BEHAVIOURAL AND PHYSIOLOGICAL RESPONSES OF SABLE ANTELOPE TO HEAT AND ARIDITY

Kiara Avelyen Haylock

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DECLARATION

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

Signed on the 24th day of October 2024

ABSTRACT

The increased probability of longer, more extreme dry seasons, due to rapidly rising temperatures and the increased frequency and intensity of droughts, threatens water-dependent, selective grazers throughout Africa. Phenotypic plasticity such as behavioural adjustments and physiological flexibility may buffer the impacts of spatiotemporal variations in resource availability and climate. My project aimed to assess variations in home range size, movement distances, behavioural states of movement, fine-scale activity, microclimate selection and body temperature of sable antelope (*Hippotragus niger niger*), a water-dependent selective grazer, in relation to spatiotemporal variation in vegetation greenness and environmental heat load.

To address the aim of my project, I measured body temperature and fine-scale activity using biologging in ten free-living GPS-collared sable antelopes in the semi-arid Bwabwata National Park of Namibia. Each collar was fitted with a miniature black globe thermometer to assess microclimate selection. A weather station with a standard black globe thermometer recorded black globe temperature and air temperature. Data collection spanned 24 months, from May 2016 to April 2018.

The dry season was a critical period for sable antelopes, particularly the late dry season when high ambient temperatures compounded reduced resource availability. As conditions became hotter and browner with the progression of the dry season, home ranges elongated towards the Kavango River and increased in size by ~50% from the early dry to the late dry season. In response to increased 24-hour mean black globe temperature and increased exposure to brown vegetation, the 24-hour mean hourly displacement distance of sable antelopes increased with progression of the dry season, mostly due to the increased frequency of long, directed movements to the Kavango River during the late dry season. One sable antelope

travelled between 13 and 30 kms every 4-5 days to access water from the river during the late dry season. Using Hidden Markov Models, four behavioural states were identified from the movement tracks of sable antelopes: resting, foraging, local movement and relocating. The long, directed movements to water, classified as a relocating behavioural state, predominated during the late dry season. Sable antelope displayed an increase in relocating behaviour and a decrease in foraging behaviour associated with high 24-hour mean black globe temperature and increased proportion of brown vegetation exposure. Sable antelopes also displayed an increase in local movement with increased exposure to brown vegetation and high 24-hour mean blackglobe temperature, but a decrease in resting behaviour with an increase in the proportion of brown vegetation exposure.

Driven by decreasing vegetation greenness and increasing black globe temperatures, sable antelopes reduced their diurnal proportion of activity with progression of the dry season, associated with a reduction in activity during the heat of the day in response to increased exposure to brown vegetation, high 24-hour mean black globe temperature and an increased proportion of time spent in the shade. Sable antelopes did not fully compensate for lost diurnal activity, despite increased nocturnal activity during hot and dry conditions, as total 24-hour activity decreased with progression of the dry season. Sable antelopes also selected higher quality microclimates (i.e. microclimates that were on average 6.7 ± 0.2 ^{o}C cooler than direct sun) when increasingly exposed to brown vegetation and high 24-hour maximum black globe temperature.

Fluctuations in 24-hour body temperature increased during the dry season with maximum amplitudes of body temperature rhythm of >5 ^{o}C within a single day during the late dry season. Sable antelopes displayed a reduction in minimum 24-hour body temperature in response to decreased 24-hour black globe temperature and increased exposure to brown vegetation during the early dry season, likely due to energy deprivation. While minimum

body temperatures remained low during the late dry season, sable antelopes displayed an increase in maximum 24-hour body temperature in response to increased mean 24-hour black globe temperature and increased exposure to brown vegetation, likely due to water deprivation. High maximum 24-hour body temperatures, indicative of dehydration-induced hyperthermia, increased the likelihood of relocating movements to the Kavango River which in turn were associated with a subsequent decline in maximum 24-hour body temperatures. By linking body temperature to a behavioural state of movement, I am the first to demonstrate a direct link between access to a water resource and maximum body temperature in a free-living antelope species.

