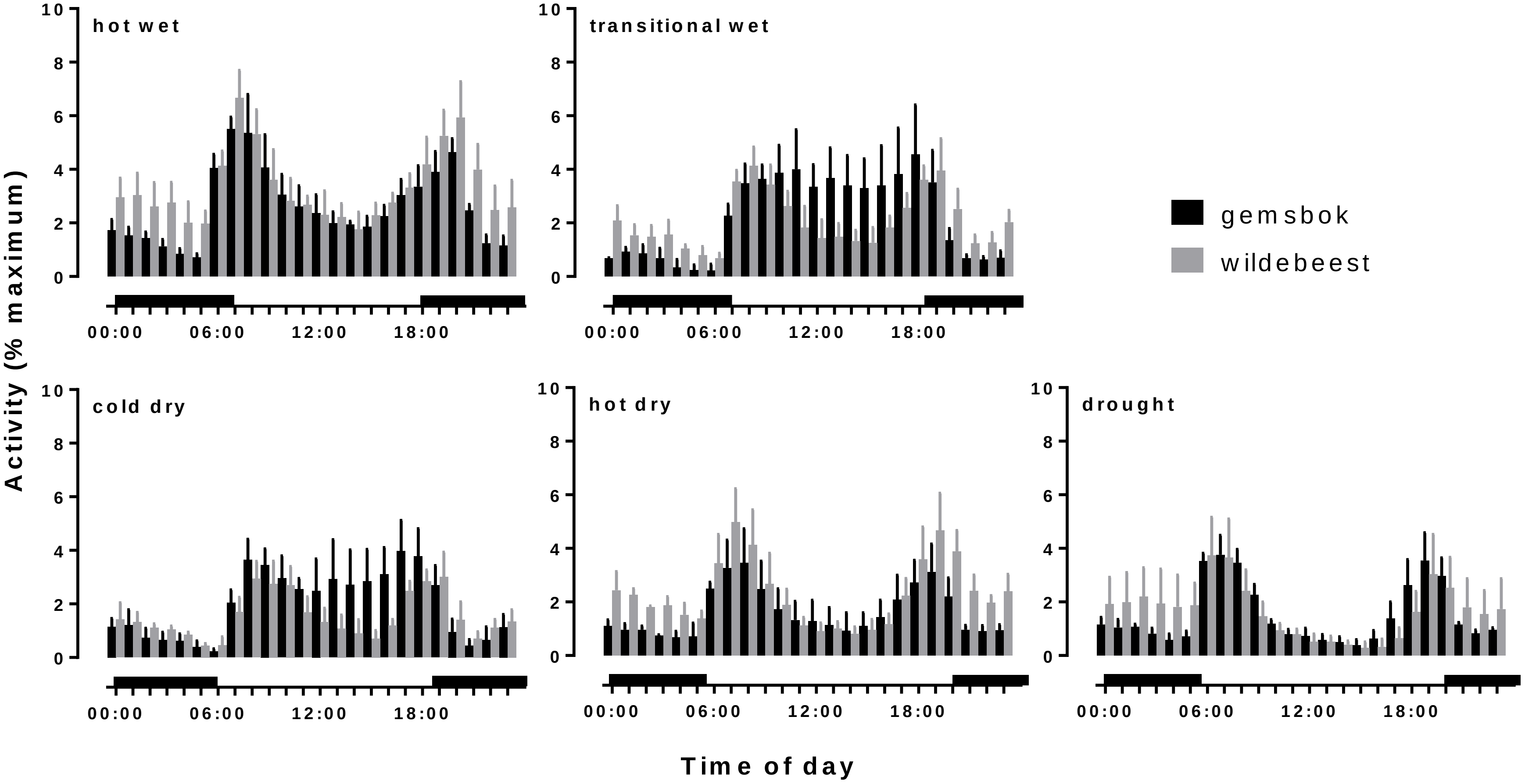

Figure 3.4: 24 h rhythm of activity (mean ± SD) in hourly bins for three gemsboks (black bars) and three wildebeest (grey bars) over the five seasonal periods. Activity was measured with a motion-sensitive data logger tethered into the abdominal muscle wall. Activity counts were expressed as a percentage of maximum counts for that logger. Horizontal black bars represent night.

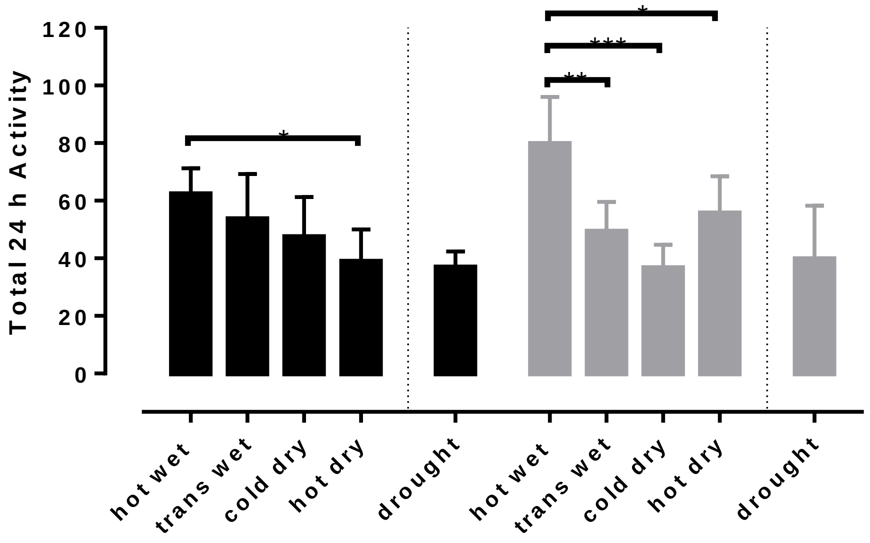

Figure 3.5: Comparison of total 24 h activity of gemsbok (mean ± SD, n=3, black bar) and wildebeest (mean ± SD, n=3, grey bar) over the four seasonal periods and the inter-annual hot dry periods separated by the dotted line. * *P* < 0.05, ** *P* < 0.01, * *P* < 0.001, Two-way repeated measures ANOVA with Tukey's multiple comparison tests. No differences were found between the inter-annual hot dry periods.**

To assess the apportioning of activity across the 24 h period, I compared the proportion of total 24h activity that occurred during the day between 7:00 and 17:00 (proportion of diurnal activity), night between 19:00 and 5:00 (proportion of nocturnal activity), and around sunrise between 5:00 and 7:00 and sunset between 17:00 to 19:00 (proportion of crepuscular activity) between species and across seasonal periods. The proportion of diurnal activity differed significantly between species ($F_{1,4} = 51$, $p < 0.002$; Figure 3.6) with gemsbok displaying a higher proportion of diurnal activity than wildebeest during transitional wet ($p < 0.0001$), cold dry ($p = 0.0003$) and hot dry ($p = 0.02$) periods but not during the hot wet period ($p = 0.09$). Consequently, the proportion of nocturnal activity differed significantly between species ($F_{1,4} = 57$, $p = 0.002$; Figure 3.6) with wildebeest displaying a higher proportion of nocturnal activity than gemsbok across all seasonal periods (Figure 3.6). However, the proportion of crepuscular activity (05:00 to 07:00 and 17:00 to 19:00) did not differ between species ($F_{1,4} = 2.5$, $p = 0.19$; Figure 3.6). In hot periods, the proportion of diurnal activity was lower ($F_{3,12} = 25$, $p < 0.0001$) and the proportion of nocturnal activity was higher

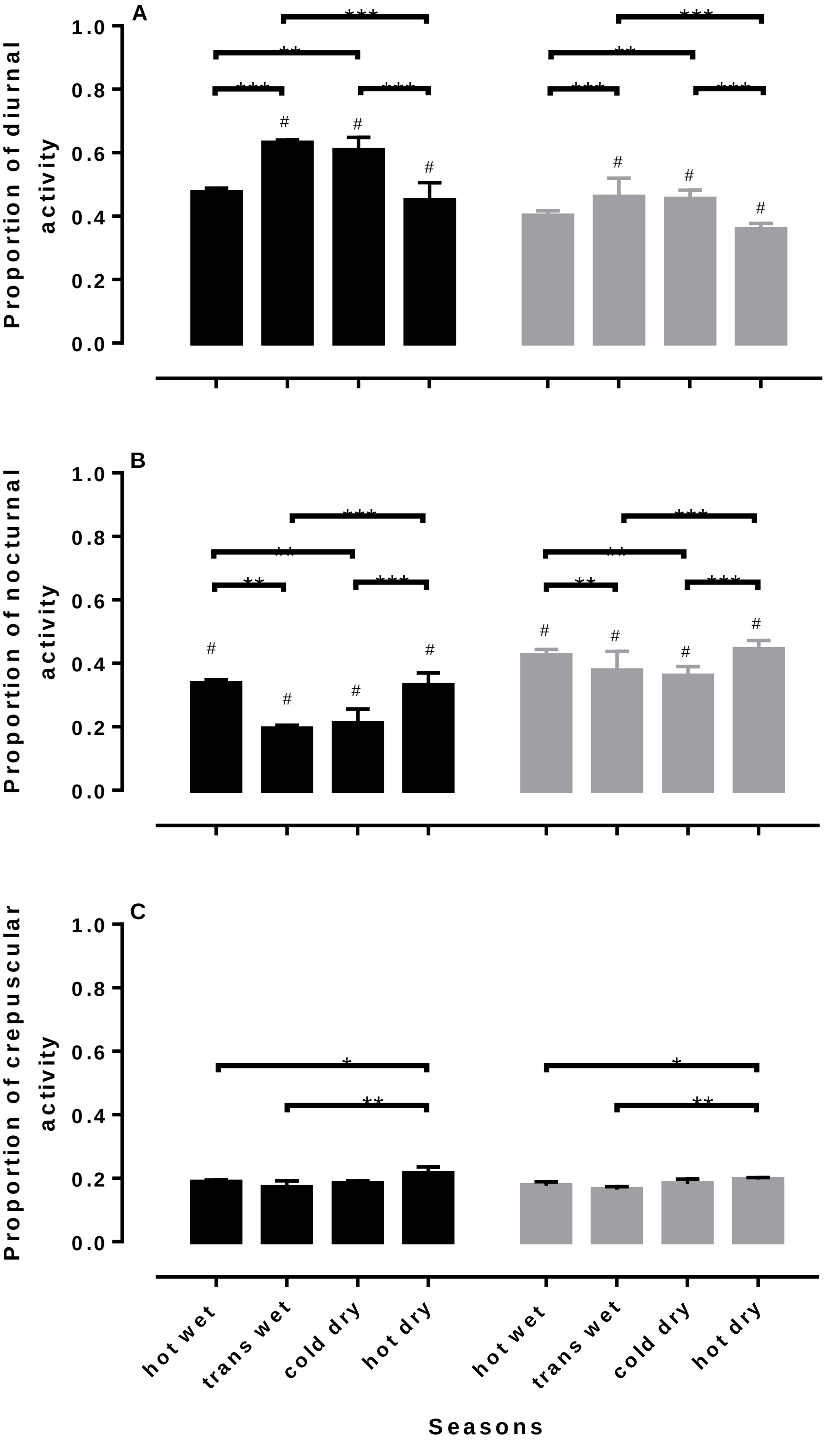

Figure 3.6: Comparison of proportion of total 24 h activity of gemsbok (mean ± SD, n=3, black bar) and wildebeest (mean ± SD, n=3, grey bar) apportioned diurnally (A), nocturnally (B) and crepuscularly (C) over the four seasonal periods. The black hashtag represents the difference between species. * *P* < 0.05, ** *P* < 0.01, * *P* < 0.001, Two-way repeated measures ANOVA with Tukey's multiple comparison tests.**

($F_{3,12}$ = 19, $p < 0.0001$) than during the cooler transitional wet and cold dry periods (Figure 3.6). Crepuscular activity also differed significantly between seasonal periods ($F_{3,12}$ = 8.5, $p = 0.003$; Figure 3.6), with hot dry period featuring a higher proportion of crepuscular activity compared to the transitional wet ($p = 0.001$) and hot wet ($p = 0.04$) period but no difference was found with the cold dry period (Figure 3.6). Both species responded similarly to the changing climatic conditions across the four seasonal periods, i.e., there was no interaction between species and season for the proportion of diurnal activity ($F_{3,12}$ = 2.6, $p = 0.10$), proportion of nocturnal activity ($F_{3,12}$ = 2.8, $p = 0.08$), or proportion of crepuscular activity ($F_{3,12}$ = 0.53, $p = 0.67$; Figure 3.6).

3.4.4 Body temperature

Body temperature generally varied between 37 °C and 39 °C for both species but on occasion reached an absolute minimum of 36.1 ± 0.7 °C and a maximum of 41.1 ± 0.1 °C for gemsbok and an absolute minimum of 35.4 ± 0.5 °C and a maximum of 41.3 ± 0.1 °C for wildebeest. Minimum body temperature dropped progressively during the dry seasons resulting in a noticeable increase in amplitude of body temperature rhythm during the drought in the first year of the study and again during the subsequent dry season (June to November) but this increase in amplitude was not as obvious as during the drought (Figure 3.7).

Peak body temperatures did not coincide with peak environmental heat load, but, in general, body temperatures increased throughout the day reaching an acrophase around sunset before decreasing throughout the night reaching a nadir around sunrise (Figure 3.8). Overall, mean ($F_{1,7}$ = 0.76, $p = 0.41$), maximum ($F_{1,7}$ = 0.74, $p = 0.42$), minimum ($F_{1,7}$ = 0.43, $p = 0.53$), and amplitude ($F_{1,7}$ = 0.17, $p = 0.69$) of 24 h body temperature rhythm did not differ between species across the four seasonal periods (Figure 3.8). Nor did the mean ($F_{1,7}$ = 5.6, $p = 0.05$) and maximum ($F_{1,7}$ = 0.18, $p = 0.69$) 24 h body temperatures differ between species during the inter-annual hot dry periods. However, wildebeest’s minimum 24 h body temperature was significantly lower than gemsbok ($F_{1,7}$ = 7.1, $p = 0.03$) during the drought period compared to the normal hot dry period (Figure 3.9C), despite ambient temperatures being similar between the two years. This low minimum 24 h body temperature resulted in a larger amplitude of 24 h body temperature rhythm ($F_{1,7} = 7.1$, $p = 0.03$) for wildebeest during this drought period compared to the hot dry period (Figure 3.9D).

Mean ($F_{3,21} = 40$, $p < 0.0001$), maximum ($F_{3,21} = 42$, $p < 0.0001$), minimum ($F_{3,21} = 32$, $p < 0.0001$) and amplitude ($F_{3,21} = 27$, $p < 0.0001$) of 24 h body temperatures differed between seasonal periods (Figure 3.8 & Figure 3.9). Both species had higher mean 24 h body temperatures during the hot wet period compared to the other periods. Yet, wildebeest had a larger decrease in mean 24h body temperature as the seasons progressed ($F_{3,21} = 4.1$, $p = 0.02$), which resulted in a lower mean 24 h body temperature during cold dry period compared to the transitional wet period (Figure 3.9A). During the inter-annual hot dry periods, mean 24 h body temperatures was similar ($F_{1,7} = 2.4$, $p = 0.17$) with no interaction between species and period ($F_{1,7} = 1.5$, $p = 0.26$; Figure 3.9A).

Maximum 24 h body temperatures of both species also responded differently to the changing climatic conditions ($F_{3,21} = 4.9$, $p = 0.01$), with gemsbok displaying higher maximum 24 h body temperatures during the hot periods compared to the cooler periods whereas wildebeest had higher maximum 24 h body temperatures during the ‘hot wet’ period compared to all the other periods (Figure 3.9B). This difference resulted primarily because of less of an increase in maximum 24h body temperature for wildebeest during the hot dry period so that maximum 24 h body temperatures during the hot dry period was higher than the cold dry period but not different to the transitional wet period. During the drought, wildebeest had a higher maximum 24 h body temperature than during the hot dry period ($F_{1,7} = 24$, $p = 0.002$), but there was no interaction between species and inter-annual hot dry periods ($F_{1,7} = 5.5$, $p = 0.05$; Figure 3.9B).

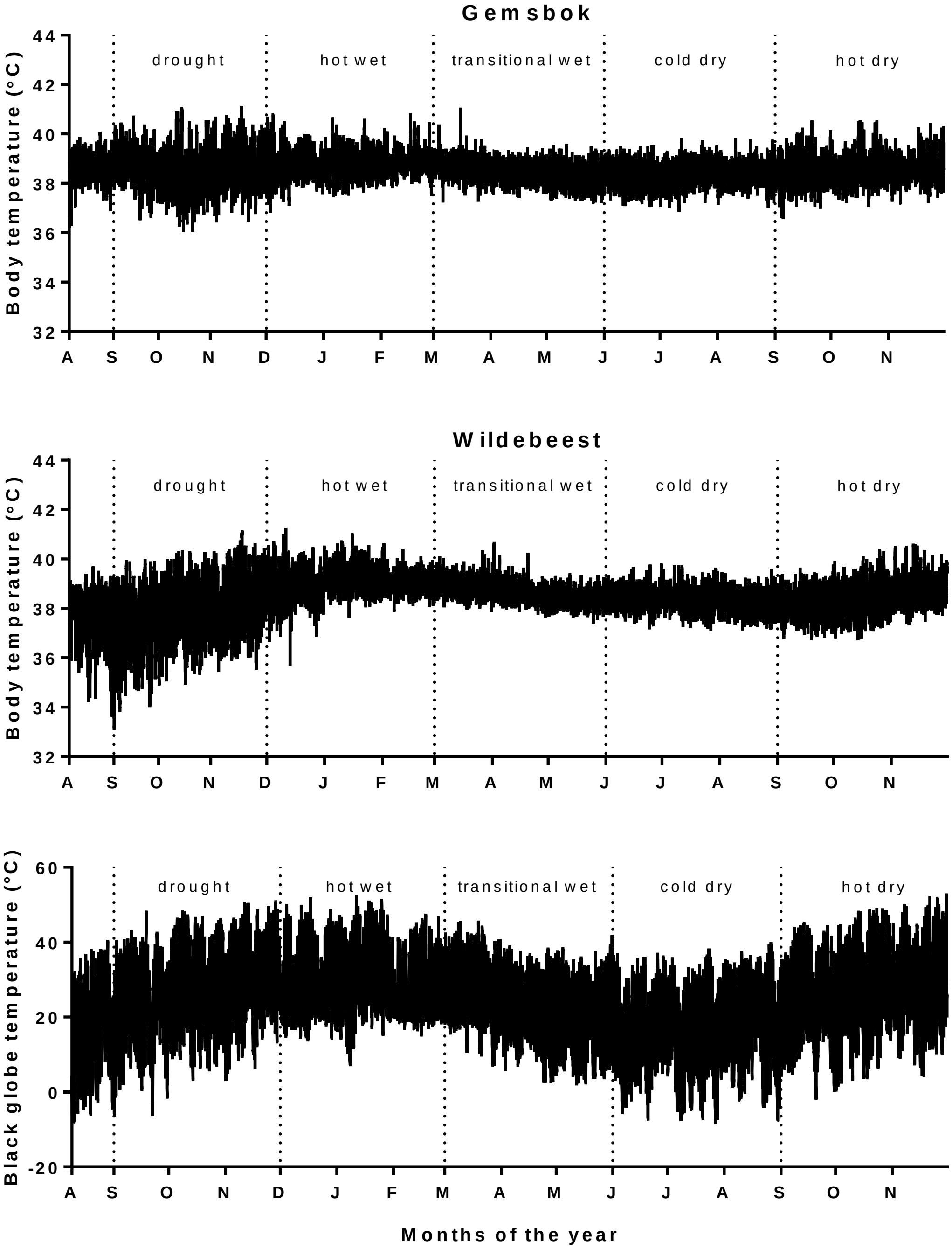

Figure 3.7: The top two panels show the original 10 min recordings of body temperature from a representative free-living female gemsbok (top panel) and a representative free-living female wildebeest (middle panel) over the 15-month study period (September 2013 to November 2014). The bottom panel shows the black globe temperature recorded at Kgalagadi Transfrontier Park, over the same period. The dotted lines separate the data into five periods analysed, namely drought, hot wet, transitional wet, cold dry, and hot dry.

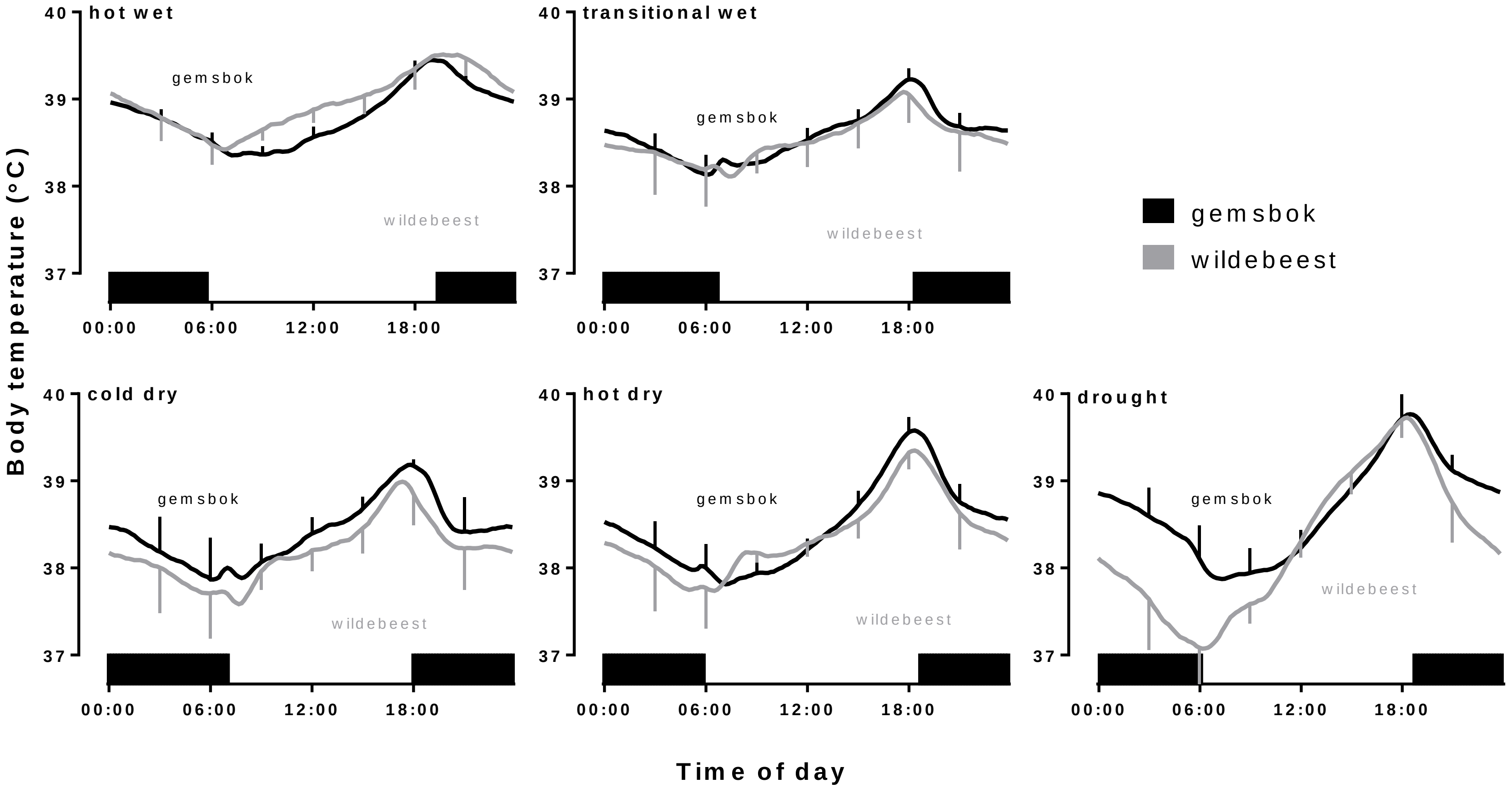

Figure 3.8: 24 h rhythm of body temperature for five free-living female gemsboks (mean ± SD, black line) and four free-living female wildebeest (mean ± SD, grey line) over the five seasonal periods. Horizontal black bars represent night time.

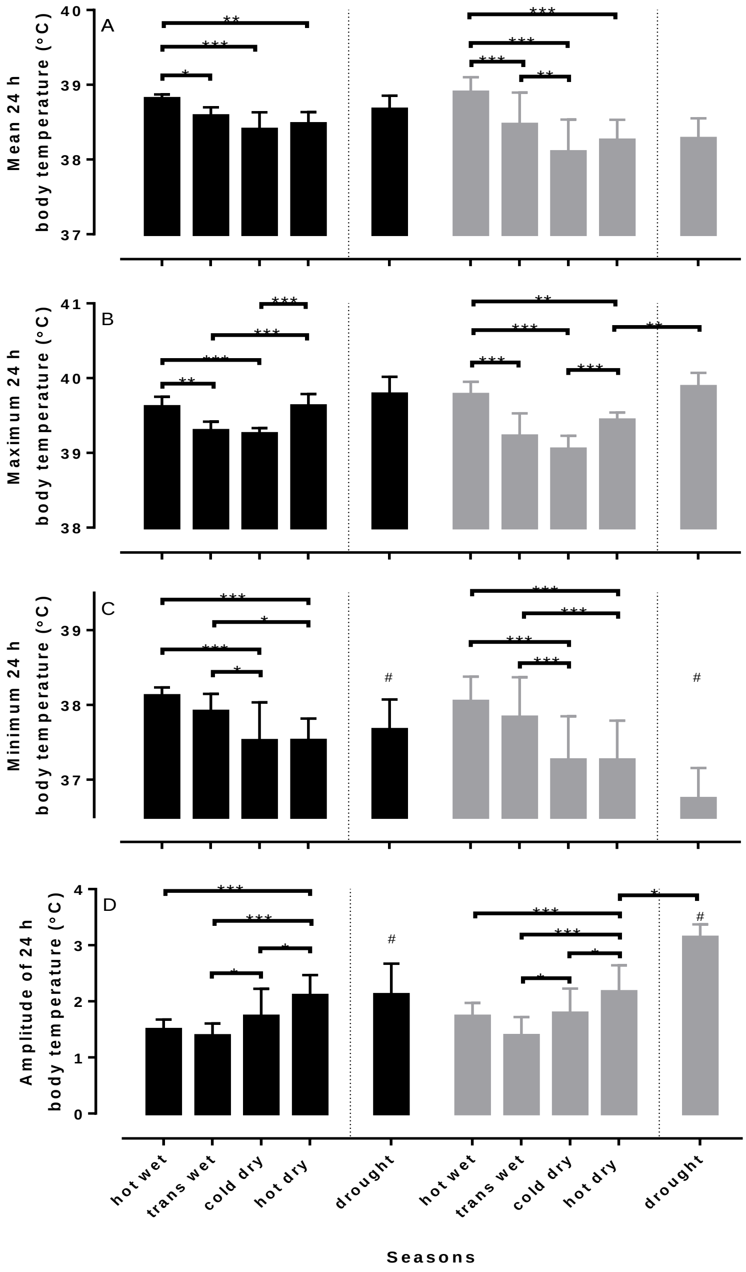

Figure 3.9: Comparison of the profile of the 24h body temperature rhythm between two sympatric species. A) 24 h mean, B) 24 h maximum, C) 24 h minimum, and D) 24 h amplitude of the body temperature rhythm of gemsbok (mean ± SD, n=5, black bar) and wildebeest (mean ± SD, n=4, grey bar) over the four seasonal periods and a comparison of the inter-annual hot dry periods separated by the dotted line. No difference was found between species during the seasonal comparison. The horizontal bars represent significant differences between seasons and the inter-annual comparison. The black hashtag represents the difference between species during the inter-annual hot dry periods. * *P* < 0.05, ** *P* < 0.01, * *P* < 0.001, Two-way repeated measures ANOVA with Tukey's multiple comparison tests.**

Both species displayed lower minimum 24 h body temperatures during the dry periods compared to the wet periods, and there was no interaction between species and seasonal period ($F_{3,21} = 0.74$, $p = 0.54$; Figure 3.9C). The low minimum 24 h body temperatures and high maximum 24 h body temperatures experienced during the hot dry period resulted in both species displaying the largest amplitude of 24 h body temperature rhythm during the hot dry period compared to the other periods (Figure 3.9D). The 24 h amplitude of body temperature rhythm was lower during the transitional wet period than during the cold dry period and there was no interaction between species and seasonal period ($F_{3,21} = 0.71$, $p = 0.56$; Figure 3.9D). During the inter-annual hot dry periods, minimum 24 h body temperature was similar for both periods ($F_{1,7} = 1.3$, $p = 0.29$) with no interaction between species and period ($F_{1,7} = 4.2$, $p = 0.08$). The high maximum and low minimum 24 h body temperatures of wildebeest during the drought resulted in a larger amplitude in 24 h body temperature compared to the hot dry period ($F_{1,7} = 5.9$, $p = 0.045$) with no interaction between species and period ($F_{1,7} = 6.0$, $p = 0.05$; Figure 3.9D).