The behavioural flexibility exhibited by sable antelopes during the dry season failed to buffer reduced resource availability as fluctuations in body temperature indicated that sable antelopes experienced nutritional and water stress. My findings highlight the importance of incorporating physiological measurements into behavioural and ecological studies to inform management decisions and improve conservation efforts in the face of climate change.

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LIST OF ABBREVIATIONS

EVI	Enhanced Vegetation Index
GPS	Global Positioning System
IUCN	International Union for Conservation of Nature
KaZa TFCA	Kavango–Zambezi Transfrontier Conservation Area
MODIS	Moderate Resolution Imaging Spectroradiometer
NDVI	Normalised Difference Vegetation Index
NOAA	National Oceanic and Atmospheric Administration
VHF	Very High Frequency

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CHAPTER 1

Introduction

1.1 Literature review

1.1.1 Introduction

African savannas are characterised by pronounced seasonality with distinct wet and dry seasons. This marked seasonality generates substantial spatiotemporal patchiness in the quantity, quality, and distribution of resources through each seasonal cycle (Bell, 1986; du Toit et al., 2003). In summer rainfall regions, the total amount and distribution of rainfall during the warm summer months not only governs savanna plant growth and water availability during the wet season but determines the persistence of water sources and key dietary components into the dry season (du Toit et al., 2003). During the dry season water availability, food availability and the nutritional value of food progressively decline (Owen-Smith, 1982; Owen-Smith, 2014). The severity of the dry season, and thus the degree of resource scarcity, varies annually depending on the rainfall received during the preceding wet season. Ambient temperatures are typically coolest during the early dry season, with temperatures peaking at the end of the dry season before rainfall resumes. Large savanna herbivores must therefore cope with substantial spatial and temporal variation in both resource availability and weather.

Spatial and temporal variations in resource availability and environmental conditions are likely to increase with climate change. Climate change and the associated bush encroachment, rising temperatures, increased drought occurrence and increased variability in rainfall threaten the persistence of African savanna herbivore assemblages as a result of habitat deterioration, disruption of ecological interactions, reduction of key resources and exacerbation of thermal stressors (Duncan et al., 2012; Fuller et al., 2014; Gordon and Prins, 2008; Ogutu and Owen-Smith, 2003; Owen-Smith and Mills, 2006; Seydack et al., 2012; Smit and Prins, 2015; van Wilgen et al., 2016). Climate-induced alterations to savanna ecosystems have contributed to the substantial decline of large ungulate populations across Africa (Craigie et al., 2010; Ogutu et al., 2009; Ogutu and Owen-Smith, 2003; Seydack et al., 2012; Smit and Prins, 2015). In particular,

drought and increased rainfall variability have been associated with substantial changes in the population dynamics of certain ungulate species with water-dependent, grazing species exhibiting resource selectivity, narrow habitat requirements and low local densities suffering the highest mortalities (Dunham et al., 2004, 2003; Harrington et al., 1999; Ogutu et al., 2008; Ogutu and Owen-Smith, 2003; Okello et al., 2016; Owen-Smith et al., 2005; Owen-Smith and Mills, 2006).

If ungulates are to survive the adverse ecological and environmental effects of increased heat and aridity associated with climate change, they will have to adapt to new conditions or shift their distribution ranges, either through genetic adaptation or phenotypic plasticity (Hetem et al., 2014). However, genetic adaptation is an unlikely option for coping with the rapid rate of climate change, particularly in the case of long-lived, large terrestrial mammals because they lack the generation time required to genetically adapt to new selective pressures (Rosenheim and Tabashnik, 1991). Shifts in their distribution ranges may also be limited in fragmented, human-dominated habitats that restrict dispersal options to track shifts in suitable environmental conditions (Thuiller et al., 2006). Phenotypic flexibility, particularly behavioural adjustments and physiological flexibility may therefore prove crucial to the persistence of large savanna ungulates in a rapidly changing world (Boutin and Lane, 2014; Fuller et al., 2016, 2010; Hetem et al., 2014). However, whether these large ungulates can demonstrate sufficient phenotypic plasticity (i.e., behavioural and physiological flexibility) to buffer the effects of climate change is still largely unknown and requires a comprehensive understanding of the ecological, behavioural, and physiological responses of large savanna ungulates to current environmental variation and stressors as well as to extreme conditions such as drought as an analogue of predicted future conditions.