3.5 Discussion

This study documents the longest record of microclimate selection, activity, and body temperature in two sympatric species with differing dependencies on water, living freely in the Kalahari. Despite their reported differences in water dependencies, both species responded remarkably similar to seasonal changes in environmental conditions during a typical year in the Kalahari. Both species prioritised behavioural thermoregulation during the hot periods (hot wet and hot dry) by seeking cooler microclimates more frequently as opposed to cooler periods, thereby becoming more efficient at selecting cool microclimates; at times both species selected microclimates that were 18 °C below that of an identical miniglobe in the sun. When conditions were hot and dry, both species further reduced environmental heat loads by seeking shade at lower ambient temperatures (thresholds) than during other periods.

Gemsbok were generally more diurnally active than wildebeest. Both species decreased the proportion of diurnal activity and increased the proportion of nocturnal activity when conditions were hot (hot wet and hot dry periods) and increased proportion of crepuscular activity when conditions were hot and dry. Despite the increased crepuscular, both species were seemingly unable to compensate for reduced diurnal activity when conditions were hot and dry since total 24h activity decreased in both gemsbok and wildebeest compared to when conditions were hot and wet. Wildebeest also showed low total 24 h activity in the transitional wet and cold dry periods. Although both species sought cool microclimates and reduced diurnal activity when conditions were hot, they both experienced higher maximum 24 h body temperature when conditions were hotter and lower minimum 24 h body temperatures when conditions were drier, resulting in a larger amplitude of 24 h body temperature rhythm during the hot dry period (Figure 3.9). Following a drought, the amplitude of 24 h body temperatures were even more pronounced for wildebeest.

Regrettably, technology failure resulted in a small sample size in microclimate selection data for wildebeest and in activity data for both wildebeest and gemsbok. Despite small sample sizes, I did find differences between seasonal periods. A season is a division of a year marked by changes in weather or ecology and could be defined in many ways, e.g., absolute (calendar months) or relative terms (amount of rainfall, dry vs. wet). For this study the meteorological calendar consisting of three-month periods was used to define the seasonal periods. Although selecting calendar months would bound continuous responses within a three-month period, this meteorological seasonal definition allowed me to compare two hot periods which differed in rainfall but not temperature. Based on these seasonal periods, I was able to highlight that it was not only ambient conditions that drove the different responses.

Shade-seeking is a common behaviour, especially during midday when ambient temperatures are highest, and has been observed in a variety of ungulates, for example, desert bighorn sheep (*Ovis Canadensis Mexicana*; Cain et al. 2008), Arabian oryx (*Oryx leucoryx*; Hetem et al. 2012a), impala (*Aepyceros melampus*; Jarman & Jarman 1973), and klipspringer (*Oreotragus oreotragus*; Dunbar 1979). I was able to quantify microclimate selection in wildebeest and gemsbok, by using a miniglobe attached to the collar, a novel technique developed by Hetem et al.

(2007). As the heat of the day increased, both species decreased the minimum temperature difference between the miniglobe on the collar and the reference globe, highlighting frequent and high-quality shade selection during hot dry and hot wet periods. By quantifying microclimate selection, I showed that there was no species difference in microclimate selection (Figure 3.2), contrary to previous observations (Knight 1991). In the southern Kalahari, gemsbok were observed (i.e., not quantified) to have a greater use of shade across all seasons, compared to wildebeest, but decreased their shade use during the hot dry periods (Knight 1991). However, minimum temperature difference between the miniglobe on the collar and the reference globe are influenced not only by the amount of time an individual spends in shade but also by the intensity or effectiveness of that shade (Hetem et al. 2007). Therefore, it is plausible that the gemsbok within this study sought shade less frequently than the wildebeest but sought more intense shade when they did.

Since the use of cool microclimates (shade-seeking) may reduce heat loads, it may also reduce the need for evaporative water loss and hence save body water (Cain et al. 2008; Hetem et al. 2012a). Indeed, Arabian oryx showed enhanced shade seeking when conditions were dry (Hetem et al. 2012a). Similarly, gemsbok and wildebeest in my study showed lower threshold temperatures (i.e., miniglobe temperature at which sought shade) when conditions were hot and dry compared to hot and wet despite similar miniglobe temperatures. This threshold temperature is the lowest recorded to date for a large mammal. Miniglobe temperatures on collars have been measured previously in a number of large mammals. In a mild climate, eland sought shade when miniglobe temperatures was above 28 °C (Shrestha 2012) and elephants (*Loxodonta africana*; Mole 2015) and kudu (*Tragelaphus strepsiceros*; Hetem et al. 2008) sought shade above 30 °C. In an extreme environment, Arabian oryx and sand gazelle (*Gazella subgutturosa marica*) have been observed to increase shade-seeking behaviour at miniglobe temperatures above 28 °C (Hetem et al. 2012b). Despite the conditions of this study being milder than those of the Saudi Arabian Desert, I found that gemsbok and wildebeest occupied microclimates cooler than the exposed thermal environment, presumably shaded microclimates, when miniglobe temperatures exceeded 23 °C. I have, therefore, shown that wildebeest and gemsbok inhabiting the Kalahari have the lowest threshold temperature, thus, are the most efficient shade seekers among large African mammals measured to date. Yet, the threshold temperature for both wildebeest and gemsbok did not decline further during the drought, suggesting that both species may already be using optimal shade so that no further flexibility in this response is possible.

Although shade seeking may conserve body water it reduces valuable foraging time during the heat of the day (Knight 1991; Hetem et al. 2012a; Shrestha et al. 2014). In this study, wildebeest consistently had a lower proportion of diurnal activity than gemsbok but with both species displaying lowest diurnal activity when ambient temperature was high, likely because of increased shade seeking during the heat of the day. If species are to maintain a positive energy balance, they will need to increase foraging during crepuscular or nocturnal periods to compensate for reduced diurnal foraging during hot periods. Both species increased the proportion of nocturnal activity during the hot seasons, as has been reported previously for gemsbok (Knight 1991) and Arabian oryx (Hetem et al. 2012a). Conversely in a previous study, wildebeest in CKGR showed no difference in nocturnal activity across three seasonal periods based on rainfall (Selebatso et al. 2017b). However, the differences found could result from a different classification of season. These low levels of nocturnal activity throughout the year may be because of high predatory pressures at night (Valeix et al. 2009; Tambling et al. 2015). Indeed, large predators (e.g., lion and hyena) are primarily active at night (Hayward & Slotow 2009; Cozzi et al. 2012) and herbivores adjust their activity times to avoid them (Valeix et al. 2009; Tambling et al. 2015; Davies et al. 2016). Despite being exposed to similar ambient temperature and predators (lions and hyena) as the wildebeest in CKGR (Selebatso et al. 2017b), my gemsbok and wildebeest increased their proportion of nocturnal foraging when conditions were hot, which implies the benefit must outweigh the risk of increased predation. There is an additional benefit of increased intake of preformed water by foraging at night (Cain et al. 2006; Nagy & Knight 1994; Taylor 1969). I found no difference in proportion of nocturnal activity between hot wet and hot dry periods.

The increased nocturnal activity when conditions were hot and wet not only compensated for the reduced diurnal activity but resulted in an increase in total 24h activity compared to the hot dry period for gemsbok and compared to all other periods for wildebeest. Wildebeest in CKGR also displayed highest activity during the wet period, compared to other seasonal periods, attributed to maximising forage intake to accumulate enough body reserves (Selebatso et al. 2017b). Both gemsbok and wildebeest are predominantly grazers, but gemsbok use a wider range of food items than wildebeest (Knight 1991). Wildebeest show little seasonal variation in the types of food eaten, but gemsbok's food sources include forbs, fruit such as Tsama melons (*Citrullus lanatus*) and browse (Knight 1991). However, gemsbok only resort to eating browse during the dry seasons to ensure a higher water content diet (Western 1975; Knight 1991), particularly once grasses have reached complete sward maturity and senescence resulting in energy deficiency (Sinclair 1975; Western 1975; Owen-Smith 2008b). Since wildebeest are associated with the denser and shorter grasses (Knight 1991), they rely quite heavily on good quality grasses. By resorting to other forage, it is plausible that gemsbok were less affected by the drying vegetation compared to wildebeest.

Minimum 24 h body temperatures were lowest during the dry periods for both species and most likely reflected a negative energy balance during these periods (Hetem et al. 2016). Similar reductions in minimum body temperature were reported for species exposed to cold, dry winters (Shrestha et al. 2011), suggesting that the low minimum 24 h body temperatures might result from a combination of low energy and cold stress. Yet, some species show low minimum body temperatures during summer months when they are not exposed to cold stress (e.g., kangaroos (Dawson et al. 2007; Maloney et al. 2011), Arabian oryx (Ostrowski et al. 2003, Hetem et al. 2012b), sand gazelle (Ostrowski et al. 2006, Hetem et al. 2012b) and camels (Grigg et al. 2009)). This response has been proposed as a preprogramed response to allow additional heat to be stored throughout the day, as has been proposed for adaptive heterothermy (Mitchell et al 2002; Grigg et al. 2009), but unlikely based on the findings of this study. If these low minimum 24 h body temperatures were a preprogramed response to the hot conditions, I would then expect minimum 24 h body temperatures to be low throughout the hot periods. Instead, minimum 24 h body temperature were low during the cold dry and hot dry period and resolved following rains during the hot wet period, implying that low minimum 24 h body temperatures are more related to energy balance than heat storage in hot conditions, as suggested for kangaroos (Dawson et al. 2007).

Similar to ungulates prioritizing energy conservation over thermoregulation when energy was limited, high maximum 24 h body temperatures result when ungulates prioritize body water conservation over thermoregulation when dehydrated and exposed to high air temperatures (Hetem et al. 2010; Fuller et al. 2016; Hetem et al. 2016). Although reducing evaporative water loss and tolerating high body temperatures (e.g., dromedary camel (*Camelus dromedarius*), Schmidt-Nielsen et al. 1957; Arabian oryx (*Oryx leucoryx*), Hetem et al. 2010) may conserve body water (Schmidt-Nielsen et al. 1957; Mitchell et al. 2002), it may increase the risk of reaching lethal body temperature (Hetem et al. 2016). Gemsbok in this study showed the highest maximum 24 h body temperatures when it was hot irrespective of aridity and wildebeest showed an unexpected pattern of lower maximum 24 h body temperatures during the hot dry compared to hot wet, which may relate to low energy reserves as seen in aardvark (*Orycteropus afer*) before their death (Rey et al. 2017).

A combination of low minimum body temperature and high maximum body temperature (adaptive heterothermy) appears beneficial to a large mammal when these animals are exposed to environmental heat stress (Taylor 1969), in that storage of heat reduces the demand for evaporative cooling and conserves body water. Under this hypothesis an endotherm that is more arid-adapted will have a larger amplitude of body temperature because maintaining body temperature is quite costly and a fluctuation of body temperature (i.e., adaptive heterothermy) would presumably reduce water use and conserve energy (Hetem et al. 2016). Yet, the more mesic kangaroo *(Macropus giganteus)* was less able to cope with dehydration and displayed greater heterothermy, characterised by an increase in maximum body temperature, than the arid adapted kangaroo (*Macropus rufus*) during hot, arid conditions (Dawson et al. 2007). The larger body temperature fluctuations in the mesic kangaroo suggests that a fluctuation in body temperature may reflect an indication of physiological stress compromising the thermoregulatory system more than a positive adaptive response. Amplitudes of 24 h body temperature rhythm were highest in both my species in hot dry period, resulting from a combined effect of increased maximum 24 h body temperatures and decreased minimum 24 h body temperatures. This heterothermy was exaggerated during the drought period for wildebeest, because of the particularly low minimum 24 h body temperatures during the drought. The larger amplitude of 24 h body temperature rhythm employed by wildebeest during the drought implies that wildebeest were more energetically and water stressed than gemsbok during the drought. Such physiological stress may ultimately result in the demise of a population, as has been recorded for wildebeest in the Kalahari during drought (Knight 1991; Ogutu et al. 2011, Owen-Smith & Ogutu 2012).

In summary, I have demonstrated that the arid-adapted gemsbok and the water-dependent wildebeest have similar behavioural responses when faced with seasonal fluctuations in air temperatures and resources. Both species prioritised behavioural thermoregulation during the hot periods by effectively selecting cooler microclimates during the heat of the day, and reducing diurnal activity and compensating at night. Increased 24h activity during wet period were more exaggerated for wildebeest. I have also shown that both species do become heterothermic (i.e. displayed a larger amplitude of 24 h body temperature) during times of aridity, since maximum 24 h body temperature was highest when conditions were hot and minimum 24 h body temperatures were lowest when conditions were dry. These seasonal analyses, which allowed me to compare two hot periods with differing amounts in rainfall but not temperature, imply that the species behavioural and thermoregulatory responses were influenced by seasonal changes in water and forage availability, but those effects have not been tested empirically for any ungulate to date. The subsequent chapters, chapter 4 and 5, focus on thermoregulation and behaviour of the same individuals in response to variability in vegetation greenness and distance to water.

CHAPTER 4

4 Behavioural and thermoregulatory responses of large herbivores to vegetation greenness variability.

4.1 Abstract

When food resources are limited, animals have to trade off the benefit of acquiring widely distributed forage against the energetic costs of searching for the food. If an endotherm is unable to maintain a positive energy balance, it may be become hypothermic (i.e., unable to maintain a high body temperature). In this study, I quantified the influence of vegetation greenness on body temperature and activity of two sympatric free-ranging ungulate species under the same environmental conditions. I then investigated if the responses of the arid adapted species, namely the gemsbok (*Oryx gazella gazella*), were enhanced in a more arid environment. I used Normalized Difference Vegetation Index (NDVI) as a standardized index of vegetation greenness, which can be considered a proxy for vegetation productivity and quality. Wildebeest (*Connochaetes taurinus*) and gemsbok, regardless of location, reduced activity when exposure to brown vegetation compare to when they were exposed to green vegetation. Minimum 24 h body temperature declined when vegetation was brown and this response was exaggerated for blue wildebeest compared to gemsbok. When exposed to more extreme aridity, gemsbok showed a decrease in minimum 24 h body temperature. I propose that under conditions of low food availability, thermoregulation may become too costly. Therefore, when food resources are limited in quality, wildebeest and gemsbok appear to prioritize the conservation of energy over the maintenance of a high body temperature.

4.2 Introduction

The vegetation across a semi-arid ecosystem is primarily constrained by precipitation (Fensholt et al. 2012). It is the seasonality, substantial differences between years, and unpredictability of precipitation that result in heterogeneity of vegetation distribution in semi-arid ecosystems (Skarpe & Bergström 1986). During the rainy season, vegetation is abundant and of high quality with peak concentrations in young, green leaves (Owen-Smith 2008). It is during the dry season that vegetation quality declines, protein content becomes more diluted and fibre increases, resulting in grass tufts being mostly brown (Sinclair 1975; Bergström 1992; Parker et al. 1999; Owen-Smith 2008). The greenness of vegetation is correlated with several variables that appear to be relevant to ungulate diet in quantity and quality (Pettorelli et al. 2011) and essentially is the energy available for mammalian herbivores (Pettorelli et al. 2005b). Since food availability closely follows precipitation in semi-arid ecosystems, large African ungulates typically experience insufficient food not only during winter but also during spring before the onset of rain and at a time when ambient temperatures are increasing.

Optimal foraging theory predicts that large mammalian herbivores should capitalise on high quality forage to maximise food intake (Gordon & Lindsay 1990) and limit energetic expenditure wherever possible (Sæther & Andersen 1990; Johnson et al. 2001). Since forage is often diverse in quality, quantity, space and time, it may act as a constraint on energy acquisition particularly during the dry seasons (Senft et al. 1987). Even though it may seem counter intuitive, many large mammalian herbivores, such as kudu (*Tragelaphus strepsiceros*; Owen-Smith 1994), increase their activity during dry periods to locate limited resources (Owen-Smith 1982; Musiega & Kazadi 2004). Yet, searching for adequate forage is often time-consuming and energetically expensive, and can put large mammalian herbivores at risk of increased water loss. Alternatively, a large mammalian herbivore can decrease energy expenditure by reducing its locomotor activity to conserve energy, as shown by northern ungulates during winter (Arnold et al. 2004; Arnold et al. 2006; Wang et al. 2006). If an endotherm cannot increase its foraging effort when resources are sparse or reduce activity to conserve energy sufficiently to maintain a positive energy balance, it may become hypothermic (i.e., a reduction of body temperature below the required temperature for normal metabolism; Tattersall et al. 2012).

Endotherms maintain a high body temperature, independently of environmental temperatures, because of endogenous heat generated as a by-product of metabolism (Tattersall et al. 2012; Lovegrove 2016). This high and relatively constant body temperature is proposed to allow endotherms to exploit seasonal environments (Lovegrove 2005) because they can maintain body temperature within an optimal range for enzyme activity irrespective of air temperature (Lovegrove et al. 1991; Kemp 2006). When air temperatures are low, endotherms are prepared to expend energy (shivering or non-shivering thermogenesis) to maintain body temperature (i.e., thermoregulate; Tattersall et al. 2012). However, when energy intake is limited, the costs of maintaining body temperature may become too high and endotherms may reduce metabolism and body temperature, particularly in small mammals with their high mass-specific metabolic rate (Geiser 2004; reviewed by Ruf & Geiser 2015). Similar mechanisms have been proposed for northern ungulates (e.g., red deer (*Cervus elaphus*; Arnold et al. 2004; Turbill et al. 2011), Przewalski horse (*Equus ferus przewalskii*; Arnold et al. 2006), and Alpine ibex (*Capra ibex ibex*; Signer et al. 2011)) when food is inaccessible under winter snow. In less temperate environments, ungulates also show a reduction in minimum body temperature during the dry season (e.g., Arabian oryx (*Oryx leucoryx*; Hetem et al. 2010), Arabian sand gazelle (*Gazella subgutturosa marica*; Hetem et al. 2012b), Dromedary camels (*Camelus dromedaries*; Grigg et al. 2009), blue wildebeest (*Connochaetes taurinus*; Shrestha et al. 2011; Chapter 3) and gemsbok (*Oryx gazella*; Chapter 3)), which has been attributed to a reduction in forage availability. However, to date no study has explicitly linked changes in body temperature to vegetation quality.

The focus of this chapter is to determine if vegetation greenness influences variability in activity and body temperature of two antelope species with differing water dependencies. Specifically, I compared activity and minimum body temperature of 1) gemsbok and wildebeest living within the same environmental conditions and 2) gemsbok in two climatically contrasting environments in southern Africa. Based on the results presented in the previous chapter (chapter 3), I hypothesis that both species will decrease activity when forage quality (indexed by NDVI) declines and this response is likely to be similar for sympatric species. In chapter 3, both species showed low minimum 24 h body temperatures during the dry season, therefore, I hypothesise that this response was more related to the poor vegetation quality than low air temperatures.

4.3 Materials and methods

4.3.1 Study areas

The study took place within the Central Kalahari Game Reserve (CKGR) in central Botswana (S 21.48°, E 23.69°), from November 2012 to July 2013, and within the Bakgalagadi Schwelle region (here after called Schwelle) of the southwestern Botswana (S 24.35°, E 20.62°), from October 2013 to December 2014. The Schwelle includes the Kgalagadi Transfrontier Park (Botswana side) and surrounding wildlife management areas. Both CKGR and Schwelle are open semiarid savannas located within the greater Kalahari and provide considerable scope for animals to exploit spatial heterogeneity in vegetation. Predators and competitors were similar between sites.

The Kalahari exhibits a gradual increase of aridity in a south-westerly direction, with CKGR experiencing an annual average rainfall of 350 - 400 mm (Makhabu et al. 2002), and Schwelle experiencing an annual average rainfall of 250 - 350 mm (Thomas & Shaw 1991; Stapelberg et al. 2007; Fynn & Bonyongo 2011). Rainfall is concentrated between November and April (Thomas & Shaw 1991). Air temperature in the Kalahari can reach extremes, with summer daytime temperatures exceeding 40 °C, and winter night time air temperatures dropping below freezing. Extreme temperatures of –11 °C and up to 45 °C have been recorded within Schwelle (Knight 1995), whereas, CKGR is slightly less extreme with air temperatures ranging between -1 °C and 37 °C (Makhabu et al. 2002). Neither site has permanent natural water sources, thus herbivores depend on ephemeral pools that form shortly after rain and moisture from vegetation or a few artificial waterholes with differing degrees of potability.

4.3.2 Data collection

Eight individual female gemsbok within the CKGR and eight individual female gemsbok and eight individual female blue wildebeest within the Schwelle, all from separate herds, were captured by a qualified veterinarian using standard procedures (see chapter 2). These individuals where collared with a satellite-based GPS collar (African Wildlife Tracking, Pretoria, South Africa) and implanted with miniature data loggers. The collars recorded the animal’s location (GPS) at hourly intervals. Miniature temperature-sensitive data loggers (DST centi-T, Star-Oddi, Iceland) implanted retroperitoneally recorded body temperature at 10 min intervals and motion-sensitive data loggers (ADXL345, Sigma Delta Technologies, Australia) tethered to the abdominal wall recorded activity counts within the first 10 seconds of each at 5 min intervals. For more details on surgical procedures, calibrations and accuracy of temperature-sensitive and motion-sensitive data loggers refer to chapter 2.

4.3.3 Weather data measurements

Black globe temperature is a better index of heat load than air temperature as it integrates the effects of air temperature, wind velocity, solar radiation and long wave radiation, which influence the animal’s thermal balance (Hetem et al. 2007). A free-standing black miniglobe thermometer was placed in direct sun, 1 m above ground, on site at each of the study sites (Schwelle: S 24.35 °, E 20.62 °; CKGR: S 21.61 ° E 24.04 °) and recorded miniglobe temperature (°C) every hour by a temperature data logger (Hobo, Onset Computer Corporation, Pocasset, MA, USA), for the duration of the study period (refer to chapter 2 for calibrations). Air temperature (°C) and rainfall (mm) during the study period were obtained from Agricultural Research Council (ARC) on site for Schwelle (S 25.4 °, E 20.6 °) and from the Central Kalahari Game Reserve Office at Matswere gate for CKGR (S 21.26 °, E 24.12 °).

4.3.4 Quantifying changes in relative greenness

Vegetation indices are mathematical combinations or transformations of spectral bands that accentuate the spectral properties of green plants so that they appear distinct from other image features (Pettorelli et al. 2005b). Normalized Difference Vegetation Index (NDVI) is a vegetation index defined by the equation:

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

where NIR is the reflectance of the Earth's surface in the near-infrared channel and RED is the reflectance in the visible portion of the red channel (Tucker &

Sellers 1986, Huete et al. 2002, Pettorelli et al. 2009). Green plants have high reflectivity in the near-infrared (NIR) wavelengths and absorb red wavelengths for photosynthesis, which results in an NDVI ratio that ranges from -1 to +1, where negative values correspond to an absence of vegetation (i.e., soil; Myneni et al. 1995). Satellite sensors can measure the absorbed and reflected radiation from the earth's atmosphere and by transforming these reflected wavelengths into NDVI values, researchers can create images that give a measure of vegetation greenness over large areas. The Moderate Resolution Imaging Spectroradiometer (MODIS) sensor is a key instrument aboard the Terra and Aqua satellites that collects data within 36 spectral bands, ranging in wavelengths from 0.4 µm to 14.4 µm, every 1 to 2 days (Tucker & Yager 2011). The MODIS products, such as MODIS MOD13Q1, that are computed from atmospherically corrected bi-directional surface reflectance that have been masked for water, clouds, heavy aerosols, and cloud shadows (Didan et al. 2015), are already compiled and freely available. The spatial resolution of the MODIS MOD13Q1 data set is 250 m^2 and daily MODIS NDVI data are composited into 16-day intervals based on product quality assurance metrics to remove low quality pixels to eliminate the effect of clouds, aerosols, and variations in sun surface-sensor geometry (Didan et al. 2015), with only the highest NDVI value per pixel selected during the composited period. MODIS MOD13Q1 data images were retrieved from EarthExplorer (NASA Land Processes Distributed Active Archive Center (LP DAAC), USGS/Earth Resources Observation and Science (EROS) Center, Sioux Falls, South Dakota, https://earthexplorer.usgs.gov/) for both the study sites from the start of the dry season in 2010 until the end of the study period in December 2014.

MODIS pixels are particularly sensitive to soil and vegetation structure, such as trees vs. grasses (Nicholson & Farrar 1994; Scanlon et al. 2002). Because trees green up before the first rains of the season, whereas grasses typically green up after the first rains (Archibald & Scholes 2007), when comparing a pixel with trees to another pixel that is composed of only grass, the tree pixel will most likely be greener (i.e., have higher NDVI values) than the grass pixel. Therefore, to assess the vegetation greenness used by each individual animal in space and time, I used a relative greenness measure.

Relative greenness represents how green (or brown) each pixel is in relation to a long-term greenness value for that pixel. The assumption is that the vegetation structure would not have changed during the period for which the long-term mean is calculated. Relative greenness, therefore, minimises the confounding effect between greenness and vegetation structure by classifying each pixel as green or brown relative to its own mean across a predefined time period (Newnham et al. 2011; Relton 2016). The optimal time interval required to calculate a long-term mean is 2.5 years of data (Newnham et al. 2011). For simplicity, I used a 3-year time series, which was sufficiently long to represent average conditions as validated previously for gemsbok living in CKGR (Relton 2016). I first estimated the long-term mean NDVI and standard deviation on a pixel-by-pixel basis for a 3-year time series, beginning from August 2010 until July 2013 for CKGR, and from January 2012 to the end of December 2014 for Schwelle. By using mean ± 0.5 standard deviation, I was able to differentiate three levels of greenness. Secondly, for each 16-day NDVI raster image, I reclassified the raster into one of the three greenness categories: 'level 1' (brown), 'level 2' (green), and 'level 3' (very green). 'Level 1' represented NDVI values less than the mean NDVI minus 0.5 standard deviation, i.e., this level represented the pixel's lowest range in greenness values during the study period, defined as brown pixels. 'Level 3' represented values greater than the mean plus 0.5 standard deviation, i.e., this level represented the pixel's highest range in greenness values during the study period, defined as very green pixels. 'Level 2' greenness was everything that fell between 'level 1' and 'level 3', i.e., mean ± 0.5 SD, defined as green pixels. Thirdly, I collated the rasters into a relative greenness time series. I then overlaid the GPS locations of each individual onto the relative greenness time series and extracted a relative greenness values coinciding with the time and position of each animal location. These data allowed me to identify and compare not only the relative greenness of locations used by each individual but also the time that the animal spent in a predefined relative greenness category.

4.3.5 Data analysis

Based on animal deaths and inability to relocate animals, I analysed three gemsbok GPS data, four body temperature loggers and three activity loggers that recorded data for the whole nine months in CKGR between November 2012 and July 2013 (see Appendix 1 for details). In the Schwelle, I analysed five individual GPS data, five body temperature loggers and four activity loggers for gemsbok (but one activity logger stopped early in July 2014) and two individual's GPS data, four body temperature loggers and two activity loggers for wildebeest that recorded data for all 15 months (see Appendix 2 for details).

To compare annual patterns ambient conditions between sites, I compared monthly averages of mean air temperature, rainfall obtained from weather stations on site (details of weather stations are in 4.3.2) and composited NDVI. NDVI data was extracted from MODIS imagery at the same locations as the weather stations and averaged per month.

To visualize the effects of vegetation greenness and ambient temperature on monthly patterns of activity and body temperature, I averaged (mean ± SD) the minimum 24 h miniglobe temperature on weather station, minimum 24 h body temperatures and total 24 h activity levels per month across all individuals per species, within each site. I also calculated the percentage of mean 24 h locations that were within 'level 1' category of relative greenness (brown vegetation) per month.

To investigate the effect that relative greenness had on total 24 h activity and minimum 24 h body temperatures, I ran a series of generalized linear mixed effects models (GLMMs). The data I included in these analyses were the values for each 24 h period for each individual over the entire study period, that is a total of 457 days per antelope (from October 2013 to December 2014) for the interspecies comparison and 273 days per antelope (from November to July) for the intraspecies (site) comparison. I included minimum 24 h miniglobe temperature as a 'control' variable in all the models because low minimum 24 h miniglobe temperature increase the cost of thermoregulation and may exacerbate 24 h body temperature fluctuations as a result of energy restriction (see chapter 3).

To test for possible variation in the effects of the explanatory variables between species or between site, I included an interaction term for these variables into the GLMMs models. Animal identity was entered as a random effect on the intercept term to avoid pseudoreplication in all models (Pinheiro & Bates 2000). An example of a model was therefore: total 24 h activity ~ minimum 24 h miniglobe temperature + relative greenness + species + minimum 24 h miniglobe temperature * species + relative greenness * species + animal identity [random intercept]. I used model selection procedures using the corrected Akaike's Information Criterion (AICc) to identify which model supported the data best (Burnham et al. 2011). AICc (corrected for small sample bias) allows comparing of potential working hypothesis models and weighting (w_i) for their level of support in the data (Anderson 2008). Of all the candidate models, all models with a difference in AICc value of <2 were considered plausible and were used for making inferences (Anderson 2008). I used R statistical software environment (R Core Team 2015) with R packages lme4 (Bates et al. 2015) to perform the GLMM analysis and AICcmodavg (Mazerolle 2016) to perform the model selection. The conditional R^2 for generalized linear mixed-effect models was calculated for the models along with 95% confidence intervals. The conditional R^2 describes the proportion of variance explained by both the fixed and random factors (Nakagawa & Schielzeth 2013).

To further compare body temperature profiles and activity levels for interspecies comparison when vegetation greenness differed, I selected one month during the dry season when forage quality was limited (October 2013 fell within the 'level 1' relative greenness (brown) category) and a month when forage was green shortly after summer rains (February 2014 fell within the 'level 3' relative greenness (very green) category). Mean 24 h miniglobe temperatures were similar during these two months (October 2013: 25.7 ± 3.2 °C; February 2014: 26.0 ± 2.7 °C; $t_{57} = 0.36$, $p = 0.72$). Using a two-way repeated measures ANOVA, I compared total 24 h activity and minimum 24 h body temperature between species across periods. Bonferroni's multiple comparisons posthoc test was used to identify sources of differences.

To further compare body temperature profiles for the intraspecies comparison, I selected the coldest month (June) during the study period for both sites and compared the relative greenness and the minimum 24 h miniglobe temperature of the two sites and then compared the minimum 24 h body temperatures of gemsbok inhabiting the two sites by using multiple unpaired t-tests.

The two-way repeated measures ANOVA, Bonferroni's multiple comparisons posthoc test and multiple t-tests were performed using GraphPad Prism (version 6.00 for Windows, GraphPad Software, San Diego, CA, USA). Values are expressed as mean and standard deviation and $p < 0.05$ was considered significant.

4.4 Results

4.4.1 Interspecies comparison

Minimum 24 h body temperature and total 24 h activity seemed to decrease as conditions got cool with further decreases evident in the late dry season when vegetation was brown (Figure 4.1). Both variables remained low in September/October when conditions were warming up before the rains (i.e., when both species were still exposed to brown vegetation; Figure 4.1). The likelihood that these responses were influenced by vegetation greenness is further highlighted by the initial months of the study; during a drought, minimum 24 h body temperatures were low, but the response was more pronounced for wildebeest than gemsbok (Figure 4.1). In general, wildebeest selected greener vegetation during a normal dry period but when conditions were particularly dry during the drought, wildebeest and gemsbok were exposed to similarly brown vegetation (Figure 4.1).

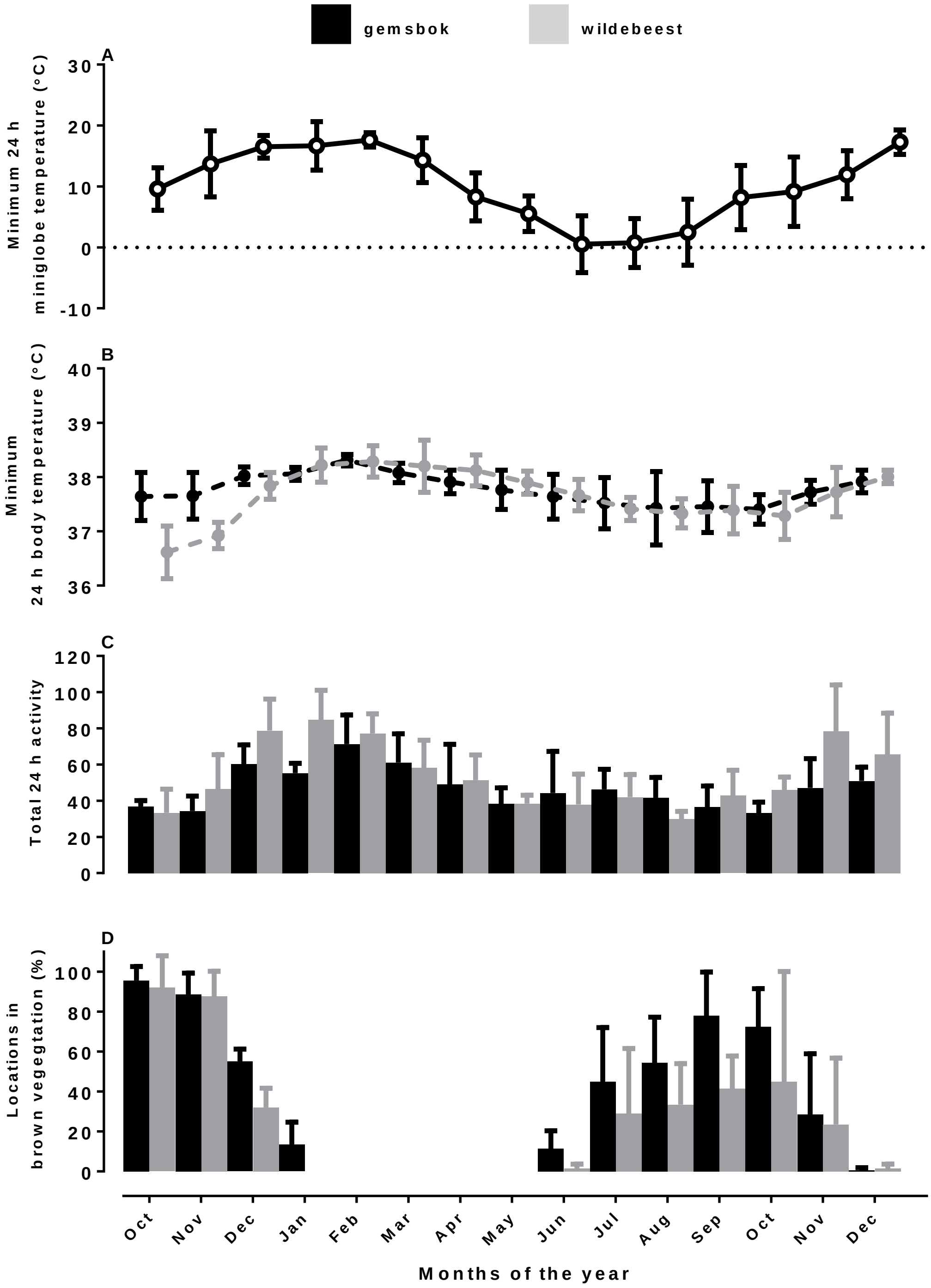

Figure 4.1: (A) Monthly (mean ± SD) minimum 24 h miniglobe temperatures (exposed to the sun on a fixed weather station); and (B) monthly (mean ±SD) minimum 24 h body temperatures for five gemsbok (black) and two wildebeest (grey); (C) total 24 h activity average per month (mean ± SD) for four gemsbok (black) and two wildebeest (grey); and (D) the proportion of locations (%) when individuals inhabited areas with brown vegetation, calculated from collar GPS positions for five gemsbok (black) and two wildebeest (grey) over the 15 month study period in Schwelle field site in Botswana. Points are offset for clarity.

To understand the influence of minimum 24 h miniglobe and/or relative greenness on total 24 h activity of sympatric species, I ran model selection on a series of GLMMs. Total 24 h activity was dependent on species, minimum 24 h miniglobe temperature and relative greenness, with the best supported model including all three of these terms as the main effects (model 1, Table 4.1, with the lowest AICc score and Akaike's weight of 0.96). The best supported model also included an interaction between minimum 24 h miniglobe temperature and species and between relative greenness and species implying that minimum 24 h miniglobe and relative greenness influenced the species activity patterns differently. However, the model was only confident in explaining 21% (Conditional R^2 = 0.21) of the variance of the total 24 h activity. After controlling for minimum 24 h miniglobe temperature, wildebeest were generally more active than gemsbok when exposed to 'very green' vegetation. As vegetation transitioned from very green to green, wildebeest showed a greater decline in total 24 h activity than gemsbok, but the decline in total 24 h activity when vegetation transitioned from green to brown was similar between the species (Figure 4.2A).

Table 4.1: Candidate generalized linear mixed models describing the response total 24 h activity for four gemsbok and two wildebeest in Schwelle study site, showing various explanatory variables and interactions (×) included. Models are listed in descending order of likelihood according to their corrected Akaike information criterion (AICc). Data were entered as one point per individual per day (N=2488). Δ_i is the delta AICc (difference between the AICc for a given model and the best fitting model), *k* is the number of estimated parameters and ω_i is the model selection probability (Akaike weights). Animal identity was included as a random effect. All models are shown except those where ω_i was zero.

Model Ranking	Fixed Effects	*k*	AICc	Δ_i	ω_i
1	minimum 24 h miniglobe + relative greenness + species + minimum 24 h miniglobe x species + relative greenness x species	10	23768.31	0.00	0.96
2	minimum 24 h miniglobe + relative greenness + species + minimum 24 h miniglobe x species	8	23775.32	7.02	0.03
3	minimum 24 h miniglobe + relative greenness + species + relative greeness x species	9	23777.77	9.46	0.01
4	minimum 24 h miniglobe + relative greenness + species	7	23794.91	26.60	0.00

To tease out the effects of minimum 24 h miniglobe and relative greenness on minimum 24 h body temperature, I ran model selection on a series of GLMMs. Two models were plausible and received a total 100% of the model weight (model 1 and model 2, Table 4.2). Both models included species, minimum 24 h miniglobe temperature, and relative greenness as the main effects explaining minimum 24 h body temperature. The second model only differed by the inclusion of the interaction term “minimum 24 h miniglobe x species” (Table 4.2). Model 1 (without the interaction term) was 2.7 times more likely (0.73 vs. 0.27) to be the best supported model than model 2 (with the interaction term). Based on the differences in AICc there was little support for a difference in species responses to minimum 24 h miniglobe as the strength of the model didn’t improve significantly when this interaction was included. These models contributed 54% (Conditional $R^2 = 0.54$) of the total variance of minimum 24 h body temperature experienced by the animals. The models also contained an interaction between relative greenness and species, suggesting that relative greenness influenced minimum body temperatures of the two species differently. When controlling for minimum 24 h miniglobe temperature, wildebeest showed a greater decline in minimum 24 h body temperature as vegetation transitioned from very green to brown (Figure 4.2B).

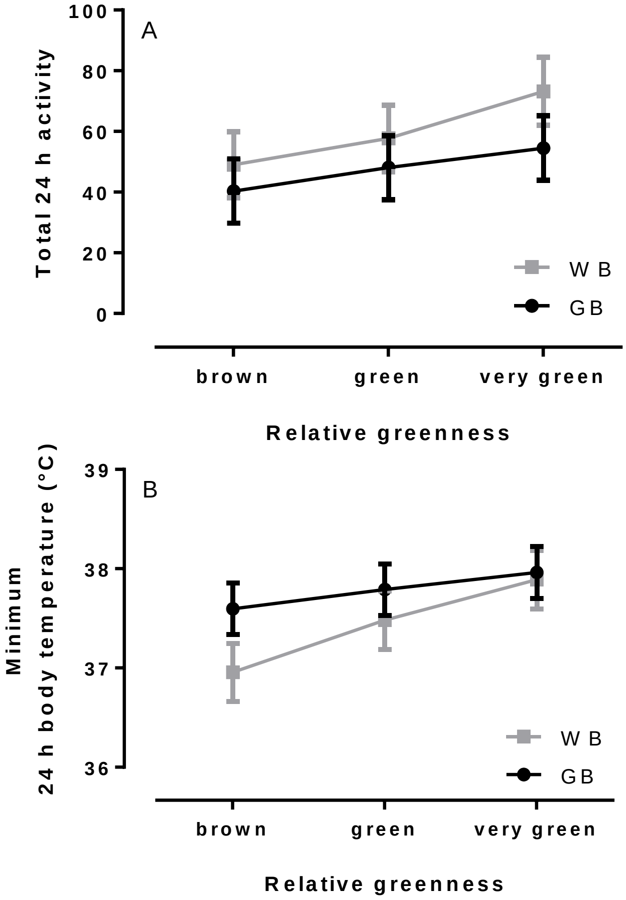

Figure 4.2: Mean with 95% CIs for the relationship between (A) total 24 h activity and relative greenness for four female gemsbok and two female wildebeest; (B) minimum 24 h body temperature (°C) and relative greenness for five female gemsbok and four wildebeest, living freely in the Schwelle study site in Botswana during October 2013 – December 2014. Each relative greenness category represents the vegetation greenness, namely ‘brown’, ‘green’ and ‘very green’, of the actual areas inhabited by the individuals based on hourly GPS data from the collars.

Table 4.2: Candidate generalized linear mixed models describing minimum 24 h body temperature for five gemsbok and four wildebeest in Schwelle study site in Botswana during October 2013 – December 2014, showing various explanatory variables and interactions (×) included in models. Candidate models are listed in descending order of likelihood according to their corrected Akaike information criterion (AICc). Data were entered as one point per individual per day (N=3433). Δ_i is the delta AIC (difference between the AIC for a given model and the best fitting model), *k* is the number of estimated parameters and ω_i is the model selection probability (Akaike weights). Animal identity was included as a random effect. All models are shown except those where ω_i was zero.

Model ranking	Fixed Effects	*k*	AICc	Δ_i	ω_i
1	minimum 24 h miniglobe + relative greenness + species + relative greenness x species	9	3640.80	0.00	0.73
2	minimum 24 h miniglobe + relative greenness + species + relative greenness x species + minimum 24 h miniglobe x species	10	3642.78	1.98	0.27
3	minimum 24 h miniglobe + relative greenness + species + minimum 24 h miniglobe x species	8	3850.90	210.10	0.00

To visualize the effects of varying vegetation greenness on 24 h body temperature and total activity, I selected two months with the same miniglobe temperature but differing in vegetation greenness, namely ‘brown’ and ‘very green’. Total 24 h activity did not differ between species ($F_{1,6}$ = 0.04, p = 0.84), and both species responded similarly to varying vegetation greenness ($F_{1,6}$ = 0.65, p = 0.45), with both species showing significantly less activity during the ‘brown’ period compared to the ‘very green’ period ($F_{1,6}$ = 45.7, p = 0.0005; Figure 4.3). Both species also showed lower minimum 24 h body temperature during the ‘brown’ period compared to the ‘very green’ period ($F_{1,7}$ = 62.2, p < 0.0001; Figure 4.3), but this drop in minimum 24h body temperature was more pronounced for wildebeest compared to gemsbok ($F_{1,7}$ = 8.2, p = 0.02) so that overall wildebeest displayed a lower minimum 24 h body temperature than gemsbok ($F_{1,7}$ = 12.55, p = 0.009; Figure 4.3).

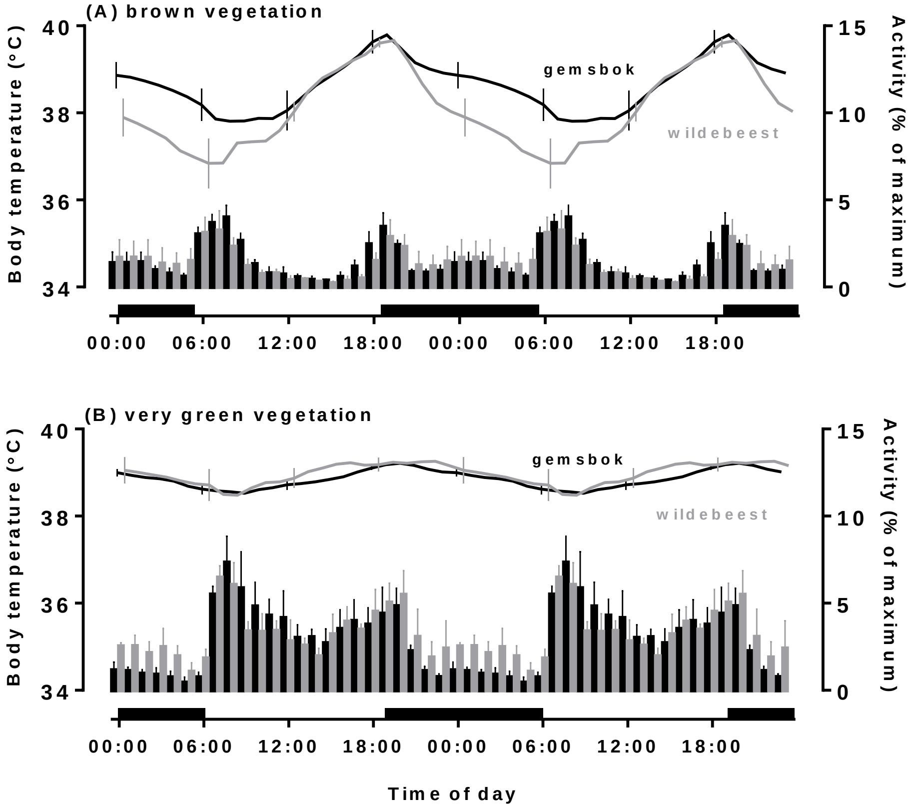

Figure 4.3: Mean (± SD) 24 h rhythm of body temperatures averaged for five free-living female gemsboks (black line) and four female wildebeests (grey line) and mean 24 h rhythm of activity averaged for four female gemsboks (black bar) and two female wildebeests (grey bar) during a (A) brown period (mean 24 h miniglobe temperature of 25.8 ± 3°C, 24 h minimum of 20.3 ± 3°C and 24 h maximum of 42.2 ± 3°C) when forage quality was low and (B) a very green period (mean 24 h miniglobe temperature of 25.9 ± 2.5°C, 24 h minimum of 20.9 ± 2.5°C and 24 h maximum of 39.9 ± 3°C) following rain. Points are offset for clarity. Data is double plotted to ease visualization of the 24 h patterns. Black bars represent night-time for each period.

4.4.2 Intraspecies comparison

In the Schwelle, miniglobe temperatures reached a maximum of 53 °C during December 2014 and dropped to as low as −8 °C in June 2014, giving a range of 61 °C. The range in miniglobe temperature was much smaller in CKGR where miniglobe temperature reached a maximum of 47 °C during November 2012 and dropped to as low as 8 °C during June 2013, giving a range of 39 °C. For comparison between sites, I selected a 9 month period that occurred during the same time of the year (grey block in Figure 4.4). During the 273 study days (from November to July), rainfall occurred in the Schwelle on 81 days, with a total rainfall of 199 mm resulting in an annual rainfall of 203 mm (calendar year), lower than the long-term mean annual rainfall. Rainfall occurred in the CKGR on 43 days, with total rainfall of 156 mm, resulting in an annual rainfall of 169 mm, less than half of the long-term mean annual rainfall (<350 mm; Figure 4.4). Although the Schwelle area is generally classed as more arid compared to CKGR, the unusually low rainfall in CKGR, resulted in CKGR being more arid than Schwelle during the study period.

As a result of the unusually dry conditions in CKGR, gemsbok were exposed to brown vegetation early in the dry season (April/May), and showed lower total 24 h activity and minimum 24 h body temperatures than gemsbok in Schwelle region (Figure 4.5). As the dry season progressed and gemsbok were increasingly exposed to brown vegetation, minimum 24 h body temperatures and total 24 h activity declined for gemsbok inhabiting both field sites, however, this drop in minimum 24 h body temperature and total 24 h activity was noticeably earlier and more extreme for gemsbok in CKGR than gemsbok in Schwelle region (Figure 4.5).

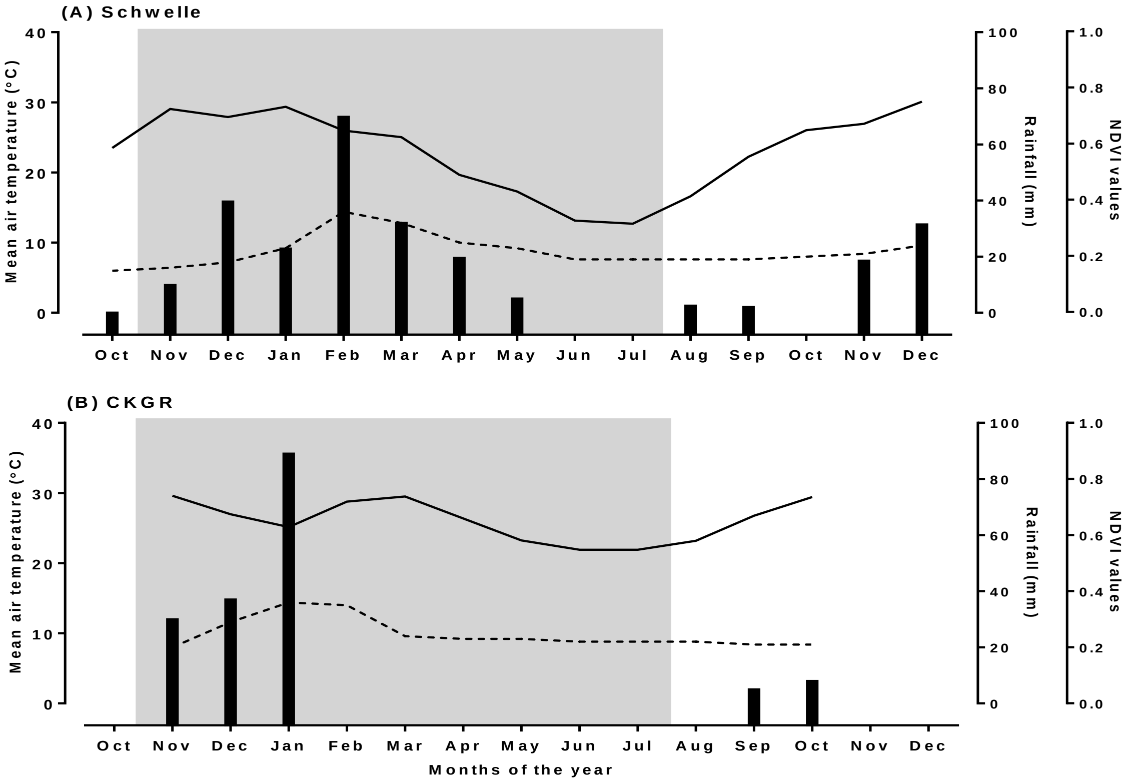

Figure 4.4: Comparison of the monthly mean air temperature (solid line), total monthly rainfall (black bars) and monthly composited greenness (NDVI) time series (dashed line) of A) Schwelle site over 15 months and B) CKGR site over 12 months, in Botswana. Rainfall and air temperature data were obtained from Agricultural Research Council (ARC) weather station located at the Nossob campsite (S 25.4, E 20.6) for Schwelle and from the Central Kalahari Game Reserve Office at Matswere gate for CKGR (S 21.26 °, E 24.12 °). NDVI data was extracted from MODIS imagery at the same locations as the weather stations. The grey box represents the time period considered for the comparison of gemsbok between two sites.

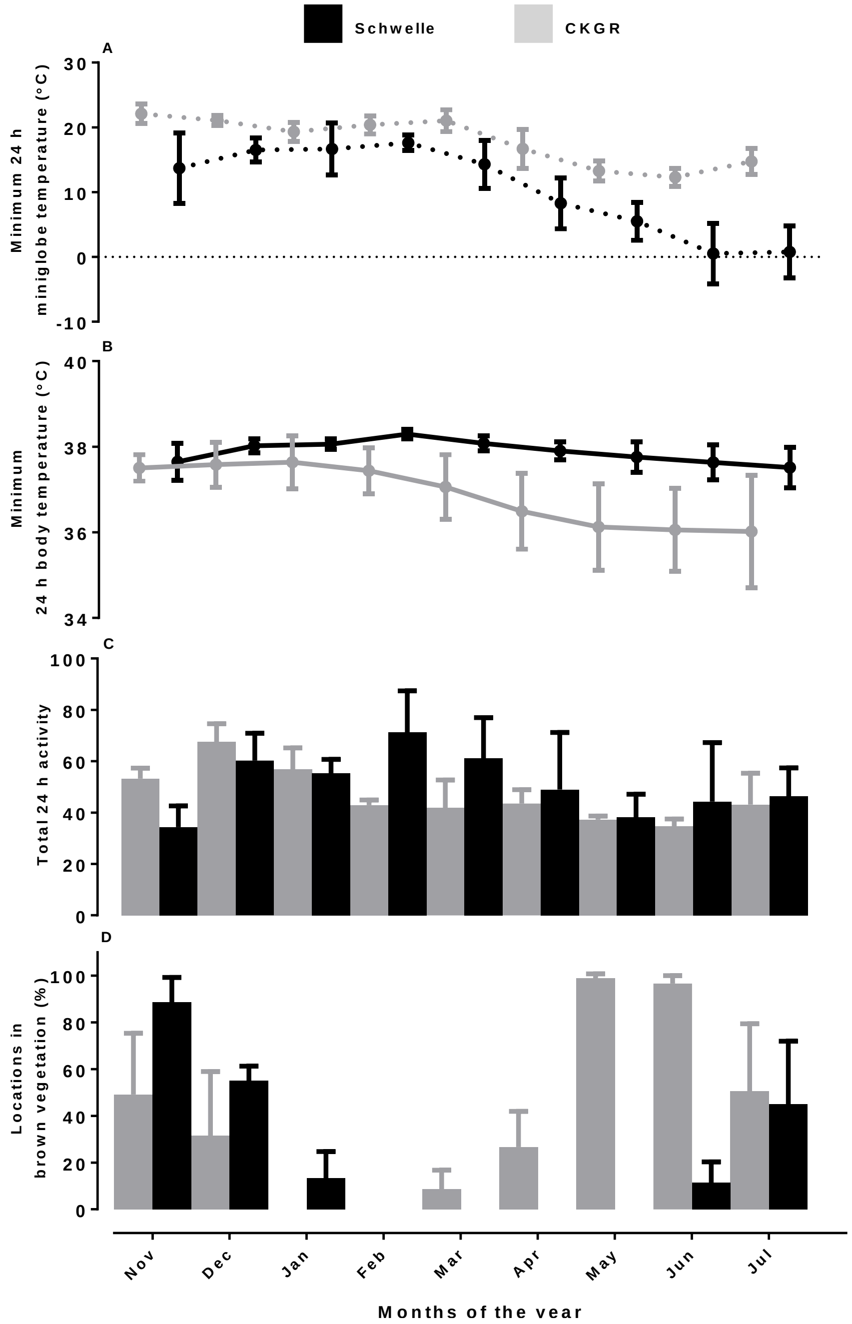

Figure 4.5:(A) Monthly (mean ± SD) minimum 24 h weather station miniglobe temperatures; (B) monthly (mean ±SD) minimum 24 h body temperatures for five gemsbok in Bakgalagadi Schwelle site (black line) and three gemsbok in Central Kalahari Game Reserve site (grey line); (C) total 24 h activity average per month (mean ± SD) for four gemsbok in Bakgalagadi Schwelle site (black bar) and two gemsbok in Central Kalahari Game Reserve site (grey bar); and (D) the proportion of locations (%) when individuals inhabited areas with brown vegetation, calculated from collar GPS positions for five gemsbok in Schwelle site (black bars) and four gemsbok in the drier Central Kalahari Game Reserve (grey bars), November to July, within each study site. Points are offset for clarity.

To investigate the effects of minimum 24 h miniglobe and relative greenness on total 24 h activity, I ran model selection on a series of GLMMs. Three models were considered plausible, all of which included minimum 24 h miniglobe temperature and relative greenness as main effects. The best supported model (model 1) included ‘site’ and the interaction term “minimum 24 h miniglobe x site” and model 3 also included the interaction term “relative greenness x site” (Table 4.3). Model 1, the best-supported model, received 37% of the model-selection weight, with an AICc score of 1.2 and 1.3 times better than the second and third best supported models respectively (32% of weight and 28% of weight; Table 4.3). Based on the differences in AICc there was little support for total 24 h activity differences between the field sites as the strength of the model didn’t improve significantly when this term with interactions were included. However, relative greenness had the strongest influence on total 24 h activity since it was present in all the top models. All three models were poor at explaining variance in 24h activity (Conditional $R^2 = 0.14$). After controlling for differences in minimum 24 h miniglobe temperature, total 24 h activity declined when conditions were brown and there was virtually no difference between sites (Figure 4.6A).

Table 4.3: Candidate generalized linear mixed models describing total 24 h activity for five gemsbok in Schwelle study site and for three gemsbok in Central Kalahari Game Reserve study site, showing various explanatory variables and interactions (×) included in models. Models are listed in descending rank according to their corrected Akaike information criterion (AICc). Data were entered as one point per individual per day (N=1634). Δ_i is the delta AIC (difference between the AIC for a given model and the best fitting model), *k* is the number of estimated parameters and ω_i is the model selection probability (Akaike weights). Animal identity was included as a random effect. All models are shown except those where ω_i was zero.