The sable antelope *Hippotragus niger niger* is one example of a water-dependent, selective grazer with narrow habitat requirements, that has experienced declines in population size across its southern African distribution range in recent years (Crosmary et al., 2015; Dunham, 2012; Kenya

Wildlife Service, 2012; Ogutu and Owen-Smith, 2003; Ogutu and Owen-Smith, 2005). These declines in population size and suppressed population recovery have mostly been attributed to enhanced predation pressure, habitat deterioration and reduced availability of key resources (Harrington et al., 1999; Ogutu and Owen-Smith, 2003; Owen-Smith et al., 2012a; Owen-Smith and Mills, 2006). Given that habitat deterioration, resource deficiencies and predation are intrinsically intertwined, disentangling the relative effects of each stressor on the performance of sable antelope has proved difficult (Owen-Smith and Mills, 2006; Seydack et al., 2012). Most previous studies overlook the potential exacerbating effect of heat load, a crucial environmental consideration with increasingly hotter and drier conditions and therefore lack sufficient and appropriate data on the behavioural and physiological responses of sable antelope to various environmental stressors.

Bwabwata National Park, located in the semi-arid Zambezi region of north-east Namibia, supports a large, thriving population of sable antelope exposed to relatively low predation pressure and seasonal fluctuations in resource availability and weather conditions. These circumstances presented a novel opportunity to investigate the influence of resource availability and climate on the behaviour and physiology of sable antelope by detailing movement patterns and recording the first-ever measurements of fine-scale activity, microclimate selection and body temperature for sable antelope. This interdisciplinary approach allowed me to i) assess the behavioural adjustments (i.e. movement, fine-scale activity and microclimate selection) employed by sable antelope to buffer changes in resource availability and ambient temperature and ii) use a physiological response (i.e. body temperature) to assess how successful sable antelope are coping with a combination of environmental stressors.

I will start by reviewing the literature on movement patterns, behavioural states of movement, fine-scale activity, microclimate selection and body temperature of ungulates in response to

changes in resource availability and ambient temperature, with specific reference to large grazing ungulates of Africa, where possible.

1.1.2 Movement patterns

An animal's movement is governed by the interplay of an organism's internal physiological state and external environmental factors (Bailey et al., 1996; Nathan et al., 2008). Two of the most important environmental factors that influence ungulate movements are ambient temperature and key resource availability, specifically food (Mueller and Fagan, 2008; Owen-Smith, 2014) and surface water (Redfern et al., 2003; Western, 1975). For African ungulates inhabiting highly dynamic and heterogenous environments (e.g. savannas), the relative and combined influence of resource availability and environmental heat load on movement will likely vary with the time of day and over the seasonal cycle. Global Positioning System (GPS) telemetry allows the movement of large ungulates to be detailed over a wide range of spatial and temporal scales, from broad-scale landscape movements to day-to-day travel distances and hourly displacements (Kays et al., 2015; Nathan et al., 2022).