Model ranking	Fixed Effects	*K*	AICc	Δ_i	ω_i
1	minimum 24 h miniglobe + relative greenness + site + minimum 24 h miniglobe x site	8	15321.73	0.00	0.37
2	minimum 24 h miniglobe + relative greenness	6	15321.97	0.24	0.32
3	minimum 24 h miniglobe + relative greenness + site + minimum 24 h miniglobe x site + relative greenness x site	10	15322.23	0.50	0.28
4	minimum 24 h miniglobe + relative greenness + site	7	15323.76	2.03	0.12
5	minimum 24 h miniglobe + relative greenness + site + relative greenness x site	9	15327.15	5.42	0.02
6	relative greenness	5	15376.78	55.04	0.00

Unlike activity, minimum 24 h body temperature did differ between gemsbok inhabiting the different areas. Field site, relative greenness and minimum 24 h miniglobe temperature influenced minimum 24 h body temperature, with the best supported model including these three main effects as well as two interaction terms between minimum 24 h miniglobe and field site and between relative greenness and field site (model 1, Table 4.4, with the lowest AICc score and Akaike's weight equal to 1, Conditional $R^2 = 0.75$). After controlling for differences in minimum 24 h miniglobe temperature, gemsbok in CKGR generally had lower minimum 24 h body temperature compared to those in Schwelle and showed a more exaggerated decline in minimum 24 h body temperature when they were exposed to brown areas (Figure 4.6B).

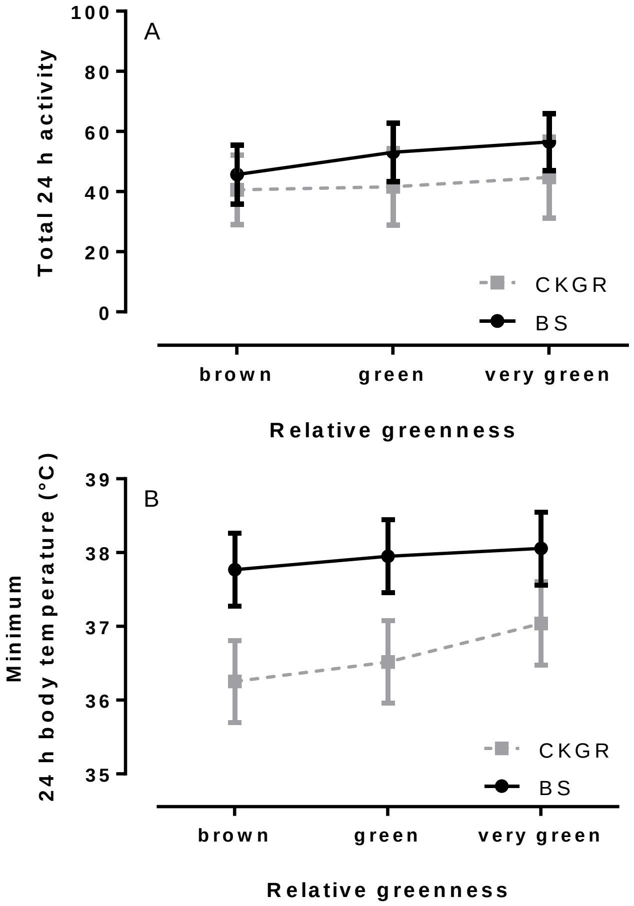

Figure 4.6: Mean with 95% CIs for the relationship between (A) total 24 h activity and relative greenness for four female gemsbok in the Schwelle study site and two female gemsbok in the CKGR study site; (B) minimum 24 h body temperature (°C) and relative greenness for five female gemsbok in the Schwelle study site and four female gemsbok in the CKGR study site. Each relative greenness category, namely 'brown', 'green' and 'very green', represents the vegetation greenness of the actual areas, occupied by the gemsbok based on GPS locations recorded on their collars.

Table 4.4: Candidate generalized linear mixed models, describing minimum 24 h body temperature for five gemsbok in Bakgalagadi Schwelle study site and for three gemsbok in Central Kalahari Game Reserve study site, showing various explanatory variables and interactions (×) included. Models are models listed in descending order ranked according to their corrected Akaike information criterion (AICc). Data were entered as one point per individual per day (N=1634). Δ_i is the delta AIC (difference between the AIC for a given model and the best fitting model), *k* is the number of estimated parameters and ω_i is the model selection probability (Akaike weights). Animal identity was included as a random effect. All models are shown except those where ω_i was zero.

Model ranking	Fixed Effects	*k*	AICc	Δ_i	ω_i
1	minimum 24 h miniglobe + relative greenness + site + minimum 24 h miniglobe x site + relative greenness x site	10	2572.72	0.00	1
2	minimum 24 h miniglobe + relative greenness + site + minimum 24 h miniglobe x site	8	2646.29	73.57	0

To visualize the effect of environmental conditions on body temperature, I selected the coldest month (June) during the study period for both sites. Despite gemsbok in CKGR being exposed to a milder winter (i.e., less extreme minimum 24 h miniglobe temperature CKGR: 12.3 ± 0.2 °C vs. Schwelle: 1.0 ± 0.8 °C; t_{58} = 13.71, $p < 0.0001$), they had lower minimum 24h body temperatures (CKGR: 36.1 ± 0.9°C vs. Schwelle: 37.6 ± 0.4°C, t_7 = 3.33, $p = 0.013$; Figure 4.7), which was likely the result of their exposure to browner vegetation compared to gemsbok in the Schwelle in June (CKGR gemsbok inhabited brown vegetation during 96% of locations vs. Schwelle gemsbok that inhabited brown vegetation during 39% of locations; Figure 4.5D).

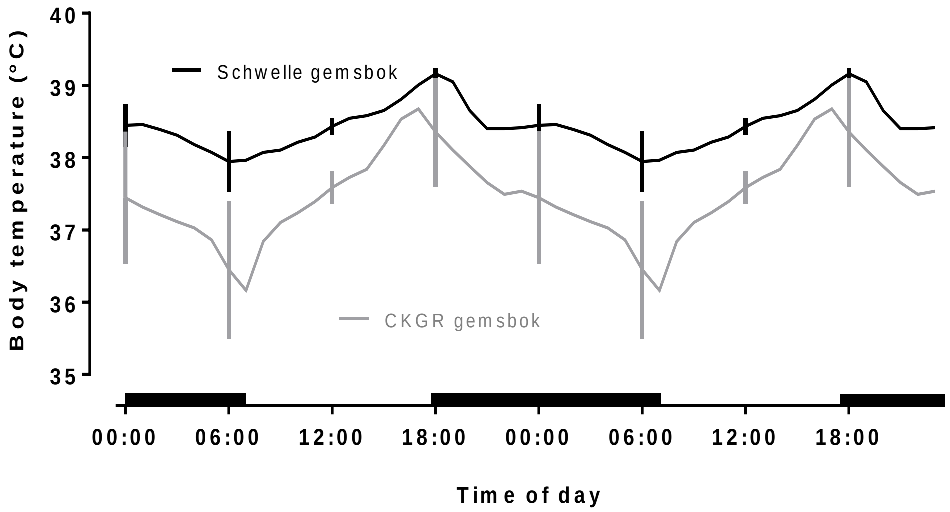

Figure 4.7: Mean ± SD of 24 h body temperatures rhythm averaged for five free-living female gemsboks from Schwelle study site (black line) and four free-living female gemsbok from the drier CKGR study site (grey line), during the coldest month of the year (June). Black bars represent night-time for each period. Data is double plotted to ease visualization of the 24 h patterns. Gemsbok in the drier CKGR had lower minimum 24 h body temperature despite being exposed to warmer minimum 24 h miniglobe temperature.

4.5 Discussion

Rather than a seasonal comparison (chapter 3), this study sought to quantitatively assess the influence of vegetation greenness on activity and thermoregulation of two sympatric free-ranging antelopes. I found that wildebeest increased their activity more than gemsbok when conditions became green (Figure 4.2A). However, when vegetation transitioned from green to brown, both species reduced their activity. Wildebeest appeared to be struggling more than gemsbok when exposed to brown vegetation, as their minimum 24 h body temperatures were lower than those of gemsbok (Figure 4.2B). However, when the arid adapted species was exposed to increased aridity, the gemsbok in the more arid site (CKGR) showed lower minimum 24 h body temperatures than the gemsbok in the less arid site (Schwelle; Figure 4.7), despite being exposed to a warmer climate. This drop in minimum 24 h body temperature suggests that wildebeest in the less arid site and gemsbok in the more arid site were temporarily abandoning homeothermy when quality of vegetation was inadequate.

The results presented here do have some limitations. Firstly, technology failure resulted in a small sample size of activity data for wildebeest in Schwelle and gemsbok in CKGR. Secondly, the activity models reported a low model confidence which could result from small sample sizes or possibly that vegetation greenness and miniglobe temperatures were not the only determinants of total 24 h activity. NDVI greenness measures are not a comprehensive measure of resources availability as it does not directly quantify any biological variable (Pettorelli et al. 2011). For example, soil minerals, tsamma melons (*Citrullus lanatus*), underground roots, gemsbok cucumbers (*Acanthosicyos naudinianus*) (Knight 1991) are a few of the resources that ungulates may rely on during brown periods which NDVI greenness measures cannot detect. Despite the small sample sizes and limitations with the use of NDVI as a proxy for forage quality, I did find differences in behavioural and thermoregulatory responses to vegetation greenness between species and between study sites of differing aridity.

When vegetation transitioned from brown to very green, there was an apparent increase total 24 h activity of both species, more so for wildebeest than gemsbok. A possible explanation for this increase in activity could be that both species are replenishing energy and protein reserves for the next dry season as suggesting for northern ungulates (Parker et al. 2009). Similarly, wildebeest in CKGR displayed the highest level of activity during the wet season compared to the dry season, which the authors attributed to accumulating energy and protein from forage to meet maintenance and reproductive requirements to survive the next dry season (Selebatso et al. 2017b). I therefore suggest that the increase of activity when vegetation was very green suggests that wildebeest, more so than gemsbok, were compensating for the lack of nutrition that could have resulted from the previous dry season rather. This response of increased activity when vegetation is very green may suggest that wildebeest (potentially more so than gemsbok) depend on green vegetation to support their energy needs, so that a larger decline in activity as conditions get brown indicates an inability to obtain sufficient energy.

There are two foraging strategies that large mammals use when faced with limited food resources: either they will increase their metabolic rate and foraging effort to allow more time to seek out better-quality food types (Owen-Smith 2008), or they will reduce their metabolic rate by reducing their activity levels to conserve energy (McCue et al. 2010; Wang et al. 2006). When faced with poor quality forage, ruminants require increased rumination time to successfully digest the food (Cain et al. 2006). In an environment where water is limited, grazers may be forced to reduce the rate of forage intake when forage quality declines (Cain et al. 2006). Since a lack of water content (Cain et al. 2006) or simply higher fibre content of senesced grasses (Wilmshurst et al. 2000) may slow down the passage rate of the forage, grazers may be restricted in the amount of food they can consume per day compared to a higher quality forage (i.e., browse; Owen-Smith 2002). Since foraging was a major contribution to activity, this finding is consistent with both species spending less time feeding, observed as a decrease in total 24 h activity, when forage quality was limited (brown). Similar to the results of this study, wildebeest in CKGR presumably conserved energy by reducing activity in forage limited dry seasons (Selebatso et al. 2017b). When conditions are unfavourable a reduction in activity may minimize depletion of body reserves and conserve energy (Milton 1998; Rezende & Bozinovic 2001). However, contrary to the results of this study, earlier observations within the southern Kalahari (Knight 1991), reported that both wildebeest and gemsbok increased their diurnal activity in response to reduced food quality and quantity in the hot dry period. This increase in activity may have been an artefact associated with human observation error since observations were made from a vehicle and for only two days per month per year. Using biologgers, I was able to obtain continuous measurements of activity of undisturbed free-living wildebeest and gemsbok. It is plausible that both species increased their diet breadth shown by the increase in activity, however, when nutrient intake falls below maintenance demands, a narrowing of the diet should occur (Owen-Smith & Novellie 1982), resulting in a negative energy balance as observed by a reduction in activity in this study.

This negative energy balance when vegetation turns brown is further supported by the low minimum 24 h body temperatures presented by both species. Minimum 24 h body temperatures and total 24 h activity of both species were lower when exposed to brown forage than during a period when exposed to very green forage, despite similar ambient temperatures during these two periods (Figure 4.3). Western grey kangaroos (*Macropus fuliginosus*; Maloney et al. 2011) and Arabian oryx (Hetem et al. 2010) in dry summer months, and wildebeest (Shrestha et al. 2011) in a cool dry season, demonstrated a similar decline in minimum body temperature. This drop in minimum 24 h body temperature during the dry season, observed in other studies, has been attributed to a reduced quality and quantity of forage. Within this chapter, I present the first quantifiable link between forage quality (indexed by NDVI) and minimum 24 h body temperature and compared to gemsbok, wildebeest had a greater decline in minimum 24 h body temperatures when exposure to brown vegetation increased (Figure 4.2B). This drop in minimum 24 h body temperature was enhanced during a drought (initial dry month), when wildebeest experienced the lowest minimum 24 h body temperatures throughout the study period; one wildebeest displayed a minimum 24 h body temperatures as low as 34.5 °C. Thus, the difference in minimum 24 h body temperature between the two species suggests that the less arid-adapted species struggled more with energy balance during the dry season when quality of forage is reduced. Gemsbok, the more arid-adapted species may have increased their diet breadth as a response to poor vegetation quality and included forbs, fruit such as tsamma melons (*Citrullus lanatus*) and browsing during the dry season (Knight 1991). Unlike grass, browse is less dependent on rainfall and can retain most of its nutrients late into the dry season (Owen-Smith 1994; Owen-Smith 2002).

If gemsbok switched to browse and widely distributed resources, such as melons, in the dry season they may still be able to maintain a positive energy balance. Yet, the gemsbok in the more arid site (CKGR), exposed to a milder winter, showed even lower minimum 24 h body temperatures compared to the gemsbok in the less arid site (Schwelle), with minimum 24 h body temperature dropping to as low as 33.3 °C for one female gemsbok. Not only did the CKGR have less rainfall; compared to Schwelle during the study period, but CKGR’s rainfall was substantially lower than the long-term mean to which the gemsbok within this region were accustomed. This reduction in rain would have reduced the preformed water in plants and vegetation quality and browse may have also have senesced earlier in the CKGR owing to less rainfall, as highlighted by their greater exposure to brown vegetation. In addition, tsamma melons are not common in the northern CKGR because of a lack of sandy soils, thus CKGR gemsbok have less ability to switch to melons during dry periods. I believe that the results indicate that the gemsbok population in the more arid site was possibly more physiologically stressed by the more arid conditions than the gemsbok population in the less arid site. Therefore, there may be limits of aridity to which the gemsbok can adapt. Similar reductions in minimum 24 h body temperature were reported for wildebeest at a more arid site compared to a colder site (Shrestha et al. 2011).

An endotherm's energy balance may become compromised either by increased energy costs (low ambient temperatures) or by reduced energy supply (inadequate forage intake; Maloney et al. 2013; Hetem et al. 2016). A common response of large mammals to insufficient energy intake appears to be a decrease in metabolic rate accompanied by a decrease in minimum body temperatures and a decrease in energy expenditure (Arnold et al. 2004; McCue 2010; Signer et al. 2011; Maloney et al. 2013). As such Alpine ibex (Signer et al. 2011), red deer (Arnold et al. 2004) and horses (Arnold et al. 2006) decreased metabolic rate during winter, when the animals must cope with inaccessible forage (i.e., buried under snow). These studies occurred during winter when cold conditions and reduced available food often coincide, making it difficult to tease out the effects of cold from the effects of reduced energy supply in free-living ungulates (Hetem et al. 2016). Interestingly, free-living western grey kangaroos displayed low minimum body temperatures during summer, presumably in anticipatory for hot days (Maloney et al. 2004), and dromedary camels displayed low minimum body temperatures during rutting (Grigg et al. 2009). Yet, both incidences occurred during a time when energy availability was likely limited. A recent study on free-living western grey kangaroos proposed that the low minimum 24 h body temperatures displayed at the end of summer likely resulted from inadequate forage intake, a time when they were not exposed to cold stress (Maloney et al. 2011). Two experimental studies on sheep (*Ovis aries*; Maloney et al. 2013) and red deer (Turbill et al. 2011) showed that both species displayed low minimum body temperatures when their diets were restricted and the ambient temperatures were controlled. However, I have shown that the forage quality (indexed by NDVI) was the primary driver of minimum 24 h body temperatures, particularly for gemsbok inhabiting an arid site (Figure 4.6B & 4.7). My results I concur with Turbill et al. (2011) and Maloney et al. (2011 & 2013) who concluded that the decline in body temperature and energy expenditure was more related to diet restriction than ambient temperature.

By using NDVI as a proxy for vegetation greenness, I was able to link changes in activity and body temperature to vegetation quality in free-living gemsbok and wildebeest. I propose that during times of low vegetation greenness (brown period), the drop in minimum body temperature is determined not by ambient temperatures alone, but also by inadequate energy intake caused by aridity. Although both wildebeest and gemsbok reduced their total 24 h activity to conserve energy when vegetation was brown, the reduction in activity was not enough to maintain a positive energy balance and possibly required them to use fat and other body reserves, as seen in sheep (Illius & Gordon 1998). When forage quality was at its lowest and they were unable to obtain sufficient energy and protein from their diets, body stores likely began to decline, which ultimately resulted in a starvation-induced hypothermic response. Under conditions of inadequate energy intake large mammals have to “trade off” energy conservation and thermoregulation (Hetem et al. 2016) and ungulates of the Kalahari appear to prioritize the conservation of energy over the maintenance of a high body temperatures.

CHAPTER 5

5 Behavioural and thermoregulatory responses of two sympatric free-ranging ungulates living in the semi-arid Kalahari in relation to distance to water.

5.1 Abstract

Access to surface water is often restricted in a semi-arid environment. This restriction is further exacerbated by high air temperatures during hot seasons. Understanding physiological flexibility of species currently occupying hot and dry environments provides an analogue for conditions likely to become prevalent in the future. In this study, I investigated how distance to water (i.e., how frequent animals were likely to have accessed the water) may influence microclimate selection, activity and body temperature of two sympatric species of antelope with different water dependencies, namely blue wildebeest (*Connochaetes taurinus*) and gemsbok (*Oryx gazella gazella*), free-living in the Kalahari. Both species selected similar microclimates when miniglobe temperature exceeded body temperature with enhanced shade seeking when water sources were likely too far to drink frequently. However, wildebeest, compared to gemsbok, were less active during the heat of the day and displayed higher maximum 24 h body temperature when the likelihood of frequently drinking water decreased with increasing distance from water. The hyperthermia resolved following first rains. I suggest that the high maximum 24 h body temperatures of wildebeest in the Kalahari was the result of dehydration during thermal stress. With climate change predicted to increase ambient temperatures and have less predictable rainfall in the semi-arid Kalahari, water-dependent wildebeest will likely experience greater thermal stress in the future.

5.2 Introduction

The most limiting factor for plants and animals in arid and semi-arid ecosystems is water (Louw & Seely 1982; Noy-Meir 1973). Indeed, distance to water is one of the primary determinant of distribution patterns of ungulate species (Bailey et al. 1996). Numerous studies have looked at the effect of distance to water on animal distribution and habitat use (Western 1975; Bailey et al. 1996; Redfern et al. 2003; Chamaillé-Jammes et al. 2007). In the Kruger National Park, where access to high-quality forage may be limited during the dry season, it was suggested that wildebeest face a trade-off between nutritional requirements and surface-water constraints (Redfern et al. 2003). Since wildebeest occurred closer to water in the dry season compared to the wet season, one could argue that wildebeest's physiological stress levels increase further from water (Western 1975; Redfern et al. 2003). Yet, no one to date has quantified differences in microclimate selection, activity and body temperature profiles in relation to distance to water.

The Kalahari, a semi-arid environment, is currently hot and semi-arid (little surface water with high evaporation rates) and likely to become increasingly hotter with less predictable rainfall under future climate change scenarios (Davis 2011; van Wilgen et al. 2016). Success in these semi-arid environments requires optimal management of body water, which all arid-zone mammals need to conserve to maintain body fluid status but also need for evaporative cooling in hot environments. Achieving optimal management of body water will become more problematic in the face of ongoing climate change. Understanding physiological and behavioural flexibility of ungulates currently occupying hot and dry environments will help to elucidate plasticity and adaptation potential of these species in the face of future climate change.

Heat loss by means of radiation, convection, and conduction, requires ambient temperature to be lower than body temperature. When ambient temperature exceeds body temperature, an endotherm must either use evaporative cooling to dissipate heat or tolerate an increase in body temperature (Cain et al. 2006; Tattersall et al. 2012). Evaporative cooling, or better known as evaporative heat loss, can occur by the evaporation of water from either the skin (through sweating/licking) or respiratory tract (panting) and is the only means of heat loss when environmental temperature exceeds body temperature of an endotherm (Hetem et al. 2016). An endotherm with sufficient water will be able to maintain thermoregulation within a fairly narrow range in most conditions (Mitchell et al. 2002), but if an endotherm is water stressed, it may not be able to maintain its body temperature within a restricted or preferred range (Tattersall et al. 2012; Boyles et al. 2011). Dehydration-induced hyperthermia results when an endotherm has insufficient body water to support evaporative cooling (Mitchell et al. 2002; Hetem et al. 2016), hence body temperatures will rise as ambient heat stress increases. This increase in body temperature will decrease the thermal differential for heat gain from the environment and subsequently conserve body water (Mitchell et al. 2002). Some arid-adapted mammals may tolerate high body temperatures resulting in a reduction in the evaporative water loss that is initially required for thermoregulation, thereby conserving body water (e.g., dromedary camel (*Camelus dromedarius*), Schmidt-Nielsen et al. 1957; Arabian oryx (*Oryx leucoryx*) and sand gazelle (*Gazella subgutturosa marica*), Hetem et al. 2012b). Both gemsbok and wildebeest showed an increase in maximum 24 h body temperature during arid conditions (Chapter 3). However, tolerance of high body temperature does not come without costs, physiological performances may need to be traded-off against hyperthermia and eventually a critical body temperature may be reached, and the animal may die (Tattersall et al. 2012).

Thermoregulatory behaviour, like cool microclimate selection or a reduction of activity, may reduce the need to evaporative cooling and are generally less costly than physiological processes to maintain homeothermy (i.e., regulation of body temperature within a narrow range). An endotherm can reduce radiant heat load by seeking shade (Cain et al. 2008; Hetem et al. 2012a). Also, an endotherm could potentially reduce metabolic heat production by not being active during times of high heat load (Cain et al. 2006; Hetem et al. 2012a). These thermoregulatory behaviours may be enhanced when water is limited. Arabian oryx in the Saudi Arabian desert increased their selection of cooler microclimates and virtually ceased daytime activity when surface water had dried up and conditions became more arid (Hetem et al. 2012a). Gemsbok and wildebeest too increased their microclimate selection and reduced daytime activity during the hot dry period (Chapter 3). Currently, little data is available on the impact that distance to water may have on potential behavioural adaptations to high ambient temperatures.

If frequent access to surface water is essential for ungulates to maintain a positive water balance (Redfern et al. 2003), species' thermoregulatory responses relative to water sources should correspond to their water dependence. For instance, in hot environments water-independent species should be able to sustain homeothermy regardless of surface water, whereas water-dependent species might only be able to sustain homeothermy within a short distance to water, yet no study has confirmed this theory. Blue wildebeest are described as being water dependent, since they exhibit daily drinking patterns (Berry 1980; Berry et al. 1982), whereas, gemsbok are reputed to be able to survive without drinking any water at all (Taylor 1968a,b). In the southern Kalahari, both gemsbok and wildebeest differed in their use of waterholes for drinking, with wildebeest using the waterholes for drinking more frequently than gemsbok (Knight 1991). Differences in water dependence among ungulate species may arise through a variety of physiological, morphological and behavioural mechanisms employed in the maintenance of temperature and water balance (Knight 1991, Cain et al. 2006). A more detailed examination of the relationship between surface water and thermoregulatory behaviour may therefore reveal insights into how individuals may respond to heat and aridity associated with climate change.

The focus of this chapter is to investigate whether individuals with less frequent access to drinking water (indexed as distance to surface water) enhance their use of thermoregulatory behaviour and are at greater risk of dehydration-induced hyperthermia. I hypothesise that gemsbok and wildebeest will seek out more intense shade more frequently when they are further away from a water source to reduce heat load and conserve body water when ambient temperature exceeds body temperature. I further predict that the water dependent blue wildebeest will seek out cooler microclimates than the arid-adapted gemsbok, particularly when far away from a water source. I also hypothesise that during the heat of the day, gemsbok and blue wildebeest will be less active diurnally when they are further away from a water source, resulting in a reduction in total 24 h activity, than when they are close to water sources. I expect that the more water dependent blue wildebeest will be less active compared to the arid-adapted gemsbok when far away from a water source. If the individual cannot conserve sufficient body water by adjusting behavioural responses (microclimate selection and activity patterns), I hypothesise that maximum 24 h body temperatures will be higher when individuals are further away from a water source. Since blue wildebeest are more dependent on surface water, I predict that they will display more extreme dehydration-induced hyperthermia (e.g. higher maximum body temperatures) than gemsbok when far away from a water source. To examine whether water was the likely driver in any observed changed in body temperature, I compared body temperature patterns before and after the first rainfall. At the end of the dry season when ambient temperatures start to increase, I hypothesise that both species will display high 24 h maximum body temperatures, which will resolve once the first rains fall and individuals have access to water to cool themselves evaporatively without compromising body water balance.

5.3 Materials and methods

5.3.1 Study area

The study took place in the Bakgalagadi Schwelle region (here after Schwelle) of the southwestern Botswana (S 24.35°, E 20.62°), from October 2013 to December 2014. Summer ambient temperatures are generally high with summer daytime air temperatures often exceeding 40 °C (Knight 1991). Rainfall is concentrated between November and April (Thomas & Shaw 1991). Natural freestanding drinking water is generally lacking and is only present occasionally after rainfall events (Knight 1995). There is no permanent natural surface water and herbivores depend upon moisture from vegetation or a few artificial waterholes, with differing degrees of potability, concentrated in a few locations along the river beds within the Kgalagadi Transfrontier Park and a few locations near villages outside the park (Figure 2.4). Ephemeral pools of surface water may collect after heavy rains between November and April but only available for a few days; at all other times both species had access to the pre-formed water in the sparse vegetation, and to metabolic water.

5.3.2 Data collection

Eight individual female gemsboks and eight individual female blue wildebeest within the Schwelle, all from separate herds, were captured. These individuals where collared and miniature movement-sensitive data loggers were implanted in the abdominal muscle wall and miniature temperature-sensitive data loggers were implanted in the peritoneal cavity, following procedures outlined in chapter 2. Surgery and collaring procedures took place in August 2013. The collars recorded the animal’s location (GPS) at hourly intervals and the miniature temperature-sensitive data loggers (DST centi-T, Star-Oddi, Iceland) recorded body temperature at 10 min intervals and the motion-sensitive loggers (ADXL345, Sigma Delta Technologies, Australia) recorded activity at 5 min intervals. Motion changes were recorded as activity counts within the first 10 seconds of each 5-min interval. Each collar supported a miniature black globe (“miniglobe”) thermometer, which quantified the microclimate that the ungulates choose to occupy (Hetem et al. 2007). For more details on calibrations, resolution and accuracy of temperature-sensitive and motion-sensitive data loggers as well as surgical procedures refer to chapter 2.

5.3.3 Weather data

I collected hourly black globe temperatures from a portable weather station (HOBO Weather Logger [H21-001], Onset Computer Corporation, USA) erected at Kaa gate, Kgalagadi Transfrontier Park (S 24.3°, E 20.6°). A free-standing black miniglobe thermometer was placed in direct sun (S 24.35 °, E 20.62), 1 m above ground, which recorded miniglobe temperature (°C) every hour by a temperature data logger (Hobo, Onset Computer Corporation, Pocasset, MA, USA), for the duration of the study period (refer to chapter 2 for calibrations). Other climatic data (including dry-bulb air temperature (°C) and rainfall (mm)) were obtained from Agricultural Research Council (ARC) at the Nossob campsite (S 25.4°, E 20.6°).

5.3.4 Environmental satellite data

For each animals’ location (GPS point), I extracted three environmental variables, namely distance to water, Normalized Difference Vegetation Index (NDVI) a proxy for vegetation greenness, and rainfall. To quantify these environmental variables, I downloaded satellite images from these three sources: Moderate Resolution Imaging Spectroradiometer (MODIS) MOD13Q1, Landsat 8 OLI/TIRS C1 Level-1 images, and Tropical Applications of Meteorological Satellites (TAMSAT). I retrieved both the MODIS MOD13Q1 data product (temporal resolution: 16 days, spatial resolution: 250 m pixels) and Landsat 8 OLI/TIRS C1 Level-1 images (temporal resolution: 16 days, spatial resolution: 30

m pixels) from EarthExplorer (NASA Land Processes Distributed Active Archive Center (LP DAAC), USGS/Earth Resources Observation and Science (EROS) Center, Sioux Falls, South Dakota, https://earthexplorer.usgs.gov/). TAMSAT daily images were downloaded from the TAMSAT website (University of Reading Research Data Archive, http://www.tamsat.org.uk/). The dataset was derived from the TAMSAT African Rainfall Climatology And Time-series (TARCAT) dataset (1983-present).