Local and regional changes in environmental conditions may influence large-scale movements, such as home range occupation, by altering the spatiotemporal availability of resources, such as food and water (Mueller and Fagan, 2008). When the availability of key resources diminishes and/or the distribution of key resources changes, such as during the dry season, ungulates may concentrate their space use resulting in a decrease in home range size (e.g., Hartmann's mountain zebra *Equus zebra hartmannae* (Muntifering et al., 2019) and African buffalo *Syncerus caffer* (Roug et al., 2020)), move more widely increasing the extent of their home range (e.g. African buffalo (Ryan et al., 2006)), make non-migratory shifts in home range occupation (e.g. African buffalo (Macandza et al., 2012a) and blue wildebeest *Connochaetes taurinus* (Yoganand and Owen-Smith, 2014)) or migrate (e.g. blue wildebeest (Thirgood et al., 2004) and plains zebra

Equus quagga (Naidoo et al., 2016)) to access food and water. However, when key resources (particularly drinking water) are accessible all year round within their home range, some ungulates may make minimal changes to seasonal home range occupation (e.g. plains zebra *Equus quagga* (Macandza et al., 2012a)).

Spatiotemporal variability in forage and water can also influence the day-to-day movements of African ungulates as they track seasonal changes in the availability and distribution of key resources. Depending on the environmental and ecological circumstances, during the dry season, ungulates may increase their daily movement distances (e.g., plains zebra (Owen-Smith, 2013) and African buffalo (Roug et al., 2020)), decrease their daily movement distances (e.g. blue wildebeest (Martin et al., 2015)), or display little variation in day-to-day movement distances, particularly when water is readily available across seasons (e.g. Hartman's mountain zebra (Muntifering et al., 2019) and African buffalo (Ryan and Jordaan, 2005)). The distribution of surface water, particularly during the dry season, influences the spatial distribution and movement patterns of ungulates, particularly water-dependent grazers, which generally occur closer to water (Redfern et al., 2003; Western, 1975) or travel more frequently to water (Cain et al., 2012) during the dry season, depending on the location of preferred foraging areas relative to the location of water sources. For example, plains zebra in Kruger National Park travelled 3-8 km every 1-2 days during the dry season to drink water (Cain et al., 2012) whereas, in the more arid Makgadikgadi, blue wildebeest grazed 10-15 km from a river which they travelled to every 2-4 days to drink water during the dry season (Curtin et al., 2018). In contrast, the less water-dependent gemsbok *Oryx gazella gazella* in the Kgalagadi, only visited permanent water sources during a drought year (Boyers, 2018). Therefore, changes in movement patterns may be useful indicators of stressful resource conditions (Owen-Smith, 2013; Owen-Smith and Cain, 2007).

To meaningfully interpret movement responses to environmental stressors, movement data should be analysed in combination with appropriate measures of key environmental factors

(Neumann et al., 2015), such as satellite-derived vegetation greenness in the form of NDVI (Normalised Difference Vegetation Index) or EVI (Enhanced Vegetation Index) (Pettorelli et al., 2011), and black globe temperature which provides a measure of experienced heat load by combining air temperature, wind speed and solar radiation (Hetem et al., 2007). Indeed, decreasing NDVI has been associated with larger home range sizes of desert-dwelling gemsbok during a drought year in north-eastern Namibia (Lehmann et al., 2020) and longer 10-day travel distances of African buffalo during the dry season in Limpopo, South Africa (Ryan et al., 2006). However, empirical evidence also shows that African grazers are attracted to new grass regrowth ("green flush") in recently burnt areas during the dry season (Gureja and Owen, 2002; O'Kane and Macdonald, 2018; Tomor and Owen-Smith, 2002), which may also influence movement patterns. While advances in remote sensing and animal tracking technology continue to improve our understanding of how vegetation influences the movement of African ungulates (Bartlam-Brooks et al., 2013; Boone et al., 2006), far less focus has been placed on quantifying the impact of high ambient temperature on the movement patterns of African ungulates (Owen-Smith et al., 2020).

Increasing aridity and temperature threaten sable antelope, which are highly selective in resource use and dependent on surface water. Sable antelopes appear sensitive to resource limitations and display substantial flexibility in seasonal movement patterns. While their movement patterns have not been assessed relative to satellite-derived vegetation indices or heat loads, their movements appear to be influenced by the distribution of areas which retain green grass for longer during the dry season (Hensman et al., 2014b; Macandza et al., 2012a; Owen-Smith et al., 2013), for example, green grass flush in recently burned areas (Magome et al., 2008; Parrini and Owen-Smith, 2010), green grass retained in vlei areas (Parrini and Owen-Smith, 2010) or green grass under tree canopies (Parrini, 2006), and the distribution of drinking water (Cain et al., 2012). When it comes to home range occupation, some sable antelope herds expand their home ranges in search of resources during the dry season (Henley, 2005; Owen-Smith and Cain, 2007; Rahimi

and Owen-Smith, 2007; Wilson and Hirst, 1977), others occupy separate wet and dry season home ranges (Hensman et al., 2014) and some herds made minimal changes to home range extent when they had year-round access to key resources, particularly water, within their home range (Cain et al., 2012; Owen-Smith and Cain, 2007; Wilson and Hirst, 1977).

Within broad landscape movements (i.e., home ranges), sable antelope can adjust their day-to-day movements at a finer scale (Owen-Smith, 2013). In Kruger National Park, the 24-hour diel displacement distances (linear displacement between locations recorded at 20:00 on consecutive days) of sable antelope were minimal during the wet season; however, as resources diminished during the dry season, sable antelope increased their proportion of diel displacements greater than 2 kms and doubled their daily movement distance (summed 6-hourly displacements) (Owen-Smith, 2013; Owen-Smith and Cain, 2007). One of these sable antelope herds travelled approximately 5-9 kms to pools remaining in a seasonal river every 3-4 days to access surface water during the late dry season once drinking water was depleted within their core range (Cain et al., 2012). The movement patterns of sable antelope during periods of resource limitations may indicate increased energy expenditure to obtain food and water (Cain et al., 2012; Owen-Smith, 2013; Owen-Smith and Cain, 2007; Owen-Smith and Goodall, 2014). However, all previous studies have neglected to include ambient temperature in their assessment of the movement patterns of sable antelope. Advancements in biologging technology have expanded the range of environmental, behavioural and physiological variables that can be measured remotely using sensors placed within the environment to measure climatic conditions (e.g. air temperature thermometers and black globe thermometers) and animal-borne sensors (e.g. accelerometers, activity tags and body temperature loggers).

1.1.3 Behavioural states of movement and fine-scale activity

If an ungulate's ability to change its distribution range is limited, then flexible behaviours such as changes in the type and timing of activity may buffer the effects of changing resource availability and climate. Assessing changes in activity patterns over time, such as the timing, quantity, and types of activity, can provide insights into how ungulates respond to larger shifts in their environment, such as seasonal changes in resource availability and climate, and how ungulates balance foraging, drinking, resting, minimising predation risk, and sheltering from thermal extremes. Diel activity patterns describe how ungulates distribute their activity, energy, and time throughout a 24-hour cycle while responding to changes in biotic (e.g. resource availability, competition, reproduction, and predation) and abiotic (e.g. temperature and photoperiod) factors. Changes in resource availability and ambient temperature may result in altered activity patterns as ungulates adjust their activity to meet resource requirements and cope with thermal challenges.

According to optimal foraging theory, large ungulates should respond to diminishing food availability by spending more time searching for remaining food and therefore are expected to increase foraging activity during the dry season when food quality and availability are poor (Owen-Smith et al., 2010). Indeed, early field observation studies noted that increased movement rates during foraging generally occurred during periods of reduced food availability, such as during the dry season (e.g. blesbok *Damaliscus dorcas* (Novellie, 1978) and kudu *Tragelaphus* (Owen-Smith, 1979)). Alternatively, ungulates may prioritise energy conservation and decrease activity to save energy during a food-limited period. This energy-conserving strategy is typically observed in cold-adapted northern hemisphere herbivores, which reduce their metabolism during low ambient temperatures and food shortages to reduce their energetic needs (Arnold et al., 2006; Signer et al., 2011). However, some African ungulates have been recorded reducing their overall activity during the dry season (e.g. blue wildebeest in the Kalahari (Selebatso et al., 2017)) and in response to increased exposure to brown vegetation during the dry season (e.g. blue wildebeest in