5.3.4.1 Delineating surface water with Normalized Difference Water Index

For analysis of surface water, I used the Semi-Automatic Classification Plugin (SCP) for QGIS. The SCP includes pre- and post-image processing capabilities and combines automated processing with minimal user interaction. To select the best imagery in terms of cloud cover and seasonal/radiometric characteristics, all available Landsat images were visually screened and pre-processed including the assessment and correction of spatial registration, cloud masking, conversion from DN (i.e. Digital Numbers) to the physical measure of Top Of Atmosphere (TOA) reflectance by importing and processing the Landsat 8 images with the SCP. As recommended by Ji et al. (2009), I followed the eight-step procedure to delineate surface water and create surface water time series maps. Because water absorbs energy at near-infrared (NIR) and shortwave-infrared (SWIR) wavelengths, the design of a spectral water index is possible. The Landsat-based Normalized Difference Water Index (NDWI) is defined as:

$$NDWI = \frac{(\rho_{green} - \rho_{SWIR})}{(\rho_{green} + \rho_{SWIR})}$$

where ρ_{green} and ρ_{SWIR} are the reflectance of green and SWIR bands, respectively. As per the above equation (Ji et al. 2009), I used the reflectance band 3 (green band) and 6 (SWIR band) of Landsat 8 to calculate the NDWI time series maps (Figure 5.1A). Generally, in satellite imagery where the resolution of the image is large, a large pixel contains multiple land-cover types within the pixel area and if a specific land-cover feature dominates 100% within the pixel area, for example water, that pixel is classed as a water pixel. If the pixel is dominated by water (>50%), then the NDWI is influenced by not only water but also by other subordinate classes, for example vegetation and/or soil. To separate water bodies from other land-cover features such as vegetation and soil, a NDWI threshold of the spectral water index is determined. NDWI threshold is a dynamic value that changes depending on the subpixel land-cover components (Ji et al. 2009). For a given water fraction (f_w = 0%, 5%, …, 95%), each NDWI has varying values depending on the fractional components of soil and vegetation (Ji et al. 2009). Thus, NDWI thresholds need to be adjusted based on the spectral signatures and proportions of the non-water components (Ji et al. 2009). Because these three components constitute major land-cover types on land surfaces, I based the water classes on the fractional water component (f_w) in the image and defined it as: water ($f_w \geq 50\%$) and non-water ($f_w < 50\%$), whereby the non-water components were made up of soil (f_s) and vegetation (f_v), each representing 25% ($f_s = f_v = 25$ %). To simplify the complexity, I assumed the soil and vegetation fractions were equal (i.e., $f_s = f_v$) for a given water fraction. Following the recommendation by Ji et al. 2009, I used the initial NDWI threshold of -0.410 (Appendix 4; Ji et al. 2009, p.1316) to density-slice the image to generate the initial water classes. This image resulted in binary water/non-water maps (Figure 5.1C) that can be used to delineate water in the landscape. To ground truth the map, I compared each water/non-water map to the false-colour composite image (as reference data; Figure 5.1B) of the same timeframe and to aerial photographs taken over the study site. I then manually adjusted the NDWI threshold to reach the best agreement with the reference data as the initial water map underestimated actual water sources. I found that when NDWI threshold was set to -0.20, the binary output water map visually agreed best with the false-colour image and aerial photographs. I noted that almost all surface water was featured within the Kalahari pan systems. Water in the pans after rain usually persists for a few weeks (Parris & Child 1973), but depending on size of pan, some of these water sources may be available only for a few days. For each image of the water/non-water time series maps, I created a distance raster (Figure 5.1D) and overlaid the animals GPS locations. I then extracted the distance from the nearest pan that featured water for each GPS location recorded on the same date as the image. Since

Landsat images are taken at 16 day intervals, I extracted the distance to water for eight days before and after each image date.

5.3.4.2 Delineating vegetation greenness with NDVI

Green plants have high reflectivity in the near-infrared (NIR) wavelengths and absorb red wavelengths for photosynthesis, therefore, it is possible to differentiate the greenness of the vegetation by using a vegetation index. This vegetation index is an indicator that describes the greenness for each pixel in a satellite image and is defined as

$$NDVI = \frac{(\rho_{NIR} - \rho_{red})}{(\rho_{NIR} + \rho_{red})}$$

where ρ_{NIR} and ρ_{red} are the reflectance of near-infrared and red channels (Tucker & Sellers 1986, Huete et al. 2002, Pettorelli et al. 2009). MODIS is a key instrument aboard the Terra and Aqua satellites that collects data within 36 spectral bands, ranging in wavelengths from 0.4 µm to 14.4 µm, every 1 to 2 days (Tucker & Yager 2011), including the ρ_{NIR} and ρ_{red} bands. NDVI, one of the MODIS products, is freely available and already computed from atmospherically corrected bi-directional surface reflectance that have been masked for water, clouds, heavy aerosols, and cloud shadows (Didan et al. 2015). Daily MODIS NDVI data are composited into 16-day intervals based on product quality assurance metrics to remove low quality pixels to eliminate the effect of clouds, aerosols, and variations in sun surface-sensor geometry (Didan et al. 2015), only the highest NDVI value per pixel is selected during the composited period. I collated a NDVI time series from the start to the end of the study period. I then overlaid the GPS locations of all individuals onto the NDVI timeseries and extracted a NDVI value for each point. Even though relative greenness was used as an index of greenness in chapter 4, continuous MODIS greenness values showed a similar trend so for simplicity I used the continuous NDVI variable in this chapter to represent a covariant (continuous predictor variable) as a control variable.

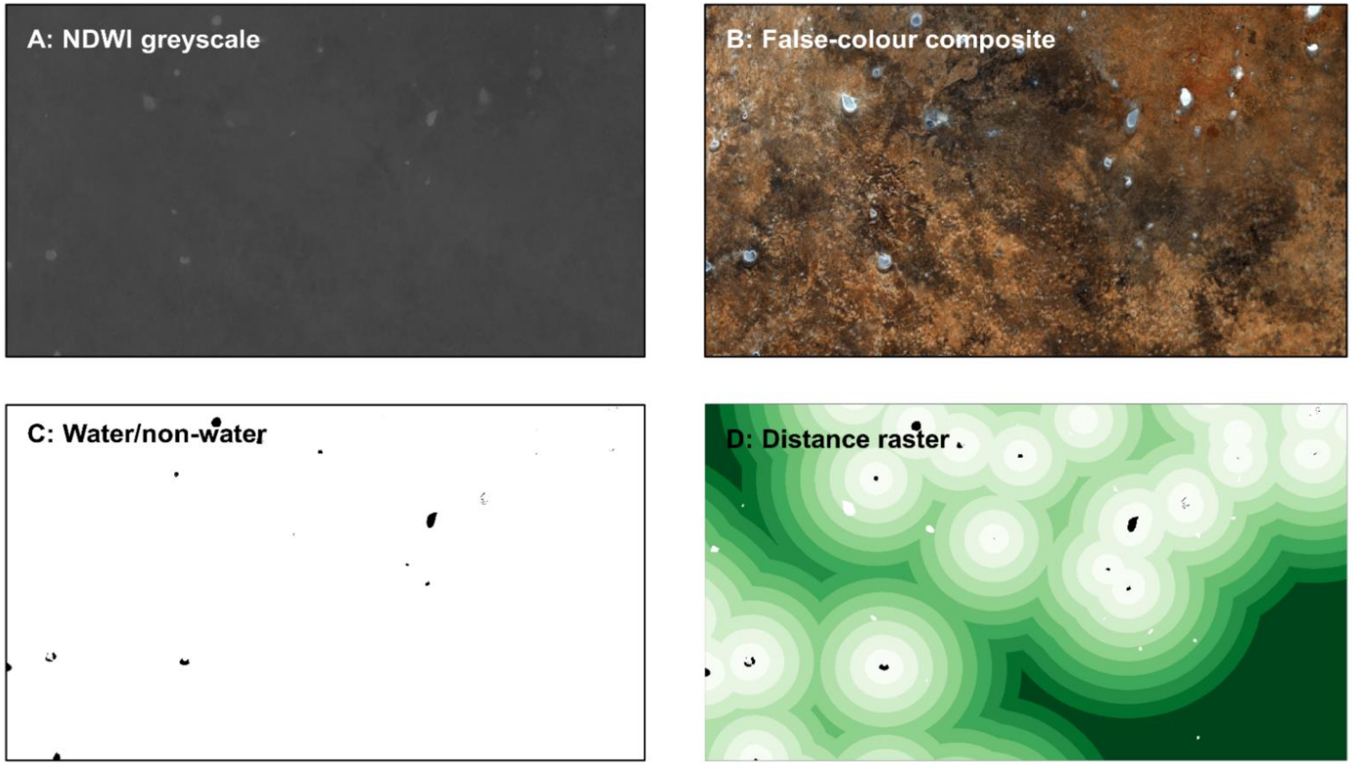

Figure 5.1: Mapping surface water features in Bakgalagadi Schwelle using Landsat 8 images. All images represented were taken on 15 October 2013 (shortly after rain). (A) Normalized Difference Water Index (NDWI; Ji et al. 2009) calculated from Landsat 8 bands, using green band (band 3) and Short-Wavelength InfraRed (SWIR) band (band 6), lighter areas represent surface water; (B) Subset of Landsat 8 image, false-colour composite (RGB 432), Image no. L50762013288, used as reference image; (C) Water/non-water binary map derived from the NDWI image, black shapes represent pans with surface water; (D) Distance raster overlaying on the water/non-water map, black shapes represent pans with surface water and ephemeral pools, white shapes represent pans with no water, each shade of green surrounding the black shapes (water) represents distances in 2km intervals from the water source with dark green areas more than 20km from all water sources.

5.3.4.3 Delineating daily rainfall

TAMSAT rainfall estimates are available for the year 1983 to a 2 week delayed present with a high spatial (4 km) and temporal (10 days) resolution for the African continent. I used this TAMSAT time series to map daily rainfall from October 2013 to December 2014. TAMSAT is derived from Meteosat thermal infrared channels with algorithms recognizing convective storm clouds and calibrated with ground based synoptic rain gauge data (Maidment et al. 2013; Maidment et al. 2014). The daily rainfall estimates are derived from the TAMSAT rainfall estimation algorithm for all of Africa at 4 km resolution (Tarnavsky et al. 2014). Rainfall estimates were obtained by extracting rainfall values for each GPS point to identify the first rains of the season based on the daily algorithm and averaged per day per individual.

5.3.5 Data analysis

Between October 2013 and December 2014, I recorded GPS positions and miniglobe temperature on the collar, body temperature and activity, for both gemsbok and wildebeest. Based on animal deaths and inability to relocate animals, I analysed data from nine (five gemsbok and four wildebeest) internal body temperature loggers; seven (four gemsbok and three wildebeest) internal motion-sensitive loggers; and seven (five gemsbok and two wildebeest) miniglobe temperature sensors from the external collars that recorded data for all 15 months (see Appendix 2). GPS data from the collars (five gemsbok and two wildebeest) was retrieved via satellite (see Appendix 2). Since my goal was to determine the influence of distance to surface water on behavioural and thermoregulatory responses when conditions were hot, I only included days when globe temperature exceeded body temperature (>38 °C; ~236 days per antelope).

To quantify microclimate selection, I calculated the hourly difference between miniglobe temperature recorded on the collar and an identical miniglobe in the sun, per animal. I then extracted the minimum 24 h difference in miniglobe temperature as an index of the coolest microclimate selected per day. To quantify activity levels, I calculated total 24 h activity, total activity that occurred during the heat of the day and maximum 24 h activity levels per individual for each 24 h periods. I defined the ‘heat of the day’ between 11:00 and 16:00 because that was when black globe temperatures exceeded 35 °C on average during summer (Figure 5.2). I also calculated maximum 24 h body temperature and 24 h mean, minimum and maximum ambient temperature (miniglobe).

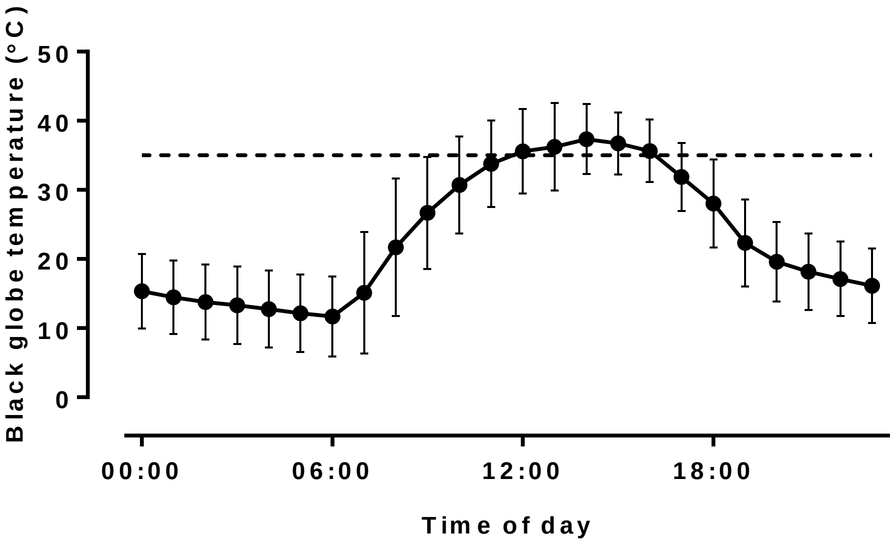

Figure 5.2: Mean hourly black miniglobe temperature (mean ± SD) during the hot period, October 2013 to December 2014, obtained on site at the Kaa gate, Kgalagadi Transfrontier Park (S 24.3°, E 20.6°). The dotted line indicates the threshold temperature of 35 °C that defined the ‘heat of the day’ between 11:00 and 16:00.

To visually assess the effect that distance to water had on microclimate selection, activity patterns, and body temperature profiles, I classified the distance to water into four categories, namely 0-2 km, 2-5 km, 5-20 km and >20 km from the nearest water source. These four categories were chosen based on the likelihood of an individual animal reaching a water source to drink within a day. From this data, the mean and standard deviation of each variable of interest were grouped into hourly bins by time of day to get the 24 h rhythm of activity, microclimate selection and body temperature profile respectively for each distance to water category for each species.

I developed a priori set of hypothesis models and used a series of generalized linear mixed effects models (GLMMs) to investigate whether likely drinking frequency (indexed as distance to water) affected minimum 24 h difference in miniglobe temperature, activity during the heat of the day, and total 24 h activity.

I entered maximum 24 h miniglobe temperature from the weather station as a ‘control variable’ for microclimate selection models because of their potential impact on microclimate selection (Chapter 3). I entered maximum 24 h miniglobe and vegetation greenness (NDVI) as ‘control variables’ in the activity models because of their potential impact on activity patterns (Chapter 3 and Chapter 4). To investigate whether distance to water influenced maximum 24 h body temperatures profiles, I used a series of generalized linear mixed effects models (GLMMs) with maximum 24 h miniglobe temperature and maximum 24 h activity as a ‘control’ variable into the models. To test for possible variation in the effects of the explanatory variables between the species, I included an interaction term for these variables into all the GLMMs. Animal identity was entered as a random effect on the intercept term to avoid pseudoreplication in all models. An example of a model was therefore: maximum 24 h body temperature ~ maximum 24 h miniglobe + NDVI + distance to water + species + maximum 24 h miniglobe x species + NDVI x species + animal identity [random intercept]. The conditional R^2 for linear mixed-effect models was calculated for the models along with 95% confidence intervals. The conditional R^2 describes the proportion of variance explained by both the fixed and random factors (Nakagawa & Schielzeth 2013). To compare the potential working hypothesis models, I used corrected Akaike’s information criterion (AICc) (corrected for small sample bias) and weighted them for their level of support in the data (Anderson 2008) and by using the AICc and model selection procedures, I was able to select the model that best supported the data (Burnham et al. 2011). I selected all models with a difference in AICc value of <2 as plausible models and interpreted the best model which had the lowest AICc value and highest weight of all the candidate models (Anderson 2008).

To test whether hyperthermia would be resolved when animals were likely to have access to water following the first rains, I extracted data, based on TAMSAT rainfall over the study area, for the first rainfall event with more than 2 mm of rain, which occurred between 6-9 December 2014. Twenty mm of rain fell over these four consecutive days during the rainfall event. Three days before and three days after the rain had occurred, I averaged mean, minimum, and maximum 24 h miniglobe temperature on the weather station and NDVI at each animal GPS location and compared each variable by using an unpaired students T-test. Because vegetation greenness selected by both species and the ambient temperatures were similar during the two periods, before and after the rainfall event (Table 1), I compared the effects of these two periods (before vs. after rain) on maximum 24 h body temperature between species by using two-way repeated measures analysis of variance (ANOVA) with Tukey's multiple comparison tests.

Table 5.1: Environmental data averaged (mean ± SD) for the three days before the rainfall event and three days after the rainfall event that occurred over four days (6th – 9th December 2014). Miniglobe temperature on the weather station and NDVI at locations selected by gemsbok and wildebeest did not differ between periods. An unpaired students T-test was used for analysis and no significant difference was found between before and after rainfall event.

	3 days before rain event	3 days after rain event	comparison
Mean 24h miniglobe temperature °C	30.2 ± 1.6	28.9 ± 1.6	$t_4 = 1.03$, $p = 0.360$
Maximum 24h miniglobe temperature °C	47.4 ± 1.9	45.2 ± 4.6	$t_4 = 0.799$, $p = 0.469$
Minimum 24h miniglobe temperature °C	15.4 ± 1.3	16.2 ± 2.2	$t_4 = 0.541$, $p = 0.617$
Mean NDVI for gemsbok	0.176 ± 0.019	0.180 ± 0.013	$t_8 = 0.392$, $p = 0.705$
Mean NDVI for wildebeest	0.223 ± 0.042	0.213 ± 0.040	$t_6 = 0.353$, $p = 0.736$

I used R statistical software environment (R Core Team 2015) and R packages: lme4 (Bates et al. 2015) to perform the GLMM analysis and AICcmodavg (Mazerolle 2016) to perform the model selection. The students t-test and two-way repeated measures ANOVA with Tukey's multiple comparison test were performed using GraphPad Prism (version 6.00 for Windows, GraphPad Software, San Diego, CA, USA). Values are expressed as mean and standard deviation and $p < 0.05$ was considered significant.

5.4 Results

5.4.1 Microclimate selection

The quality of microclimates selected by gemsbok and wildebeest, assessed by the minimum 24 h difference between collar and weather station miniglobe temperature, increased when both species increased their distance from known water sources (Figure 5.3), i.e. both species selected cooler microclimates when they were further away from the water source.

To test whether distance to water influenced microclimate selection, I ran a series of GLMMs. Two models were considered plausible and received a total 92% of the model weight (Table 5.2), with very similar structures, differing only by the inclusion of the interaction term “distance to water x species” in the second best-supported model (Table 5.2). Both models included species, maximum 24 h miniglobe temperature, NDVI and distance to water as main effects, as well as an interaction between maximum 24 h miniglobe and species and between NDVI and species. However, the probability of model 1 to be the best supported model was 2.5 times more likely (0.66 vs 0.26) than model 2, yet both models only explained 40% (Conditional $R^2 = 0.40$) of the proportion of variance in microclimates selected by the animals. If ‘distance to water’ was excluded as a variable, the model AICc weakened considerably ($\Delta_i = 10.33$; 4th ranking; Table 5.2). After controlling for maximum 24 h miniglobe temperature and NDVI, both species selected slightly cooler microclimates when they were located further away from known water sources; the inclusion of the interaction between distance to water and species did not significantly improve the model (Figure 5.4B).

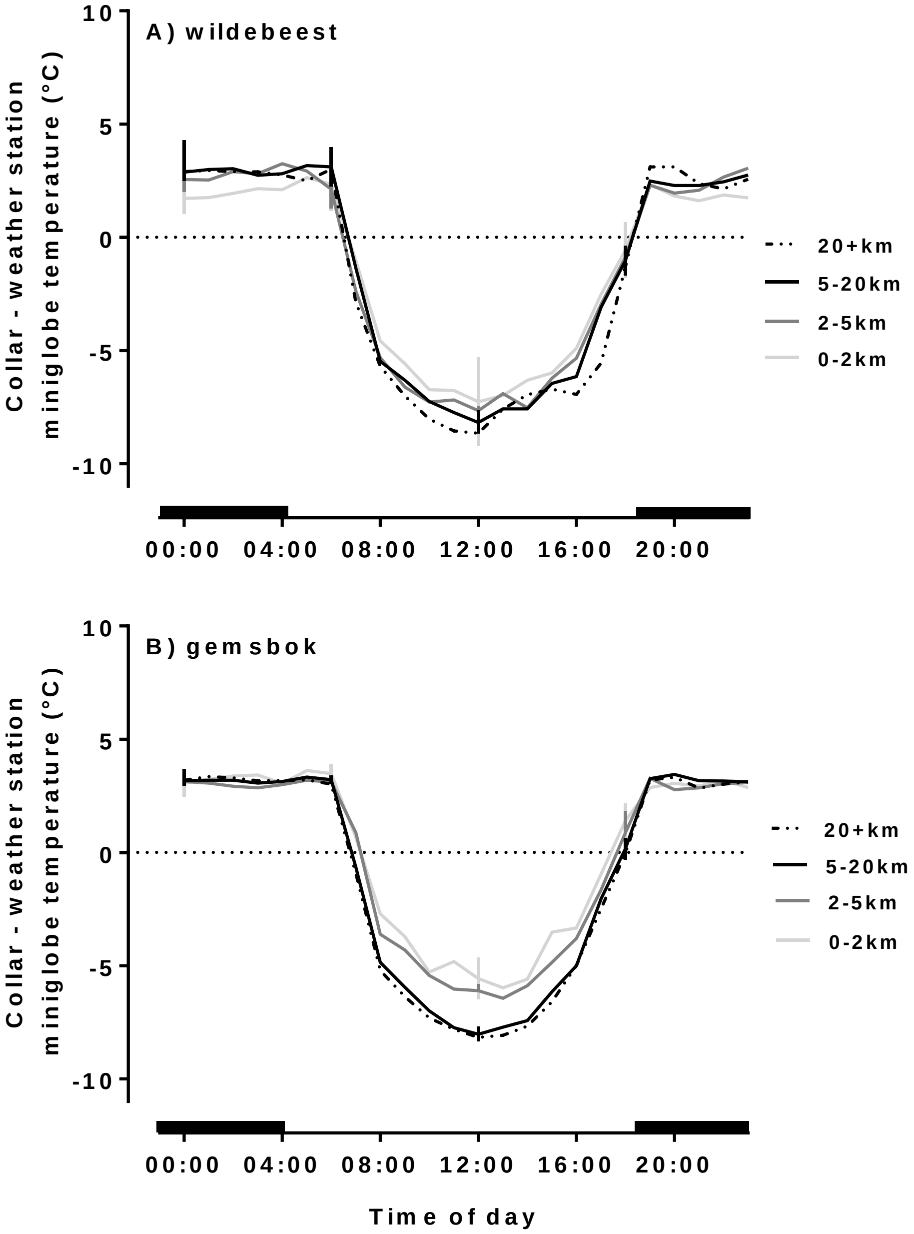

Figure 5.3: 24 h rhythm (mean ±SD) of microclimate selection in hourly bins, expressed as the difference between miniglobe temperature at the site occupied by the animal and the temperature of an identical miniglobe exposed to the sun at a nearby weather station, chosen by (A) two wildebeest and (B) five gemsbok free living at different distances from water within the Bakgalagadi Schwelle study area. Black bars represent night periods. Data consisted only of days when globe temperature exceeded body temperature of all individuals.

Table 5.2: Candidate generalized linear mixed effects models, and their coefficients, describing the response minimum 24h difference in miniglobe temperature (collar – weather station) for five gemsbok and two wildebeest in Bakgalagadi Schwelle study site, showing various explanatory variables and interactions (×) included in models. Models are listed from higher to lower ranked according to their corrected Akaike information criterion (AICc). Models are based on one point per day per individual (N=1841). Δi is the delta AICc (difference between the AICc for a given model and the best fitting model), k is the number of estimated parameters and ωi is the model selection probability (Akaike weights). Animal identity was included as a random effect.

Model ranking	Fixed Effects	k	AICc	Δ_i	ω_i
1	maximum 24 h miniglobe + NDVI + distance to water + species + maximum 24 h miniglobe x species + NDVI x species	9	8286.0	0.00	0.66
2	maximum 24 h miniglobe + NDVI + distance to water + species + maximum 24 h miniglobe x species + NDVI x species + distance to water x species	10	8287.9	1.89	0.26
3	maximum 24 h miniglobe + NDVI + distance to water + species + NDVI x species + distance to water x species	9	8290.3	4.32	0.08
4	maximum 24 h miniglobe + NDVI + species + NDVI x species	7	8296.3	10.33	0.00
5	maximum 24 h miniglobe + distance to water + species + maximum 24 h miniglobe x species + distance to water x species	8	8305.3	19.28	0.00
6	maximum 24 h miniglobe + species + maximum 24 h miniglobe x species	7	8306.6	20.67	0.00
7	maximum 24 h miniglobe + NDVI + distance to water + species + distance to water x species	8	8309.9	23.86	0.00
8	maximum 24 h miniglobe + distance to water + species + distance to water x species	7	8311.2	25.16	0.00
9	maximum 24 h miniglobe + distance to water	5	8311.8	25.83	0.00
10	maximum 24 h miniglobe + NDVI	5	8314.4	28.36	0.00
11	maximum 24 h miniglobe	4	8314.6	28.65	0.00
12	NDVI	4	9187.5	901.49	0.00

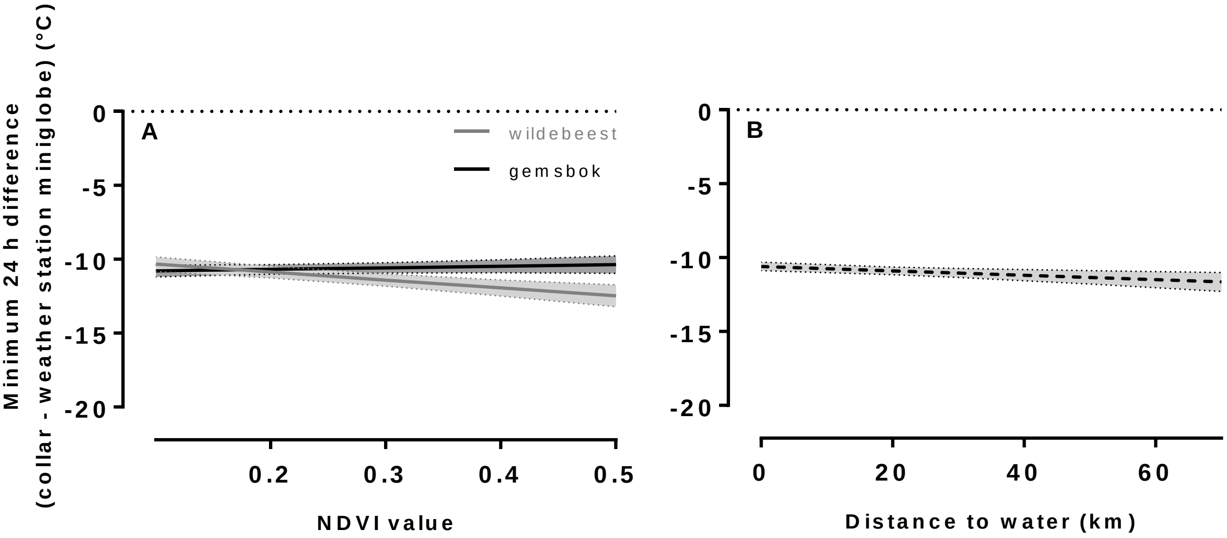

Figure 5.4: Predictive margins with 95% CIs for the influence of (A) vegetation greenness (NDVI) and (B) distance to known surface water on the microclimate selection (minimum 24 h difference between collar and weather station miniglobe) (°C) for five female gemsbok and two female wildebeest, living freely in the Bakgalagadi Schwelle study site. No significant interaction effect between species and distance to water hence responses of both species are combined in B.

5.4.2 Activity

Both species showed higher activity levels when they were located within 2 km of water compared to when they were located further away, with wildebeest consistently showing higher levels of activity than gemsbok during the night (Figure 5.5). Both species decreased their activity levels, particularly during the middle of the day, when they were further away from a water source. When wildebeest were further than 20 km from water, they were virtually inactive during the middle of day (Figure 5.5).