the Kalahari (Boyers, 2018)), likely because increased activity (e.g. foraging or searching for resources) would not have been an effective or energy-efficient response given the resource scarcity in these arid environments during the dry season. When reduced resource availability (particularly drinking water) is coupled with high ambient temperature, such as during the late dry season, African ungulates may reduce their diurnal activity, particularly over the heat of the day, and/or shift activity to the crepuscular or nocturnal period to reduce diurnal heat loads. Historically, nocturnal observations of activity were limited by the need for direct observations however, advancements in GPS and biologging technology now allow for the continuous and unbiased measure of activity throughout the 24-hour cycle (Kays et al., 2015; Nathan et al., 2022; Wilmers et al., 2015).

GPS tracking and biologging technology present several ways to record and analyse the fine-scale activity of large ungulates, from deriving movement modes or activity states from GPS movement rates using statistical models (Joo et al., 2020; Langrock et al., 2012; Owen-Smith et al., 2012b; Patterson et al., 2017), to activity sensors or accelerometers on collars (Augustine and Derner, 2013; Brown et al., 2013; Kirchner et al., 2023; Nielsen et al., 2010) and internally implanted activity loggers (Boyers et al., 2019; Hetem et al., 2012a). Ungulate trajectories (i.e. movement tracks) recorded by GPS technology can be deconstructed into a series of activity modes and probable behavioural states based on the step length (distance or velocity) and turning angle (direction) between sequential GPS locations using quantitative statistical methods such as Hidden Markov Models (Langrock et al., 2012; Michelot et al., 2016). In other words, the movement rate between sufficiently short GPS locations (i.e. an hour or less) can be used to infer the activity states underlying the movement between GPS fixes (e.g. resting, foraging, travelling, relocating). Assessing switches between activity modes or behavioural states provides important insight into how the movement behaviour of ungulates may be influenced by environmental variability, such as resource availability and climate. Although the field of movement ecology is rapidly growing, for large herbivores the literature is dominated by studies conducted on cold-

adapted ungulates inhabiting northern temperate latitudes (e.g. caribou *Rangifer tarandus* (Franke et al., 2004), elk *Cervus elaphus* (Morales et al., 2004), mule deer *Odocoileus hemionus* and plains bison *Bison bison bison* (Prima et al., 2022)). Using quantitative analytical methods to interpret movement and activity patterns of ungulates has been underutilised for African ungulates (Owen-Smith et al., 2020, 2012b; Owen-Smith and Goodall, 2014).

In African environments, ungulates that face an increased risk of predation at night, generally exhibit peaks in foraging activity during the early morning and late afternoon with resting prevailing over midday and through most of the evening (Owen-Smith, 2014; Owen-Smith and Goodall, 2014). However, diel activity patterns may change with seasonal changes in resource availability and climate. For example, using movement rates to define different activity states, Owen-Smith and Goodall (2014) found that during resource-limited dry periods, African buffalo, plains zebra and sable antelope increased their foraging activity with some foraging activity continuing into the early evening or at night during hot and dry periods when high diurnal temperatures likely suppressed diurnal activity. During the dry season, ungulates may also need to travel to surface water if water supplies dry up within their core range (Redfern et al., 2003). Indeed, sable antelope in Kruger National Park spent an increased proportion of time in a travelling state/movement mode to access a distant water source during the late dry season (Cain et al., 2012; Owen-Smith and Goodall, 2014). However, movements to distant water sources may displace other activities, such as foraging for food, leading to compensatory shifts in activity or trade-offs (Owen-Smith and Goodall, 2014), particularly when reduced resource availability is coupled with high daytime temperatures in the late dry season.