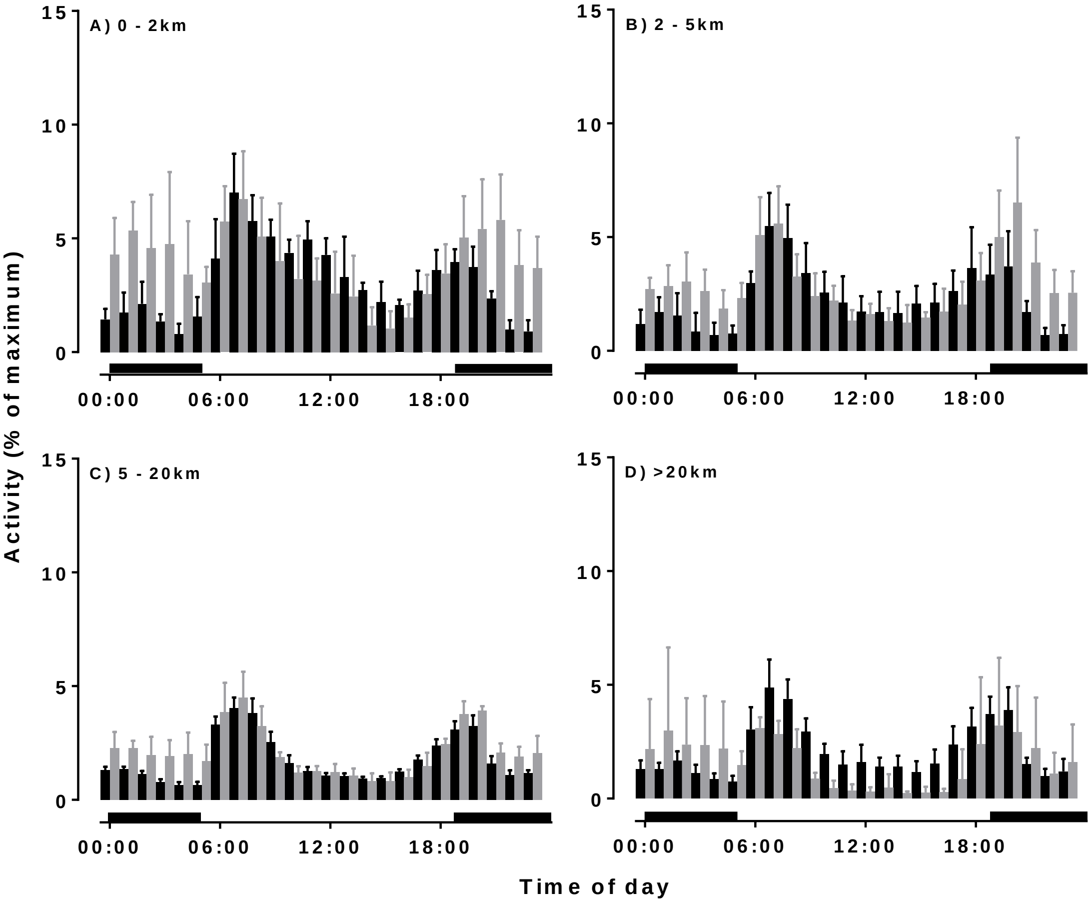

Figure 5.5: 24 h rhythm of activity (mean ± SD) in hourly bins for four gemsboks (black bars) and three wildebeest (grey bars) living freely within the Bakgalagadi Schwelle study area, on days when they occurred within 2km (panel A), within 5km (Panel B), within 20km (panel C) and more than 20 km (panel D) from water. Black bars represent night periods. Activity was measured over the abdomen with an activity data logger tethered into the abdominal muscle wall. Activity counts are expressed as a percentage of maximum counts for that logger. Data consisted only of days when ambient temperature exceeded body temperature.

To test whether distance to water influenced activity during the heat of day (between 11:00 and 16:00), I used a series of GLMMs and model selection to select the best supported model for the data. Two models with very similar weighting (0.52 vs 0.48), differing only in the exclusion of the interaction term “maximum 24 h miniglobe x species” in the second-best model, were considered plausible (Table 5.3). Activity during the heat of day was associated with species, maximum 24 h miniglobe temperature, NDVI and distance to water, with both models including all four of these terms as the main effects. Yet, the proportion of variance explained by the fixed and random factors by both models was 29%, therefore 71% of the variance of activity during the heat of the day were unexplained. However, if I excluded the term ‘distance to water’ the model weakened considerably (Δ_i = 20.94; 5th ranking, Table 5.3). While controlling for the effect of NDVI and maximum 24 h miniglobe temperature, both species decreased their activity during the heat of the day when they were located further away from known water sources, with wildebeest showing a steeper decline in activity than gemsbok as distance to surface water increased (Figure 5.6A).

To test whether the reduced activity during the heat of the day resulted in a decrease in total 24 h activity, I used a series of GLMMs to compare a priori set of hypothesis models. Two models supported the data best (model 1 and 2; Table 5.4). Total 24 h activity was associated with species, NDVI and distance to water, with both models including all three of these terms as the main effects. However, the probability of model 1 was 2.7 times more likely (0.60 vs 0.22) than model 2, which excluded the main effect “Maximum 24 h Miniglobe”, to be the best supported model (Table 5.4). Yet, these models only explained 24% (Conditional R^2 = 0.24) of the proportion of variance in total 24h activity experienced by the animals. However, the model weakened considerably if the ‘distance to water’ term was excluded in the model (Δ_i = 85.01; 5th ranking; Table 5.4). When controlling for maximum 24 h miniglobe temperature and NDVI in the best supported model, wildebeest decreased their total 24 h activity when they were located further away from known water sources, yet gemsbok’s total 24 h activity levels were similar regardless of how far they ventured from surface water (Figure 5.6B).

Table 5.3: Candidate generalized linear mixed effects models, and their coefficients, describing the response 'activity during heat of day (between 11:00 and 16:00)' for four gemsbok and three wildebeest in Bakgalagadi Schwelle study site, showing various explanatory variables and interactions (×) included in models. Models are listed from higher to lower ranked according to their corrected Akaike information criterion (AICc). Models are based on one point per day per individual (N=1406). Δi is the delta AICc (difference between the AICc for a given model and the best fitting model), k is the number of estimated parameters and ωi is the model selection probability (Akaike weights). Animal identity was included as a random effect.

Model ranking	Fixed Effects	k	AICc	Δ_i	ω_i
1	maximum 24 h miniglobe + NDVI + distance to water + species + NDVI x species + distance to water x species + maximum 24 h miniglobe x species	10	10677.20	0.00	0.52
2	maximum 24 h miniglobe + NDVI + distance to water + species + NDVI x species + distance to water x species	9	10677.34	0.14	0.48
3	maximum 24 h miniglobe + NDVI + distance to water + species + maximum 24 h miniglobe x species + distance to water x species	9	10688.22	11.02	0.00
4	maximum 24 h miniglobe + NDVI + distance to water + species + distance to water x species	8	10690.39	13.20	0.00
5	maximum 24 h miniglobe + NDVI + species + NDVI x species	7	10698.14	20.94	0.00
6	maximum 24 h miniglobe + NDVI + species + maximum 24 h miniglobe x species	7	10700.13	22.94	0.00
7	maximum 24 h miniglobe + NDVI	5	10706.47	29.28	0.00
8	NDVI	4	10722.10	44.91	0.00
9	maximum 24 h miniglobe + distance to water + species + maximum 24 h miniglobe x species + distance to water x species	8	11004.21	327.01	0.00
10	maximum 24 h miniglobe + distance to water + species + distance to water x species	7	11010.62	333.42	0.00
11	maximum 24 h miniglobe + species + distance to water x species	6	11064.28	387.08	0.00
12	maximum 24 h miniglobe	4	11082.39	405.20	0.00

Table 5.4: Candidate generalized linear mixed effects models, and their coefficients, describing the response 'total 24 h activity' for four gemsbok and three wildebeest in Bakgalagadi Schwelle study site, showing various explanatory variables and interactions (×) included in models. Models are listed from higher to lower ranked according to their corrected Akaike information criterion (AICc). Models are based on one point per day per individual (N=1406). Δi is the delta AICc (difference between the AICc for a given model and the best fitting model), k is the number of estimated parameters and ωi is the model selection probability (Akaike weights). Animal identity was included as a random effect.

Model No.	Fixed Effects	k	AICc	Δ_i	ω_i
1	NDVI + distance to water + species + distance to water x species	7	13061.84	0.00	0.60
2	maximum 24 h miniglobe + NDVI + distance to water + species + distance to water x species	8	13063.83	1.99	0.22
3	maximum 24 h miniglobe + NDVI + distance to water + species + NDVI x species + distance to water x species	9	13065.28	3.44	0.11
4	maximum 24 h miniglobe + NDVI + distance to water + species + maximum 24 h miniglobe x species + NDVI x species + distance to water x species	10	13066.05	4.21	0.07
5	maximum 24 h miniglobe + NDVI + species + maximum 24 h miniglobe x species	7	13146.85	85.01	0.00
6	maximum 24 h miniglobe + NDVI + species + NDVI x species	7	13147.82	85.97	0.00
7	NDVI	4	13149.75	87.91	0.00
8	maximum 24 h miniglobe + NDVI	5	13149.95	88.11	0.00
9	maximum 24 h miniglobe + distance to water + species + maximum 24 h miniglobe x species + distance to water x species	8	13192.37	130.53	0.00
10	maximum 24 h miniglobe + distance to water + species + distance to water x species	7	13193.45	131.61	0.00
11	distance to water x species	6	13196.09	134.25	0.00
12	maximum 24 h miniglobe	4	13334.09	272.25	0.00

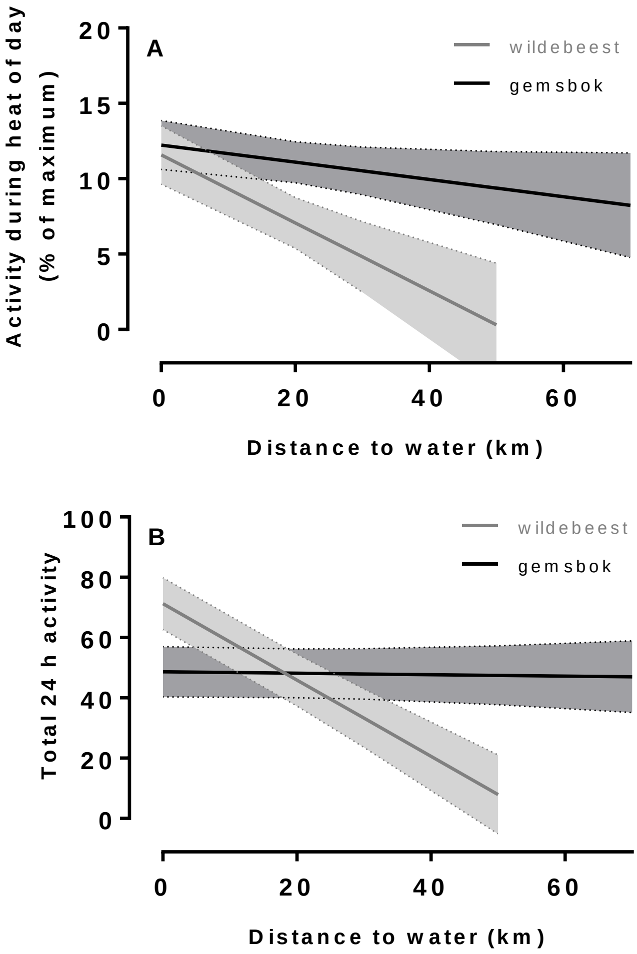

Figure 5.6: Predictive margins with 95% CIs for the influence of distance to known water sources on (A) activity during the heat of the day (between 11:00 and 16:00) and (B) total 24 h activity for four female gemsbok and three female wildebeest, living freely in the Bakgalagadi Schwelle study site.

5.4.3 Body temperature

On hot days when black globe temperature exceeded body temperature, the 24 h amplitude of body temperature rhythm of wildebeest, but not gemsbok, increased when animals were located further from surface water. When animals were located within <20 km of a known water source, both wildebeest and gemsbok were able to maintain an amplitude of body temperature rhythm within ~2 °C (Figure 5.7). However, when wildebeest were located further than 20 km from known water sources their body temperatures fluctuated more widely (3 ± 0.6 °C) with a noticeable increase in maximum and decrease in minimum 24 h body temperatures (Figure 5.7A). Gemsbok, however, only displayed a slight increase in maximum 24 h body temperature when located further than 20 km away from surface water (Figure 5.7B).

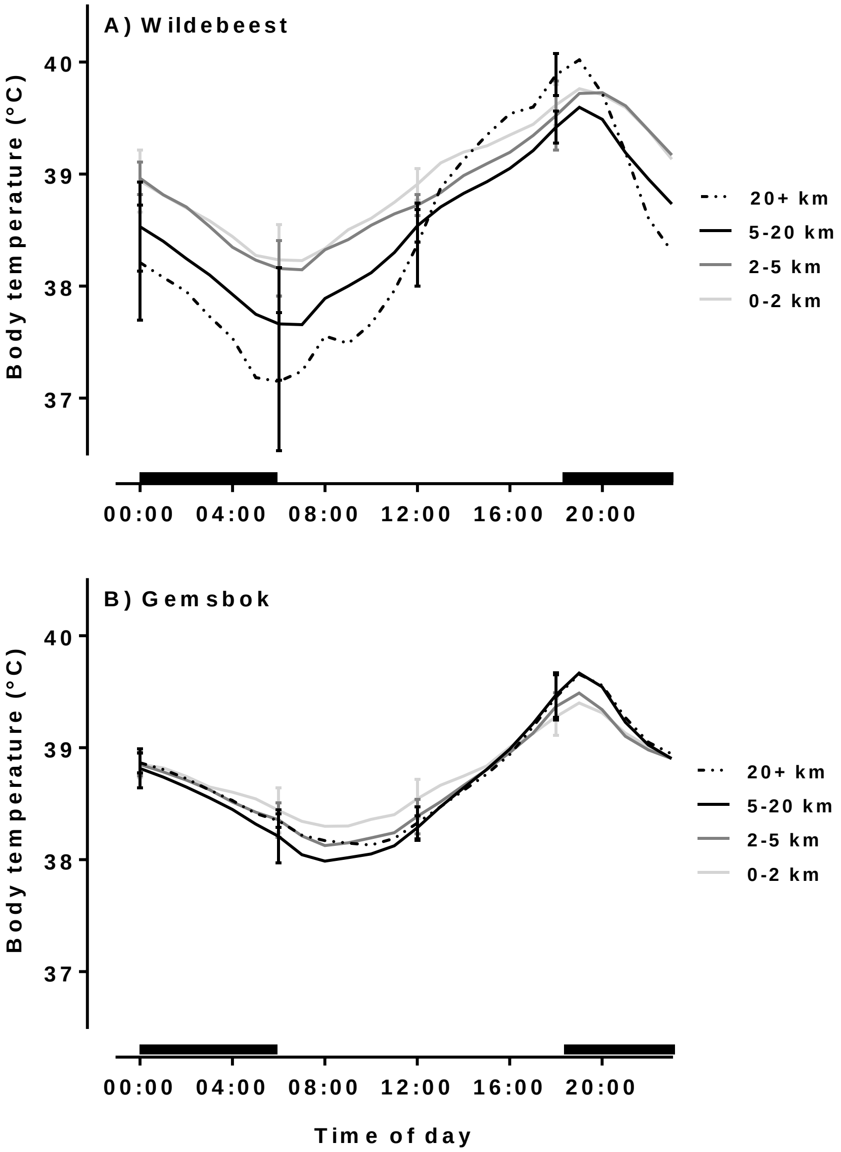

Figure 5.7: 24 h rhythm of body temperature (°C) (mean ± SD) in 10 minute intervals for (A) four wildebeest and (B) five gemsboks living freely within the Bakgalagadi Schwelle study area, on days when they occurred at different distances from water. Data included only days when black globe temperature exceeded body temperature. Body temperature was measured retroperitoneally. Black bars represent night periods.

To test whether distance to water influenced maximum 24 h body temperatures, I used a series of GLMMs. Two models were considered plausible and received a total 99% of the model weight, with very similar structures, differing only by the exclusion of the interaction term “maximum 24 h activity x species” in the most parsimonious model (Table 5.5). Thus, maximum 24 h body temperatures were associated with species, maximum 24 h miniglobe, NDVI, maximum 24 h activity and distance to water, with both models including all five of these terms as the main effects and interactions between maximum 24 h miniglobe temperature and species, between NDVI and species, and between distance to water and species. However, the probability of model 1 to be the best supported model was 1.6 times more likely (0.61 vs 0.38) than model 2, yet these models explained only 28% (Conditional $R^2 = 0.28$) of variance in the maximum 24 h body temperatures. If ‘distance to water’ was excluded as a variable, the model AICc weakened considerably ($\Delta_i = 32.78$; 4th ranking; Table 5.5). After controlling for the effect of NDVI, maximum 24 h miniglobe temperature and maximum 24 h activity, both species’ maximum 24 h body temperatures increased when they were located further away from known water sources, with wildebeest’s maximum 24 h body temperature increasing faster than gemsbok as distance to surface water increased (Figure 5.8).

Table 5.5: Candidate generalized linear mixed effects models, and their coefficients, describing the response 'maximum 24 h body temperature' for five gemsbok and four wildebeest in Bakgalagadi Schwelle study site, showing various explanatory variables and interactions (×) included in models. Models are listed from higher to lower ranked according to their corrected Akaike information criterion (AICc). Models are based on one point per day per individual (N=1371). Δi is the delta AICc (difference between the AICc for a given model and the best fitting model), k is the number of estimated parameters and ωi is the model selection probability (Akaike weights). Animal identity was included as a random effect.

Model No.	Fixed Effects	k	AICc	Δ_i	ω_i
1	maximum 24 h miniglobe + NDVI + distance to water + species + maximum 24 h activity + maximum 24 h miniglobe x species + NDVI x species + distance to water x species	11	1466.83	0.00	0.61
2	maximum 24 h miniglobe + NDVI + distance to water + species + maximum 24 h activity + maximum 24 h miniglobe x species + NDVI x species + distance to water x species + maximum 24 h activity x species	12	1467.81	0.98	0.38
3	maximum 24 h miniglobe + NDVI + distance to water + species + maximum 24 h activity + maximum 24 h miniglobe x species + NDVI x species	10	1476.88	10.05	0.01
4	maximum 24 h miniglobe + NDVI + species + maximum 24 h activity + maximum 24 h miniglobe x species + NDVI x species	10	1499.61	32.78	0.00
5	maximum 24 h miniglobe + NDVI + species + maximum 24 h activity + NDVI x species + maximum 24 h activity x species	9	1527.71	60.89	0.00
6	maximum 24 h miniglobe + NDVI + maximum 24 h activity	6	1529.50	62.67	0.00
7	maximum 24 h miniglobe + NDVI + distance to water + species + maximum 24 h miniglobe x species + NDVI x species + distance to water x species	10	2033.51	566.68	0.00
8	maximum 24 h miniglobe + NDVI	5	2090.19	623.36	0.00
9	maximum 24 h miniglobe + distance to water + species + maximum 24 h miniglobe x species + distance to water x species	8	2113.49	646.66	0.00
10	maximum 24 h miniglobe	4	2144.963	678.14	0.00
11	NDVI	4	2270.532	803.71	0.00
12	distance to water x species	6	2346.344	879.52	0.00

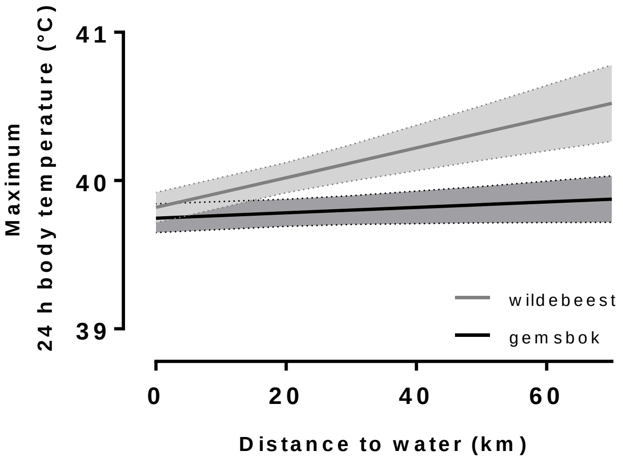

Figure 5.8: Predictive margins with 95% CIs for the influence of distance to known water sources on the maximum 24 h body temperature for five female gemsbok and two female wildebeest, living freely in the Bakgalagadi Schwelle study site on days when globe temperature exceeded 38 °C.

5.4.4 Did hyperthermia resolve following the first rains?

To test whether hyperthermia would be resolved when animals were likely to have access to water following the first rains, I compared maximum 24 h body temperatures when access to water changed (i.e., before and after the first rains) when black globe temperature and NVDI were similar. Maximum 24 h body temperature decreased after the first rainfall of the season ($F_{1,7}$ = 6.266, p = 0.040), there was no difference between species (wildebeest: 0.4 ± 0.5 °C; gemsbok: 0.4 ± 0.3 °C; $F_{1,7}$ = 1.043, p = 0.341) and there was no interaction, i.e., both species responded similarly ($F_{1,7}$ = 0.3267, p = 0.586; Figure 5.9).

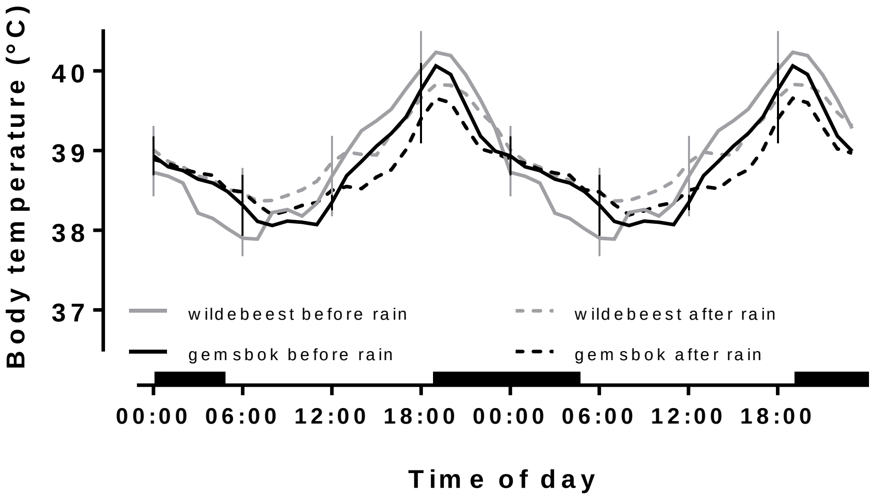

Figure 5.9: 24 h body temperatures for five gemsbok and four wildebeest averaged over three days before and three days after the first rainfall event of the season. This rainfall event occurred during the first week of December 2013. Based on TAMSAT rainfall over the area, 20mm rain fell over four consecutive days during the rainfall event. The vegetation greenness at sites selected by gemsbok was on average 0.180 ± 0.013 and for wildebeest on average 0.213 ±0.040 and did not differ from that selected prior to or after the rains. Mean 24 h miniglobe temperature did not differ before or after the rainfall event (30.2 ± 1.6 °C vs. 28.9 ± 1.6 °C). Data are double plotted to ease visualization of the 24 h pattern. Maximum 24 h body temperature for both species decreased following the rains.

5.5 Discussion

My study is the first to quantify differences in microclimate selection, activity and body temperature for two ungulate species with differing water dependencies in relation to distance to surface water. It is widely held that gemsbok do not depend on drinking water to supply their physiological needs (Taylor 1968a,b), whereas wildebeest require access to water regularly (Berry 1980). During days when miniglobe temperature exceeded body temperature, both species selected high quality microclimates during the heat of the day and selected slightly cooler microclimates when access to drinking water was less frequent compared to when water sources were near. However, when both species were located more than 20 km from surface water (i.e., at distances where they were unlikely to be accessing drinking water on a regular basis), wildebeest displayed exaggerated behavioural and thermoregulatory responses more so than gemsbok. Wildebeest were less active during the heat of the day and their total 24 h activity was reduced substantially compared to gemsbok in relation to water. When near a water source, total 24 h activity patterns were higher for wildebeest than gemsbok. Despite these enhanced behavioural responses predicted to conserve body water, at similar distances from water, wildebeest displayed higher maximum 24 h body temperature than gemsbok. In addition, maximum 24 h body temperatures were significantly higher, for both species, before the onset of the first rain compared to after rain. Thus, access to surface water from rain has the potential to resolve hyperthermia during high thermal heat loads.

The results presented do have some limitations. Firstly, sample size was small for both of our study species because of technical failures of the collars and activity loggers ending earlier than expected. Secondly, the use of satellite imagery may lead to an underrepresentation of water availability. Landsat imagery can provide the appropriate spatial detail for many water mapping applications (Frazier & Page 2000; Tulbure & Broich 2013), but its temporal frequency of 16 days may have missed small ephemeral pools that formed and dried up between 16 day images and the imagery can be often limited by cloud cover during rainfall events. In addition, the spatial resolutions of Landsat imagery (30 x 30 m pixel) are not always suited to small pools of water. Despite these limitations, I did find interesting behavioural and thermoregulatory responses as distance to water increased.

An animal can minimize the effect of high air temperatures and possibly conserve body water by selecting cool microclimates (Jarman & Jarman 1973, Dunbar 1979, Cain et al. 2008, Hetem et al. 2012a,b). The use of shaded microclimates reduces the heat load from radiation, reducing the need for evaporative cooling and minimizing evaporative water loss (Cain et al. 2006, Hetem et al. 2012a). Previous observations on Arabian oryx revealed that selection of cool microclimates was not only dependent on high ambient temperature but was also enhanced by aridity when they did not have access to water (Hetem et al. 2012a), highlighting the potential for shade seeking to conserve body water. During high thermal heat loads, both species within this study showed enhanced microclimate selection when distances to water increased and therefore were likely to be drinking less frequently, compared to when they were near surface water. These cool microclimates selected by both species may have enhanced body water conservation.

Shade seeking behaviour may come at a cost of reduced foraging (i.e., inactivity during the day). When both species were located more than 5 km away from a potential water source, they became less active during the heat of the day, which resulted in a reduction in total 24 h activity (Figure 5.5). This decline in activity during the heat of the day and total 24 h activity was enhanced with increasing aridity, and the response was more pronounced for wildebeest than gemsbok (see Figure 5.6). A reduction in activity during the heat of the day would potentially reduce the amount of evaporative water loss by lowering metabolic heat production (e.g., Topi (*Damaliscus korrigum*; Jarman 1977); moose (*Alces alces*; Belovsky & Jordan 1978); giraffe (*Giraffa camelopardalis*; Leuthold & Leuthold 1978) and gerenuk (*Litocranius walleri*; Leuthold & Leuthold 1978) reduced activity during the heat of the day). Similar responses in reduced activity during times of heat stress where water was lacking was reported for Arabian oryx (Hetem et al. 2012b), sand gazelle (Hetem et al. 2012b) and blesbok (Klein & Fairall 1986). However, compared to the arid-adapted gemsbok, wildebeest's activity responses were more enhanced when distances to water exceeded 20 km. Since wildebeest are rarely more than a few kilometres from the nearest available water (Western 1975; Berry 1980), I suggest that such differences in activity displayed by wildebeest, compared to gemsbok, could potentially be explained by their different water dependencies. Water-independent species showed little change in their distribution patterns with varying distances from water, whereas distribution patterns of water-dependent species, such as wildebeest, were constrained by distances to water (Western 1975; Redfern et al. 2003).