Accelerometers and implanted activity loggers enable continuous measurement of fine-scale activity (seconds to minutes resolution) allowing for a better measure of overall activity levels and identification of compensatory shifts in activity over the 24-hour cycle in response to prevailing environmental conditions, such as high ambient temperature (Rutz and Hays, 2009;

Williams et al., 2020; Wilmers et al., 2015). Measurements of activity recorded by internally implanted activity loggers have shown that gemsbok in the Kalahari increased their nocturnal activity during the hot, dry season; while blue wildebeest showed no seasonal difference in their nocturnal proportion of activity (Boyers et al., 2019). In the Arabian desert, Arabian oryx *Oryx leucoryx* and Arabian sand gazelle *Gazella subgutturosa marica*, inhabiting a predator-free environment, shifted to a predominantly nocturnal activity pattern without reducing total 24-hour activity when resources were limited and ambient temperature high (Hetem et al., 2012a). Measurements of activity recorded by accelerometers attached to the collars of springbok *Antidorcas marsupialis*, kudu and eland *Tragelaphus oryx*, in a dryland savanna showed that during the hot dry season, springbok decreased both their day- and night-time activity, kudu displayed little variation in their diel activity pattern and eland compensated for reduced daytime activity by increasing night-time activity such that 24-hour activity did not change (Berry et al., 2023).

A reduction in diurnal activity during the dry season generally results from decreased mobile activity (or increased resting) over the hottest part of the day when the radiant heat load is highest. Blue wildebeest in the Kalahari, with accelerometers attached to their collars, displayed the greatest reduction in diurnal activity during the hot, late dry season, reducing their mean activity level over the hottest part of the day, without increasing nocturnal activity to make up for lost diurnal activity, likely because of high predation risk (Selebatso et al., 2017). In a dryland savanna, the activity of springbok, kudu and eland declined with increasing afternoon temperatures (assessed by black globe temperature) during the hot dry season (Berry et al., 2023), such that rising afternoon temperatures suppressed time spent feeding and increased time spent resting and ruminating, with little change in walking activity (Berry et al., 2024). Across all three antelope species, there was a general decrease in active behaviours (foraging and walking) and an increase in low-activity behaviours (resting and ruminating) on hot days versus cool days during the hot, dry season (Berry et al., 2024). Reduction in activity during the heat of the day usually

corresponds to animals using thermal refuges, such as shade, to reduce radiant heat exposure and experienced heat load.

1.1.4 Microclimate selection

Microclimate selection is a primary thermal defence used by large mammals to buffer changes in ambient temperatures (Fuller et al., 2014; Hetem et al., 2014). In response to high environmental temperatures, mammals typically select cool microclimates, with shade being particularly important for large herbivores (Fuller et al., 2016). The use of shade allows large herbivores to reduce their heat load and evaporative water loss during the heat of the day, particularly during hot periods when water is limited such as the late dry season (Cain et al., 2006; Fuller et al., 2016, 2014). However, thermoregulatory behavioural adjustments such as shade-seeking may incur costs for other activities such as resource acquisition (e.g. foraging). Shade-seeking behaviour in ungulates, associated with high ambient temperature, was historically recorded by direct field observations (e.g. impala (Jarman and Jarman, 1973), blue wildebeest and red hartebeest *Alcelaphus buselaphus* (Ben-Shahar, 1987)). Unfortunately, these historic behavioural observation studies were somewhat limited by observer presence, lacked the technology to quantify the quality of the shade or the time spent in that shade and did not allow for the assessment of the trade-offs associated with shade-seeking behaviour.

Advances in biologging technology allow for the remote and continuous measurement of the time spent in shade and the quality of that shade. Biologging can be used to quantify microclimate selection by correlating black globe temperatures obtained from a miniature black globe thermometer ("miniglobe") attached to an animal's collar with black globe temperatures obtained from miniglobes located throughout the surrounding environment (e.g. in direct sunlight) (Hetem et al., 2007; Mole et al., 2016). Black globe temperature provides a measure of experienced heat load by combining air temperature, wind speed and solar radiation (Hetem et al., 2007). Biologging therefore allows us to measure the degree to which free-living ungulates exploit