Despite both species demonstrating such changes in behaviour, the combined effect of high miniglobe temperatures, large distances to surface water (i.e., exceeded 20 km) and lack of green vegetation resulted in the wildebeest being unable to maintain homeothermy. When ungulates have free access to water, sweating and panting generally increases with an increase in air temperatures as ungulates become more reliant on evaporative cooling to maintain body temperature within a narrow range (Taylor 1970a,b). However, when access to water is limited, ungulates must “trade off” osmoregulation (control of body water) with thermoregulation (control of body temperature; Tattersall et al. 2012). Some species (e.g., Grant's gazelle (*Nanger granti*), Thomson's gazelle (*Eudorcas thomsonii*), oryx (*Oryx beisa*), eland (*Tragelaphus oryx*), and camel (*Camelus dromedarius*)) can reduce evaporative cooling (sweating) by as much as 89% by allowing body temperature to fluctuate over a wide range (Schmidt-Nielsen et al. 1957; Taylor 1970b). Gemsbok are traditionally viewed as water-independent because they are able to use a flexible body temperature (i.e., adaptive heterothermy) and store heat that would otherwise need to be evaporated (Taylor 1969; Knight 1991). However, one previous study, in a milder climate with free access to water, did not find evidence for adaptive heterothermy in free-living gemsbok (Maloney et al. 2002). Similarly, I have shown that gemsbok in the Kalahari, a more extreme environment, display less extreme increases in maximum 24 h body temperatures compared to wildebeest when distances to water increased. It is plausible that gemsbok may have alternate sources of water to prevent hyperthermia, for example, by selecting succulents or browse with higher water content (Cain et al. 2006), as observed for gemsbok in the southern Kalahari (Knight 1991). Therefore, gemsbok would have been less dehydrated if they were able to access greater preformed water in their food. Wildebeest, like gemsbok, are primarily grazers however they have a higher component of grass in their diet (Knight 1991), thus are more dependent on green vegetation. Compared to gemsbok, I have shown that the water-dependent wildebeest displayed higher maximum 24 h body temperatures when distances to water increased. Maximum 24 h body temperature progressively increases when mammals are deprived of water (Fuller et al. 2016), as shown for camels (Schmidt-Nielsen et al. 1957). When high air temperature was combined with dehydration, the mesic adapted eastern grey kangaroo (*Macropus giganteus*) had significantly higher body temperatures than the arid adapted red kangaroo (*Macropus rufus*; Dawson et al. 2007). The authors argued that the larger increase in maximum body temperature of the mesic species when exposed to heat and dehydration imply that the mesic species was more physiologically stressed than the arid-adapted species (Dawson et al. 2007). Although I did not quantify dehydration in my species, I suggest that the increased maximum 24 h body temperatures reported for wildebeest, when miniglobe temperature exceeded body temperature and distances to water exceeded 20 km, may have resulted from dehydration-induced hyperthermia. My results concur with Hetem et al. (2016) who concluded that higher maximum 24 h body temperature, in the face of insufficient water supply and heat exposure, may reflect a pathophysiological state, highlighting an animal which is struggling to maintain its water balance.

Three days before the first rainfall event at the end of the dry season, miniglobe temperature exceeded body temperature at sites selected by gemsbok and wildebeest, forcing the animals to rely on evaporative cooling to dissipate heat. During the three days before rain, maximum body temperatures peaked around 40.5°C. However, after the first rains, both species' maximum 24 h body temperatures dropped suggesting that the animals could employ evaporative cooling after replenishing their body water reserves by drinking water following rains. Similarly, baboon (*Papio hamadryas*) body temperatures dropped immediately after drinking water was returned after three days of water deprivation (Mitchell et al. 2009) and a similar response was noted when water was returned to dehydrated sheep and goats (Fuller et al. 2007). In addition, other studies have revealed that body temperature returns to normal following an initial taste of water (e.g., goats and sheep; McKinley et al. 2009); i.e., the dehydration-induced hyperthermia can resolve even before any physiological changes occur. Interestingly, ruminants can regain all lost water during one drink by retaining a large amount of water in the rumen which is then released slowly into the blood and body tissues allowing the animal to quickly rehydrate (Silanikove 1994, Cain et al. 2006). Therefore, access to surface water, particularly after the first rains, appears to have resolved the dehydration-induced hyperthermia experienced by wildebeest and gemsbok during times of aridity and thermal stress.

In conclusion, I have shown that both wildebeest and gemsbok selected similar microclimates when miniglobe temperature exceeded body temperature with slightly enhanced microclimate selection when further from water. Compared to gemsbok, wildebeest showed a greater decline in activity during the heat of the day and a greater hyperthermia when they were further from water sources and less likely to be drinking frequently. However, when both species were close to potential water sources, they both sustained homeothermy (i.e., regulating their body temperature within a narrow range) despite black miniglobe temperatures exceeding body temperature. I therefore propose that, in hot and dry environments, gemsbok may have physiological adaptations to better conserve body water, e.g., enhanced reabsorption of water in kidneys or eating melons. Conversely, wildebeest abandoned homeothermy and displayed dehydration-induced hyperthermia when access to drinking water was likely to be less frequent because of large distances to water. The findings of this study suggest that heterothermy associated with dehydration-induced hyperthermia, may be an indication of dehydration compromising the thermoregulatory system; that is, an indication of water stress. Wildebeest responses exaggerated when access to drinking water was likely to be less frequent, suggesting that their response to aridity might be migration. Wildebeest are known to migrate large distances to access surface water (Wilmshurst et al. 1999), but movements between wet and dry seasonal ranges have been restricted by veterinary fences, resulting in periodic large-scale die-offs during severe droughts (Child 1972; Parry 1987). The decline in wildebeest populations as a result of limitations in movement (Owen-Smith & Ogutu 2012) may suggest that they may already be at the edge of its physiological limit and, with climate change predicted to increase ambient temperatures and have less predictable rainfall in the semi-arid Kalahari (Davis 2011; van Wilgen et al. 2016), its thermoregulatory competence may not be sufficient to ensure long-term survival.

CHAPTER 6

6 Conclusion

The general aim of my thesis was to contribute to the understanding of physiological and behavioural strategies that enable large mammals to survive aridity. Warming trends are predicted to be accompanied by reduced precipitation and increased frequency of droughts (IPCC 2014), and these climatic changes may result in reduced food and water availability in semi-arid ecosystems. Since long-lived large mammals do not have access to micro-evolution as an adaptation strategy to cope with these changing climatic conditions, understanding the plasticity of behavioural and physiological responses of large mammals will improve modelling of ecological responses and predictions of the impact of future climate change (Kearney & Porter 2009; Kearney et al. 2010; Buckley et al. 2012; Chown 2012; Seebacher & Franklin 2012; Urban et al. 2016). In the Kalahari, anthropogenic barriers limit migratory movements thus large mammals that currently live in this environment would need to show phenotypic flexibility in their behavioural and thermoregulatory responses. The drought conditions at the beginning of this study provided an analogue of conditions likely to become prevalent. Wildebeest (*Connochaetes taurinus*) showed enhanced responses in behaviour and thermoregulation compared to those of arid-adapted gemsbok (*Oryx gazelle gazelle*), in a semi-arid savanna region where annual rainfall is variable and surface water is restricted.

6.1 Seasonality

Most of environmental conditions occur seasonally, affecting resource availability for ungulates (Owen-Smith 2008b). For instance, in the wet season, there are abundant resources on which animals thrive. However, during the dry season, animals have to cope with seasonal bottlenecks and spatial variation in resources (Parker et al. 1999; Owen-Smith 2002; Pettorelli et al. 2003). In the Kalahari, the dry seasons starts in autumn and continues into summer until the onset of the first rains. Not only do the animals that live in the Kalahari have to deal with diminishing resources at the end of the dry season but also high thermal stress. However, these seasonal patterns in resources will be exacerbated by the changing climatic conditions and in particular the dry season. In chapter three, I quantified the effects of seasonal variation on behavioural and thermoregulatory responses of two ungulate species with differing degrees of water dependency. I have shown that both gemsbok and wildebeest prioritised behavioural thermoregulation during the hot periods by seeking shade during the heat of the day and reducing diurnal activity. Both species compensated for the reduced diurnal activity by increasing their nocturnal activity. More exaggerated nocturnal responses were observed for the Arabian oryx (*Oryx leucoryx*; Hetem et al. 2012b) and sand gazelle (*Gazella subgutturosa marica*; Hetem et al. 2012b), but they were not exposed to natural predators as in this study. During the hot dry season, both gemsbok and wildebeest showed increased fluctuations in 24 h body temperature rhythm (Gemsbok: 2.1 ± 0.4 °C; Wildebeest: 2.2 ± 0.5 °C), which coincided with a time when water was lacking and forage is of poor quality within the environment. Increased fluctuations in body temperature during the dry season have been observed in kangaroos (Dawson et al. 2007; Maloney et al. 2011), Arabian oryx (Ostrowski et al. 2003, Hetem et al. 2010), and sand gazelle (Ostrowski et al. 2006, Hetem et al. 2012b). Body temperature fluctuations were exaggerated during the drought period compared to a similar period the following year, suggesting that aridity rather than temperature was the likely driver. Furthermore, the water-dependent wildebeest showed larger fluctuations in body temperature compared to gemsbok (3.14 ± 0.23 °C vs. 2.11 ± 0.55 °C), suggesting that wildebeest may be more vulnerable to changing climatic conditions. Similarly, the mesically-adapted eastern grey kangaroo (*Macropus giganteus*) displayed higher fluctuations in body temperature, compared to its counterpart, the desert-adapted red kangaroo (*Macropus rufus*; Dawson et al. 2007). I therefore showed that heterothermy (i.e., a large fluctuation in amplitude of body temperature) appear to be influenced by seasonal changes in water and forage availability, but those effects have not been tested empirically for any ungulate to date.

6.2 Vegetation greenness

Although a number of studies have proposed that an increase in fluctuations of body temperature, characterised by low minimum body temperatures, may result from an energy deficit during the dry season (e.g., see Hetem et al. 2010), with some correlating lowering of minimum 24 h body temperature with days since winter solstice (Maloney et al. 2011), no study to date has explicitly linked changes in body temperature of long-lived endotherms, such as ungulates, to available energy within the environment. High temperatures combined with changes to precipitation can lead to climatic moisture stress, reducing food availability (Biggs et al. 2008; Girvetz & Zganjar 2014). Because Normalized Difference Vegetation Index (NDVI) provides an index of vegetation quality (Huete et al. 2002; Pettorelli et al. 2005b), changes in vegetation greenness can reflect the individual or combined influence of factors such as seasonal precipitation, temperature and soil moisture conditions, with poor quality forage corresponding to brown vegetation in areas of low moisture (Suzuki et al. 2006). To investigate the behavioural and thermoregulatory consequences of poor quality forage during the dry season, in chapter four I investigated the influence that vegetation greenness (indexed as NDVI) may have on activity and thermoregulatory strategies of the arid-adapted gemsbok and water-dependent wildebeest under the same environmental conditions and then investigated whether responses were enhanced when the arid adapted species was exposed to a more arid region. I found that during times of low vegetation greenness (brown periods), both gemsbok and wildebeest showed a drop in minimum 24 h body temperature and a reduction in activity. However, wildebeest appeared to be more influenced by brown vegetation, as their activity and minimum 24 h body temperatures were lower than those of gemsbok inhabiting the same environment. Although gemsbok showed a slight decrease in minimum 24 h body temperature and activity when inhabiting a milder environment, when conditions were more extreme the arid-adapted gemsbok showed an even lower drop in minimum 24 h body temperatures when vegetation greenness was low. This reduction in minimum 24 h body temperatures observed by the gemsbok in the more arid site were not driven by air temperature because minimum 24 h body temperatures were lower in gemsbok in the more arid site compared to the gemsbok in the less arid site. I believe that when food quality becomes limited in the environment, antelope may reduce the precision of body temperature regulation to conserve energy. Since high ambient temperatures and low levels of precipitation affect the nature of the vegetation in both quantity and quality, lower quality food is likely to become more apparent because of aridification. Brown vegetation is not only likely to be of low quality during the dry season but also may be low in water.

6.3 Access to water

Rainfall in the Kalahari is constrained to three to five months during summer, thus water is largely limited in these semi-arid environments. As the dry season progresses food quality and quantity declines and surface water becomes restricted to a few perennial sources (Owen-Smith 2008a; Cain et al. 2011). Numerous studies have looked at the effect of distance to water on animal distribution and habitat use (Redfern et al. 2003; Western 1975; Bailey et al. 1996), but no one to date has identified the mechanistic components driving the distributions. Quantifying behavioural and thermoregulatory responses comparative to distance to water may provide a mechanism for observed species distributions. In chapter five, I quantified microclimate selection, activity and body temperature profiles of two sympatric ungulates with different water dependencies in relation to distance to water, particularly during high ambient temperatures. Shade-seeking behaviour and the timing of activity represent flexible behavioural processes, which are likely to become increasingly important and may act to buffer the adverse effects of aridity predicted to occur with climate change (Mitchell et al. 2008; Kearney et al. 2009; Huey et al. 2012; Hetem et al. 2012a). I showed that both wildebeest and gemsbok sought out shade and avoided activity during the heat of the day when access to drinking water was less frequent compared to when water source was near. For the arid-adapted gemsbok, I showed that selecting cool microclimates and reducing its activity allowed them to conserve sufficient body water to prevent dehydration-induced hyperthermia (i.e., high maximum 24 h body temperatures). Conversely, the water dependent wildebeest displayed higher maximum 24 h body temperature when potential water sources were too far to access regularly (i.e., more than 20 km) despite seeking shade and reducing activity during the heat of the day. Despite similar behavioural responses between the species, gemsbok were coping, whereas wildebeest appeared to become dehydrated based on body temperature. I therefore suggest that gemsbok may be better able to conserve body water (e.g., enhanced ability to reabsorb water from kidneys has been reported) which they could then use to maintain body temperature through evaporative cooling. Contrary to the initial ideas of heterothermy being a primary response to conserve body water in arid adapted species (see Mitchell et al. 2002). Further studies on hydration state would therefore need to establish whether changes in water dependency resulted in the physiological changes observed.

Distance from water is likely to be associated with differences in behavioural states (foraging vs migrating), habitat use (Bleich et al. 2010; Rainho & Palmeirim 2011) and seasonality of use (Bleich et al. 2010). For instance, various plant species that are favoured by many ungulates may be grazed less often when such landscapes are far from permanent water sources (Sianga et al. 2017). Habitat heterogeneity further from water sources may potentially allow spatial refuges in the landscape during times when water is limited. Sable (*Hippotragus niger*) avoid higher concentrations of predators by forging in these spatial refuges (Hensman et al. 2014). Thus, is it possible that wildebeest select habitats further from water to reduce predation risk (Sianga et al. 2017), or forage may be more abundant far from water providing dry season refuges (Selebatso et al. 2017b), disturbance by people may be less far from water. Or might they simply be unable to access water sources in some seasons because of territories? Further studies into habitat heterogeneity and seasonality of use could reveal as to why wildebeest would venture more than 20 km away from a water source when they started to struggle physiologically, since wildebeest are not commonly found further than 15 km from water (Western 1975; Berry 1980).

6.4 Adapting to climate change

When the conditions were hot and dry, the behavioural and thermoregulatory responses observed for gemsbok and wildebeest during this study, were most likely a result of access to energy (indexed as NDVI) and water (indexed as distance to water). The findings of this thesis therefore suggest that the drivers behind the seasonal changes in body temperature observed within earlier studies result from forage and water limitations. However, I can demonstrate that the responses observed may be representative of an even bigger response to climate change than what was generalized for a seasonal response in other studies (e.g., Hetem et al. 2010; Shrestha et al. 2011). During the drought period, the large fluctuations in body temperature for both gemsbok and wildebeest were even more noticeable, particularly for the water-dependent wildebeest, reflecting a compromised thermoregulatory ability during water and forage deprivation caused by aridity. Since many arid regions of Africa are predicted to get both hotter and drier with climate change (Niang et al. 2014; Engelbrecht et al. 2015), species inhabiting these semi-arid areas may already be pushed to the limit of their ability to cope with widely fluctuating climatic conditions (Hetem et al. 2010).

Species respond to climatic changes at different rates, or may experience different interactions (i.e., predation) and some may even fail to keep pace (Feeley et al. 2012). As such, I have shown that the water-dependent wildebeest is more physiologically stressed by water and forage limitations than the arid-adapted gemsbok in the Kalahari and may not have the capacity to cope with changing climatic conditions. Mass mortalities of wildebeest have been recorded when they attempted to escape harsh conditions, such as after the erection of the veterinary cordon fences when access to water and better foraging conditions were cut off (Williamson & Williamson 1981; Spinage 1992) and during the drought of 1985 when conditions were more arid compared to a normal year (Knight 1995; Thouless 1998). Perhaps they only inhabited the Kalahari transiently in the past and moved out during bad years, as suggested by Williamson 2002, but fences have restricted that option to move and have attempted to keep them in Kalahari permanently. Those that remain in the Kalahari appear to be physiologically stressed by the lack of water, as indicated by the large fluctuations of body temperatures during the dry season. They may be able to survive average years, but dry years, which are likely to become increasingly frequent with future climate change, is likely to be fatal for large numbers of wildebeest in the Kalahari. Since rainfall determines vegetation growth in this semi-arid savanna, and the secondary effect of reduced rainfall on annual food production for large herbivores will undoubtedly be substantial (See Ogutu & Owen-Smith 2003). Thus, water-dependent species may be under a greater risk of extirpation from future increases in drought intensity under climate change than water-independent species (Duncan et al. 2012). Yet, it’s not only the water dependent species that will struggle with climate change in the Kalahari, I have revealed that even the famously arid-adapted gemsbok will become physiologically stressed with increased aridity.

6.5 Conceptual framework and future directions

Since movement is one of the first behavioural responses of animals to environmental change (Parmesan & Yohe 2003), it is important to identify and understand the mechanistic components driving the decisions behind such movement. Within this thesis, I was able to partially address two of the four mechanistic components of the Movement Ecology Framework, proposed by Nathan et al. (2008). The decision of why (i.e., internal state), how (i.e., motion) and when and where (i.e., navigation) to move is determined by the capacity of the individual animal and how it interacts with the external environment (abiotic and biotic factors; Nathan et al. 2008). By using remote sensing and GPS data, I was able to identify external factors such as vegetation greenness, distance to water and microclimate experienced that would act upon the decisions to move (i.e., internal state; Figure 6.1). Knowing what is available in terms of spatial and temporal resources, such as forage, water and microclimate, will allow us to better understand the biotic and abiotic factors influencing the movement path of that individual.

Ungulates often move between areas of key resources during the wet and dry seasons (Fynn 2012). For instance, the best quality forage occurs in the lowest rainfall regions because this is where soils are less leached and provide the highest mineral content in forage (Fynn 2012). Lower production in low rainfall areas results in more digestible forage and ungulates often move towards these low rainfall areas during the wet season (Sinclair & Fryxell 1985) because this is the time when pregnant and lactating females need high minerals, energy and protein therefore they dependent upon these areas to maximize nutrient and energy intake (Hopcraft et al. 2010; Fynn & Bonyongo 2011; Fynn 2012). High rainfall regions provide more reliable but lower quality forage for the dry season (Fynn 2012) but drinking water is often more reliable in high rainfall areas, thus herbivores

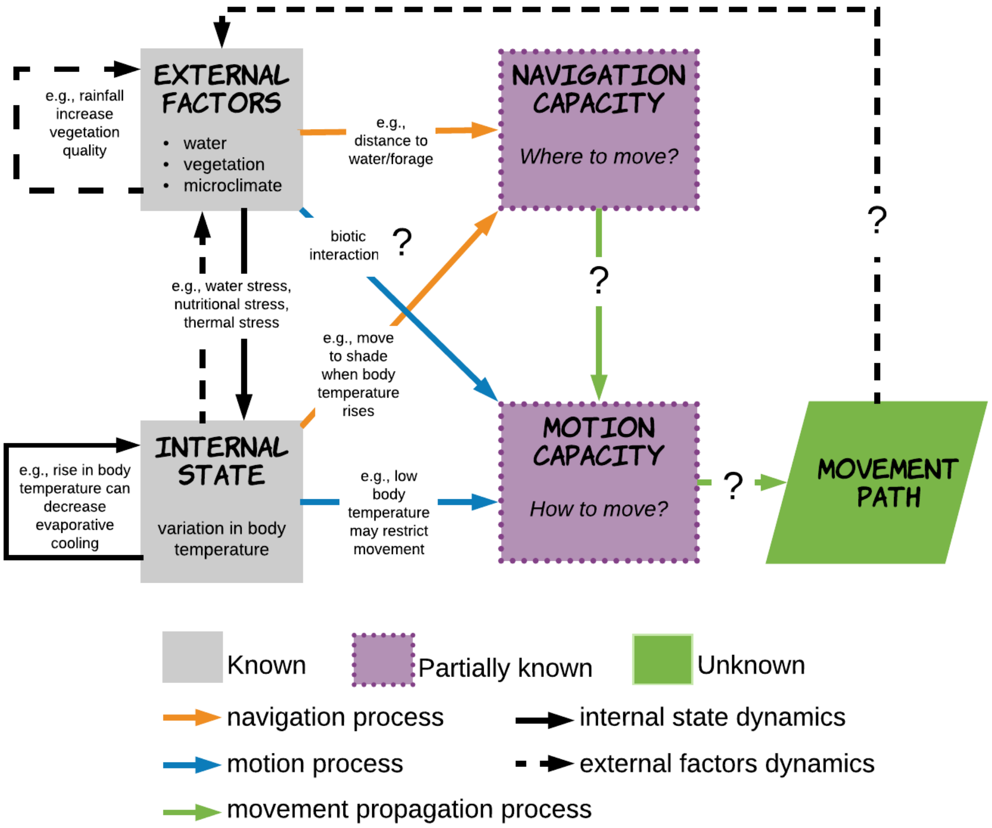

Figure 6.1: The movement ecology framework (adapted from Nathan et al. 2008) applied to this thesis, showing the processes and relationships (indicated by arrows) between the four basic components (internal state (physiology and neurology), motion capacity (biomechanical or morphological machineries), navigation capacity (cognitive or sensory machineries to obtain and use information) and external factors (biotic and abiotic environmental factors)) of movement. Arrows indicate the different processes included in the movement: the motion process in blue, the navigation process in orange, the observed movement resulting from the motion and the navigation processes in green. The grey blocks identify what has been achieved. The purple blocks identify what was partially achieved within this study and require further investigation into the links between processes. The green block identifies what is unknown and require further investigation into the links between processes (Copyright (2008) National Academy of Sciences).

migrate to high rainfall areas for the dry season (Fynn 2012). As such, green forage appears to be a major driver in ungulate seasonal range shifts during the dry season, as seen in the Kruger National Park (Fynn & Bonyongo 2011). The famous annual migration of blue wildebeest, zebra (*Equus* spp.) and Thomson’s gazelle (*Eudorcas thomsonii*) in the Serengeti can be explained largely in terms of their food requirements, such as food quality, which is largely dependent upon rainfall (Maddock 1979). But, we generally lack an understanding of the motivation to move. It is unclear as to what are the physiological costs and benefits perceived when moving between resources (see Bolger et al. 2008). Understanding the interaction between the internal state of the animal and external environment can improve our understanding of movement and navigation capacity and how these will dictate the movement path.

6.5.1 Why move?

Theoretically, the main reason to move is related to the internal state of the animal, which is seldom quantified, i.e., the physiological drivers of movement (Nathan et al. 2008). This includes the need to eat, find shade, evade predation or avoid competition (Doherty & Driscoll 2017). By using biologgers, I measured the individuals internal state by means of body temperature. The variation of body temperature is potentially an indicator of animal wellbeing (Fuller et al 2016) and fitness (Maloney et al. 2017) and could motivate the animal to fulfil one or more goals (Nathan et al. 2008). For instance, an increase in body temperature could initiate the response to seek shade or search for green patches or search for water when conditions get hot; hence, it contributes to the motivation to move (Figure 6.1). I have shown that maximum 24 h body temperature may increase as species find themselves further from water and unable to maintain their water balance, therefore, should they just wait for rain or might there be a threshold body temperature at which species start searching for water? Similarly, I have shown that minimum 24 h body temperature may decrease when an energy resource declines in the environment, therefore, would the animal move to other resources or reduce energy expenditure to maintain their energy balance. I believe I have enhanced our existing knowledge and created the link between body temperature, vegetation quality and distance to surface water for antelope of the Kalahari and effectively assessed a functional trait. The link between physiological traits and environmental factors provide the first step deciphering the basic determinants of movement patterns and processes (Nathan et al. 2008) and since a species' biological traits can mediate climate-change-induced stresses, trait-based approaches for climate change impacts could highlight the vulnerability of the species (Foden et al. 2013). For example, gemsbok were able to conserve sufficient body water by use of flexible behaviours to prevent dehydration-induced hyperthermia when access to water was limited, but wildebeest could not, highlighting that wildebeest may be more vulnerable to changing conditions than gemsbok. A mechanistic understanding of movement will enhance trait-based approaches for climate change impacts (Foden et al. 2013).

6.5.2 How to move?

Once an animal decides to move, the ability to move becomes the next challenge. To fully understand the series of processes shaping species movements we would also need to understand the motion capacity of the individual (Figure 6.1), the ability to move in various ways through its landscape (Nathan et al. 2008). Certain species may have specific adaptations in their motion capacity necessary to capture (predators) or evade (prey) capture (Wilson et al. 2018). For example, predators have higher muscle power, are faster and have a greater capacity to accelerate and decelerate than their prey (Wilson et al. 2018). Since fitness is impacted by energy and water balance (Maloney et al. 2017), healthy individuals with good body condition will have a greater motion capacity (Doherty & Driscoll 2017). Consequently, reductions in forage quality can decrease fitness and motion capacity, resulting in reduced energy available to move. For instance, I have shown that an animal may decrease its activity to conserve energy when resources are declining in the environment. However, the links between motion capacity in movement and landscape structure or conditions is not fully understood or addressed and require further investigation.

6.5.3 Where to move?

Animals have the ability to obtain and use information from the environment to decipher where to move; that is, the navigation capacity of the individual (Nathan et al. 2008). Wildebeest are known to migrate over large distances to access high-quality grazing (Hopcraft et al. 2010). Zebra time their migration according to rainfall patterns and therefore avoid adverse conditions and/or exploit renewed resource availability (Bartlam-Brooks et al. 2013). Knowing what is available in terms of spatial and temporal resources and whether animals head in that direction, will allow us to better understand the navigation capacity of that individual. Say for instance, knowing how far an animal is from water or green forage could give a probability of that animal moving in that direction. For example, gemsbok located more than 20 km away from surface water would more than likely search for higher water content forage than when close to surface water. In addition, knowing the microclimate of that individual would increase the understanding of why, where and when to move. For example, wildebeest and gemsbok would seek out shade or potential water sources when air conditions exceeded 23 °C during hot dry seasons. However, the links between navigation capacity of the individual and how and where or when they move within their landscape or under different environmental conditions is not fully understood or addressed and require further investigation.

6.5.4 When to move?

One way to understand the reasons behind movement would be by understanding the biotic interactions of species modulated by climate (Bozinovic & Pörtner 2015), such as species competition or predator-prey interactions (Trainor et al. 2014). Besides acquiring food and other resources, animals must remain safe from predation (Owen-Smith & Traill 2017). For example, the selection of thermally suitable microclimates or shifting foraging time to night may increase the risk of being predated upon and may result in a trade-off between predation risk and well-being (Godvik et al. 2009; Hebblewhite & Merrill 2009). Wildebeest in CKGR were unable to forage at night because of the high predation risk as was shown by Selebatso et al. 2017b. Although this study did not directly investigate the risk of predation for gemsbok and wildebeest, it would be inappropriate to overlook predation risk as a key component of ungulate survival, fitness and movement within the semi-arid Kalahari. Fear of predation can have a significant impact on how prey animals move within their landscape (Valeix et al. 2009). Thus, understanding the landscape of fear could identify the movement path of the animal, such as the decision to run or walk, so in all essence “when to move”. For effective conservation strategies, it is imperative to understand species interactions to accurately depict current and future species distributions (Kearney and Porter 2009; Trainor et al. 2014; Bozinovic & Pörtner 2015).

6.6 Perspectives and significance

My study is unique in that I have looked at where the animal is in space and linked it to their physiological and behavioural responses. I have, therefore, quantified microclimate selection, activity and body temperature responses in relation to NDVI and distance to water and have shown that the driving mechanisms behind the seasonal changes of body temperature and activity patterns is access to energy and water. Furthermore, the present study supports previous findings (e.g., Hetem et al. 2016) and contributes additional evidence that suggests that the fluctuation in body temperature in response to environmental conditions reflect an indication of physiological stress compromising the thermoregulatory system more than a positive adaptive response originally suggested for adaptive heterothermy.

However, physiological and behavioural studies are often short-lived, we therefore need to expand the duration to observe inter-annual variability and ultimately detect responses to climate change (see Hetem et al. 2016; Fuller et al. 2016). If the first response to hot and dry conditions, which may become more prevalent as climate change increases, is likely be behavioural adjustments, which if insufficient at buffering climate change may result in physiological stress, then long-term monitoring of these behavioural and physiological traits would be beneficial and valuable to biodiversity conservation in the light of a changing climate. We could potentially use behavioural and physiological responses as indicators of potential stress to identify possible vulnerability to changing climates. For instance, long-term monitoring of body temperature may provide a sensitive index of physiological stress, in terms of energy and water stresses, because of changing climatic conditions. Since long-term monitoring is considered as an essential tool for biodiversity management (Gitzen et al. 2012), future studies should therefore focus on the inclusion of physiology of ungulates in long-term monitoring, particularly for species that are exposed to habitat transformation and extreme environmental conditions.

If we are to successfully conserve biodiversity under changing climatic conditions, we would need a better understanding of how sensitive species are to changing climatic conditions, specifically to identify which species we would need to be prioritised for conservation in the future. The majority of prediction models (i.e., bioclimatic envelope models) to date have provided climate change extinction risks based on observed distributions and climate variables (e.g., Pearson & Dawson 2003; Root et al. 2003; Thuiller et al. 2006). Yet, climate-change-related stresses are not fully reflected in bioclimatic envelope models as they do not include the species' biological traits (Foden et al. 2013; Urban et al. 2016). However, assessing a species' functional traits such as physiological and ecological characteristics, and incorporating such functional traits that dictate a species vulnerability into distribution models may identify which species are at risk of extirpation from climate change (Foden et al. 2013; Garcia et al. 2014). To do so, we would need ecologists, physiologists and conservation practitioners to work together in developing models that incorporate all possible aspects, such as why, how, when and where to move, influencing species distribution patterns (Cooke et al. 2014; Evans et al. 2015). Increasing emphasis has been place on mechanistic species distribution models that incorporate behavioural and physiological data to create an in-depth understanding of the thermoregulatory physiology and energetics of a species (Levesque et al. 2016). Not only will these mechanistic models will allow us to better predict how species will respond to climate change (Kearney & Porter 2009; Kearney et al. 2010; Buckley et al. 2012; Chown 2012; Seebacher & Franklin 2012; Urban et al. 2016), but will ultimately contribute towards effective management and conservation of Africa's biodiversity in the face of future climate change.

CHAPTER 7

References

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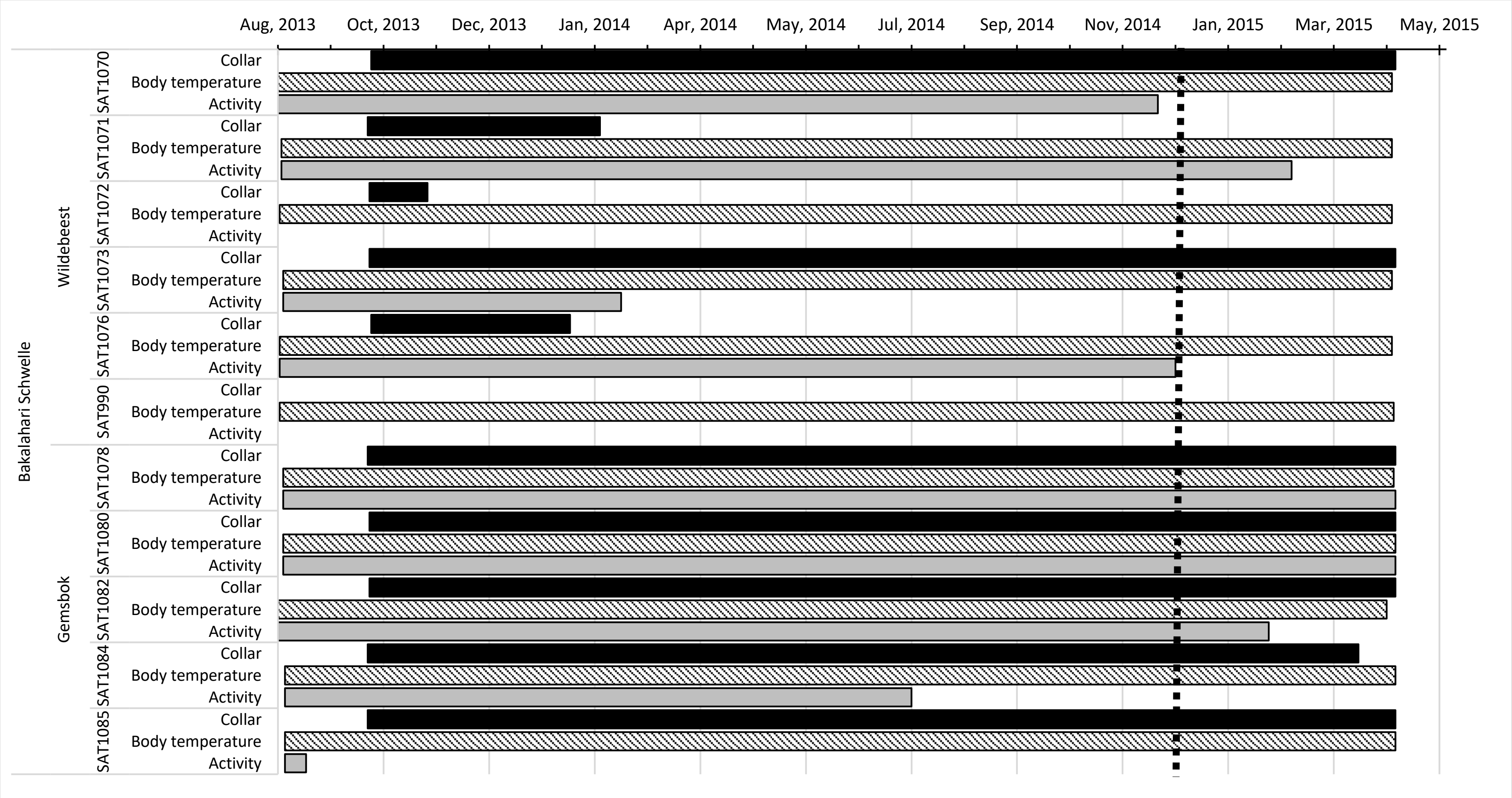
Appendix 1: Gantt chart of data collected from data loggers (body temperature and activity) and collars (GPS and microclimate selection) per individual animal throughout the study period for Central Kalahari Game Reserve. The dotted line indicates nine month mark.

Appendix 2: Gantt chart of data collected from data loggers (body temperature and activity) and collars (GPS and microclimate selection) per individual animal throughout the study period for Bakgalagadi Schwelle. Individuals had to be recollared in last week of September 2013 due to technical failure. The dotted line indicates 15 month mark.



Appendix 3: Ethical clearance certificates

AESC3

STRICTLY CONFIDENTIAL

ANIMAL ETHICS SCREENING COMMITTEE (AESC)

CLEARANCE CERTIFICATE NO. 2012/24/04

APPLICANT:	Ms M F Boyers
DEPARTMENT:	APES
PROJECT TITLE:	Trade-offs between thermoregulation and fine scale behavioural decisions of free-ranging ungulates

Number and Species

12 Gemsbok (Oryx gazelle) and 6 Blue Wildebeest (Connochaetes taurinus)

Approval was given for the use of animals for the project described above at an AESC meeting held on 26 June 2012. This approval remains valid until 30 June 2014.

The use of these animals is subject to AESC guidelines for the use and care of animals, is limited to the procedures described in the application form and to the following additional conditions:

Conditions

- FIO is used as the 'insecticide' on the wound to prevent fly infestation.
- Details of the telemetry equipment (e.g., make, dimensions and batterylife) are provided before commencement of the study

Signed: ______________________________ Date.
(Chairperson, AESC)

31/7/12

I am satisfied that the persons listed in this application are competent to perform the procedures therein, in terms of Section 23 (1) (c) of the Veterinary and Para-Veterinary Professions Act (19 of 1982)

Signed: ______________________________ Date: 31/7/12
(Registered Veterinarian)

cc: Supervisor:

Director: CAS

AESC 2012 M&E A

Please note that only typewritten applications will be accepted.

UNIVERSITY OF THE WITWATERSRAND

ANIMAL ETHICS SCREENING COMMITTEE MODIFICATIONS AND EXTENSIONS TO EXPERIMENTS

a. Name: Ms. Melinda Boyers

b. School and email address: School of Animals, Plants and Environmental Sciences

melinda.boyers@telkomsa.net

c. Experiment to be modified / extended **AESC NO**

Original AESC number	**2012**	**24**	**04**
Other M&Es :	N/A		

d. Project Title: Trade-offs between thermoregulation and fine scale behavioural decisions of free-ranging ungulates.

		No.	**Species**
e.	Number and species of animals originally approved:	12 6	*Oryx gazelle gazelle* *Connochaetes taurinus*
f.	Number of additional animals previously allocated on M&Es:	0	N/A
g.	Total number of animals allocated to the experiment to date:	12 6	*Oryx gazelle gazelle* *Connochaetes taurinus*
h.	Number of animals used to date:	0	N/A

i. Specific modification / extension requested:

MSc student, Miss Claire Relton, will make used of the data collected by the GPS and radiotelemetry tracking devices which will be placed around the neck of each animal used in Ms. Melinda Boyers' PhD study. No additional procedures or equipment are required.

j. Motivation for modification / extension:

The additional MSc project will assess the movement ecology of arid savanna herbivores in response to environmental variability across the central Kalahari. This project will be a predominantly desktopbased study, which will make use of vegetation index MODIS satellite data, as well as GPS coordinates of the animals, which is transmitted via satellite to a website developed by the collar manufacturer.

Date: 24 July 2012

Moyers

Signature:

RECOMMENDATIONS

Approved. Claire Relton is added as a co-worker

Date: 26 July 2012

Signature:

Chairman, AESC

AESC 2012 M&E B

Please note that only typewritten applications will be accepted.

UNIVERSITY OF THE WITWATERSRAND

ANIMAL ETHICS SCREENING COMMITTEE
MODIFICATIONS AND EXTENSIONS TO EXPERIMENTS

a. Name: Ms. Melinda Boyers

b. School and email address: School of Animals, Plants and Environmental Sciences

melinda.boyers@telkomsa.net

c. Experiment to be modified / extended **AESC NO**

Original AESC number	**2012**	**24**	**04**
Other M&Es :			Yes

d. Project Title: Trade-offs between thermoregulation and fine scale behavioural decisions of free-ranging ungulates.

	No.	**Species**
e. Number and species of animals originally approved:	12 6	*Oryx gazelle gazelle* *Connochaetes taurinus*
f. Number of additional animals previously allocated on M&Es:	0	
g. Total number of animals allocated to the experiment to date:	12 6	*Oryx gazelle gazelle* *Connochaetes taurinus*
h. Number of animals used to date:	8	*Oryx gazelle gazelle*

i. Specific modification / extension requested:

Addition of four gemsboks (*Oryx gazelle gazelle*) two blue wildebeest (*Connochaetes taurinus)* to increase our sample size to eight individuals per species per areas.

Change field site from Khutse (southern Central Kalahari Game Reserve) to the Kgalagadi Transfontier Park (South Africa and Botswana) as a study area.

j. Motivation for modification / extension:

Addition of animals:

The additional animals will increase our sample size to eight individuals per species per areas and allows for better comparative analysis between sites and species. Although six is the minimum sample size required for statistical analyses of this sort, a sample of eight individuals per comparison would increase our statistical power and compensate for potential losses resulting from predation and disease, which may occur in freeliving wild ungulates.

Change of field site:

Unfortunately we were unable to obtain the necessary permits from the Botswana government to work on blue wildebeest in the Central Kalahari Game Reserve, we did receive the necessary permits to work on gemsbok. We therefore looked into other areas where wildebeest and gemsbok co-occur and which would still allow for a comparison between gemsbok across a rainfall/aridity gradient. The Kgalagadi Transfontier Park represents a region with lower rainfall compared to the Central Kalahari Game Reserve. Furthermore, there are no barriers to animal movement from the Central Kalahari Game Reserve south-west towards the Kalagadi Transfrontier Park extending into South Africa (see Fig. 1 below). The greater Kalahari therefore provides considerable scope for animals to exploit spatial heterogeneity in vegetation. The Kalahari therefore provides the perfect location at which to monitor species that currently live within this semi-arid environment and their responses to the current climatic conditions in order to gain a better understanding of the behavioural and thermoregulatory mechanisms which species will need to employ as conditions become hotter and drier as a result of future climate change. We have received permission from the Botswana government and SANParks to conduct the proposed research in the Kgalagadi Transfrontier Park.

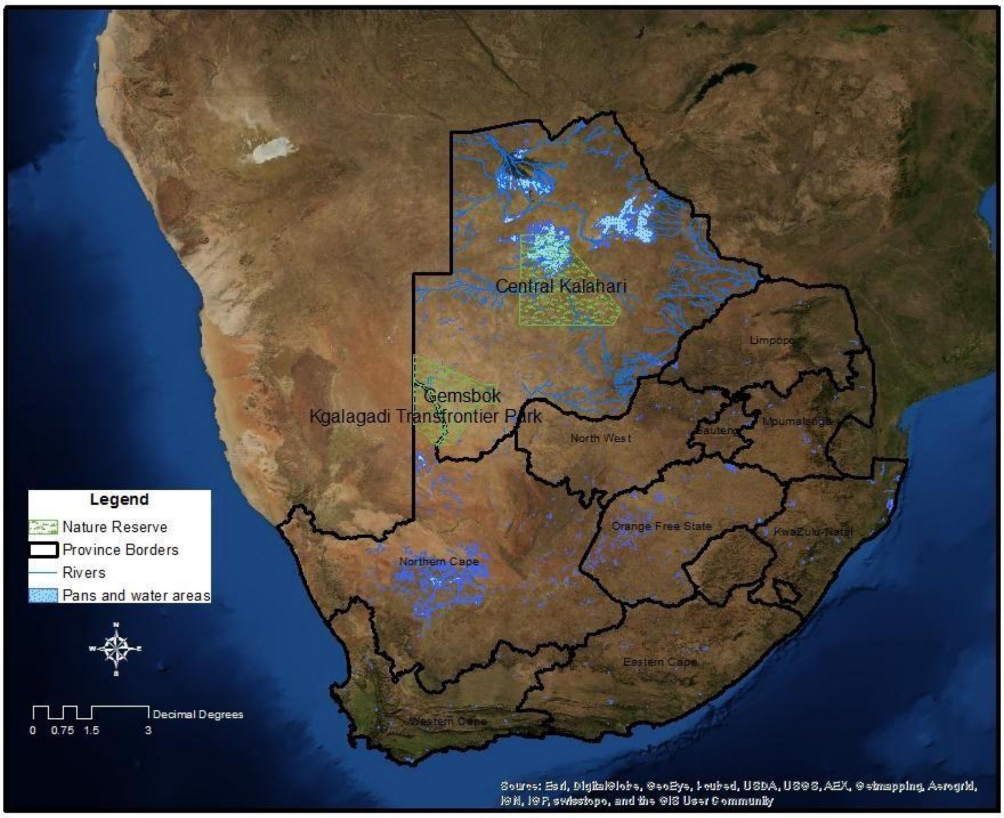


Figure 1: Map of study sites. The Central Kalahari (CKGR) is situated centrally of Botswana and the Kgalagadi Transfontier Reserve lies on the border of South Africa and Botswana. The CKGR is only fenced on the northern boundary of the reserve allowing animal movement south-west towards the Kalagadi Transfrontier Park extending into South Africa. The game fences along the Kgalagadi Transfontier Game Reserve were erected in 1983 along the park's western and southern boundaries. The eastern boundary remained unfenced leaving this border open to animals that needed to migrate from east to west.

Date: 24 May 2013

Moyers

Signature:

RECOMMENDATIONS

Approved: additional 4 gemsbok and 2 wildebeest; change of study site.

Date: 24 May 2013

Signature:

Chairman, AESC

AESC 2012 M&E C

Please note that only typewritten applications will be accepted.

UNIVERSITY OF THE WITWATERSRAND

ANIMAL ETHICS SCREENING COMMITTEE MODIFICATIONS AND EXTENSIONS TO EXPERIMENTS

a.	Name:	Ms. Melinda Boyers
b.	School and email address: Environmental Sciences	School of Animals, Plants and melinda.boyers@telkomsa.net

c. Experiment to be modified / extended **AESC NO**

Original AESC number	**2012**	**24**	**04**
Other M&Es :			Yes

d. Project Title: Trade-offs between thermoregulation and fine scale behavioural decisions of free-ranging ungulates.

	No.	**Species**
e. Number and species of animals originally approved:	12 6	*Oryx gazelle gazelle* *Connochaetes taurinus*
f. Number of additional animals previously allocated on M&Es:	4 2	*Oryx gazelle gazelle* *Connochaetes taurinus*
g. Total number of animals allocated to the experiment to date:	16 8	*Oryx gazelle gazelle* *Connochaetes taurinus*
h. Number of animals used to date:	16 8	*Oryx gazelle gazelle* *Connochaetes taurinus*

i. Specific modification / extension requested:

Permission to dart and recollar eight female gemsbok and eight female blue wildebeest in the Kgalagadi/Schwelle study area.

j. Motivation for modification / extension:

After we implanted data loggers and collared eight gemsbok and eight blue wildebeest between 2 - 9 August 2013, a system failure switched off the GPS and satellite upload capability of all of the collars. Because the supplier of the collars is unable to rectify the problem remotely, I would like to request permission to dart and replace the collars of all 16 animals in the Kgalagadi/Schwelle area. The aim is to use the VHF radio transmitter to locate all 16 study animals, then to recapture and replace the collars of eight female gemsbok and eight female blue wildebeest in the Kgalagadi Transfontier Park and Schwelle region of Botswana. I plan to replace the collars at the end of September 2013 (22nd September 2013 till 5th October 2013) when a fixed wing pilot (to locate the animals), experienced helicopter pilot and Botswana vet (to dart the animals) are able to assist with the capture operation. The GPS collars will have the same specifications as originally approved; they will be manufactured by Africa Wildlife Tracking in South Africa (see http://www.awt.co.za/) and will have satellite downloading facilities together with VHF radio transmitters to allow the location of animals for removal of the collars at the end of the study period.

Date: 18 September 2013

Moyers

Signature:

RECOMMENDATIONS

Approved: permission to recollar.

Date: 20 September 2013

Signature:

Chairman, AESC

AESC 2012 M&E D

Please note that only typewritten applications will be accepted.

UNIVERSITY OF THE WITWATERSRAND

ANIMAL ETHICS SCREENING COMMITTEE
MODIFICATIONS AND EXTENSIONS TO EXPERIMENTS

a. Name: Ms. Melinda Boyers

b. School and email address: School of Animals, Plants and Environmental Sciences

melinda.boyers@telkomsa.net

c. Experiment to be modified / extended **AESC NO**

Original AESC number	**2012**	**24**	**04**
Other M&Es :			Yes

d. Project Title: Trade-offs between thermoregulation and fine scale behavioural decisions of free-ranging ungulates.

	No.	**Species**
e. Number and species of animals originally approved:	12 6	*Oryx gazelle gazelle* *Connochaetes taurinus*
f. Number of additional animals previously allocated on M&Es:	4 2	*Oryx gazelle gazelle* *Connochaetes taurinus*
g. Total number of animals allocated to the experiment to date:	16 8	*Oryx gazelle gazelle* *Connochaetes taurinus*
h. Number of animals used to date:	16 8	*Oryx gazelle gazelle* *Connochaetes taurinus*

i. Specific modification / extension requested:

We request permission to extend the project until June 2016. We wish to dart, reimplant and recollar the eight female gemsboks in the Central Kalahari Game Reserve area in April/May 2014 and extend the period of data collection for a further two years. We also request permission to test new real-time technology by implanting a test unit (temperature and activity tag) and collaring one blue wildebeest on a private game farm in Bela Bela in February 2014.

j. Motivation for modification / extension:

The specific aim of this project is to compare the long-term physiological and behavioural thermoregulation and movement ecology of free-ranging sympatric gemsbok and blue wildebeest, through the use of miniature data loggers. I would like to request permission to extend the date of this ethics clearance certificate till 30th June 2016 (current expiry is on the 30th June 2014). This type of research requires measurements and monitoring of individual animals for long periods of time (multiple years). Thus we request for the project approval to be extended for another two years.

Unfortunately the collars that were originally placed on eight female gemsboks in CKGR in November 2012 have stopped sending a GPS signal as the batteries within the collar ran low. In order to continue this study I request permission to dart and replace the collars and data loggers of the eight female gemsbok originally allocated to the study or alternativelyto dart additional female gemsbok to make up our sample size of eight individuals if any of the original gemsbok have died or are in poor body condition at the time of darting. The aim is to use the VHF radio transmitter to locate all 8 study animals, then to recapture and replace the implants and collars of eight female gemsboks in the Central Kalahari Game Reserve of Botswana. I plan to replace the implants and collars at the end of April 2014 (28th April till May 10th) when a fixed wing pilot (to locate the animals), experienced helicopter pilot and Botswana vet (to dart the animals) are able to assist with the capture operation and a surgical team (including Dr Anna Haw and Sr Mary-Ann Costello) is able to assist with the surgical removal and reimplantation of data loggers. The GPS collars will have the same specifications as originally approved; they will be manufactured by Africa Wildlife Tracking in South Africa (see http://www.awt.co.za/) and will have satellite down-loading facilities together with VHF radio transmitters to allow the location of animals for removal of the collars at the end of the study period.

As previously approved each collar is linked up to a data 'tag' wirelessly which sends internal body temperature and activity readings to the collar which in turn sends the data (body temperature, activity, ambient temperature and GPS location) via satellite so that real time data is retrievable. This data 'tag' was manufactured by AWT and is 90mm x 35mm in diameter and weighs 150 grams. As these AWT 'tags' made use of new technology, we underestimated the signal strength required for the signal from the implanted tag to reach the collar and we have thus been unable to obtain realtime body temperature and activity data. Since then the suppliers have improved the technology and strengthened the signal from the tag. However, before we implant these new tags into the eight free-living female gemsbok in CKGR I would like to request permission to test this new tag in a male blue wildebeest inhabiting a private hunting game reserve in Bela Bela. Unfortunately the farm doesn't stock gemsbok and the female blue wildebeest are currently calving, nevertheless we believe a male blue wildebeest will provide an ideal surrogate in which to test the new tag. Once the tag has been surgically implanted (following the same procedures as originally approved), the wildebeest will be monitored on the farm and real time data, body temperature and activity, will be downloaded via a satellite link. After a one-month period the wildebeest will be hunted as is standard practice on the farm and the tag and collar will be retrieved. We hope to dart and collar and implant the blue wildebeest in the beginning of February 2014 (7th February till 9th February) when the vet (Dr Anna Haw) and helicopter are available.

Date: 23 January 2014

Meyers

Signature:

RECOMMENDATIONS:

Approval granted for a.

extension of time until

December 2016

b. **darting, re-implanting and re-collaring eight female gemsboks in the Central Kalahari Game**

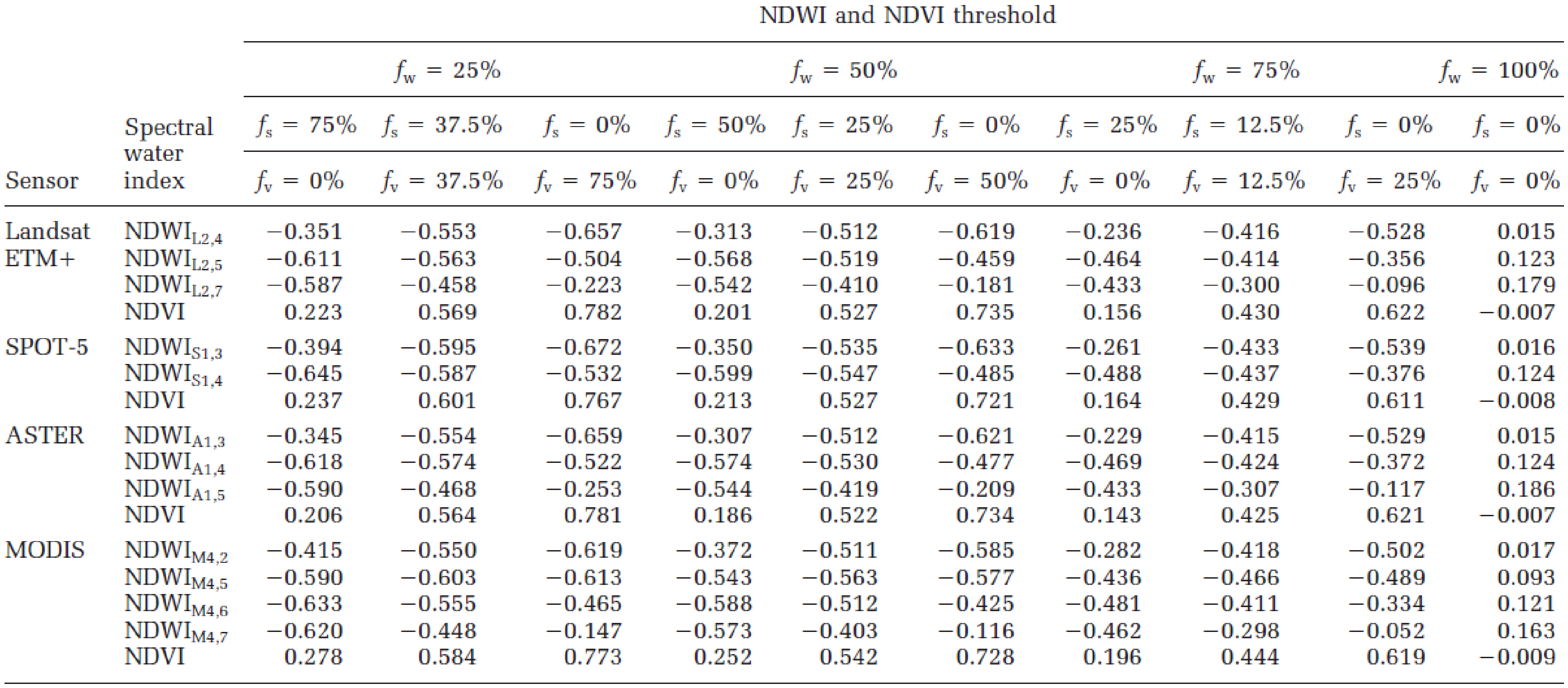
Reserve area

c. **testing new real-time technology by implanting a test unit (temperature and activity tag) and collaring one blue wildebeest on a private game farm in Bela Bela.** Date:27 January 2014

Signature:

Chairman, AESC

Appendix 4: Spectral data analysis of NDWI and NDVI thresholds for pure water (F_w = 100%) and mixed water (F_w = 25%, 50%, and 75%) components.



		NDWI and NDVI threshold									
		$f_w = 25\%$			$f_w = 50\%$			$f_w = 75\%$			$f_w = 100\%$
	Spectral water	$f_s = 75\%$	$f_s = 37.5\%$	$f_s = 0\%$	$f_s = 50\%$	$f_s = 25\%$	$f_s = 0\%$	$f_s = 25\%$	$f_s = 12.5\%$	$f_s = 0\%$	$f_s = 0\%$
Sensor	index	$f_v = 0\%$	$f_v = 37.5\%$	$f_v = 75\%$	$f_v = 0\%$	$f_v = 25\%$	$f_v = 50\%$	$f_v = 0\%$	$f_v = 12.5\%$	$f_v = 25\%$	$f_v = 0\%$
Landsat ETM+	$NDWI_{L2,4}$	−0.351	−0.553	−0.657	−0.313	−0.512	−0.619	−0.236	−0.416	−0.528	0.015
	$NDWI_{L2,5}$	−0.611	−0.563	−0.504	−0.568	−0.519	−0.459	−0.464	−0.414	−0.356	0.123
	$NDWI_{L2,7}$	−0.587	−0.458	−0.223	−0.542	−0.410	−0.181	−0.433	−0.300	−0.096	0.179
	NDVI	0.223	0.569	0.782	0.201	0.527	0.735	0.156	0.430	0.622	−0.007
SPOT-5	$NDWI_{S1,3}$	−0.394	−0.595	−0.672	−0.350	−0.535	−0.633	−0.261	−0.433	−0.539	0.016
	$NDWI_{S1,4}$	−0.645	−0.587	−0.532	−0.599	−0.547	−0.485	−0.488	−0.437	−0.376	0.124
	NDVI	0.237	0.601	0.767	0.213	0.527	0.721	0.164	0.429	0.611	−0.008
ASTER	$NDWI_{A1,3}$	−0.345	−0.554	−0.659	−0.307	−0.512	−0.621	−0.229	−0.415	−0.529	0.015
	$NDWI_{A1,4}$	−0.618	−0.574	−0.522	−0.574	−0.530	−0.477	−0.469	−0.424	−0.372	0.124
	$NDWI_{A1,5}$	−0.590	−0.468	−0.253	−0.544	−0.419	−0.209	−0.433	−0.307	−0.117	0.186
	NDVI	0.206	0.564	0.781	0.186	0.522	0.734	0.143	0.425	0.621	−0.007
MODIS	$NDWI_{M4,2}$	−0.415	−0.550	−0.619	−0.372	−0.511	−0.585	−0.282	−0.418	−0.502	0.017
	$NDWI_{M4,5}$	−0.590	−0.603	−0.613	−0.543	−0.563	−0.577	−0.436	−0.466	−0.489	0.093
	$NDWI_{M4,6}$	−0.633	−0.555	−0.465	−0.588	−0.512	−0.425	−0.481	−0.411	−0.334	0.121
	$NDWI_{M4,7}$	−0.620	−0.448	−0.147	−0.573	−0.403	−0.116	−0.462	−0.298	−0.052	0.163
	NDVI	0.278	0.584	0.773	0.252	0.542	0.728	0.196	0.444	0.619	−0.009

Note. **NDWI and NDVI Thresholds. Reprinted from "Analysis of Dynamic Thresholds for the Normalized Difference Water Index," by L. Ji, L. Zang, & B. Wylie, 2009, *Photogrammetric Engineering & Remote Sensing, 75*, p. 1316. Copyright 2009 by the American Society for Photogrammetry and Remote Sensing.**