environmental thermal heterogeneity by quantifying the selection of cool microclimates at high environmental heat loads. With the use of biologging, the selection of increasingly cooler microclimates during periods of high environmental temperature has been shown in free-living African ungulates including kudu (Hetem et al., 2008), Angora goats *Capra aegagrus hircus* (Hetem et al., 2011), eland (Shrestha, 2012), blue wildebeest and gemsbok (Boyers et al., 2021, 2019), as well as free-living Arabian oryx (Hetem et al., 2012b) and Arabian sand gazelle (Hetem et al., 2012a). Depending on the environment, the shaded microclimate can be significantly cooler than direct sunlight. Arabian oryx selected microclimates ~12^{o}C cooler than the open desert environment (Hetem et al., 2012b), and blue wildebeest and gemsbok selected microclimates ~10^{o}C cooler than in the Kalahari sun during hot conditions (Boyers et al., 2019). While using cooler microclimates would reduce experienced heat load, it may come at a cost to diurnal activity.

Spending more time in the shade during hot and dry conditions may constrain the time available for foraging during daylight, especially when ungulates cannot compensate for lost daytime foraging by increasing nocturnal foraging activity due to predation risk (Tambling et al., 2015). For example, blue wildebeest and gemsbok spent 50-60% more time in cooler microclimates during the hot seasons compared to the cooler seasons (Boyers et al., 2019) and spent longer (1.5 hours more per day) in microclimates that were cooler during the dry season of a drought year compared to a non-drought year (Boyers et al., 2021). However, while gemsbok compensated for reduced diurnal activity by increasing their nocturnal proportion of activity, so that 24-hour activity remained unchanged, blue wildebeest displayed a substantial reduction in 24-hour activity (Boyers et al., 2021, 2019). Should high ambient temperature constrain foraging activity during periods of low food availability, such as during the late dry season, ungulates may face energy deprivation (Fuller et al., 2016). However, should ungulates prioritise foraging during the heat of the day, they risk exposure to high radiant heat loads during a period when water is limited which may result in heat stress (Fuller et al., 2016).

1.1.5 Body temperature

Behavioural flexibility helps to buffer the impact of changes in resource availability and climate on the thermal physiology of large-bodied endotherms (Hetem et al., 2014). Endotherms maintain a stable body temperature (i.e. homeothermy) with sufficient resource availability (i.e. food and water) (Hetem et al., 2016). Even under high heat loads, endotherms can maintain a reasonably stable body temperature, provided they have access to water for evaporative cooling (Fuller et al., 2016). Food and water limitations, often exacerbated by thermal stressors, compromise maintaining a stable body temperature. During resource-limited periods, fluctuations in 24-hour body temperature (i.e. heterothermy) provide a useful index of energy and water stress (Hetem et al., 2016). Biologging enables remote and continuous measurements of core body temperature, which can be analysed in response to changing environmental conditions such as resource availability and climate.

When ambient temperature exceeds core body temperature, the primary way an endotherm can cool itself is by evaporative cooling (e.g. sweating or panting) (Tattersall et al., 2012) however, when water is limited, body fluid homeostasis (i.e. osmoregulation) may be prioritised over thermal homeostasis (i.e. thermoregulation) (Cain et al., 2006) and so evaporative water loss is abandoned (McKinley et al., 2008), causing a rise in maximum body temperature (i.e. hyperthermia). Experimental manipulations involving ungulates have shown that a reduction in the rate of evaporative water loss was accompanied by an increase in maximum body temperature in response to dehydration and hot conditions (e.g. eland and hartebeest *Alcelaphus buselaphus cokii* (Finch and Robertshaw, 1979), Bedouin goat *Capra hircus* (Jessen et al., 1998), Grant's gazelle *Gazella granti*, oryx *Oryx beisa*, Thompson's gazelle *Gazella thomsonii*, African buffalo, zebu steer *Bos indicus* and blue wildebeest (Taylor, 1970)). Indeed, a reduction in high body temperature with rehydration has been observed in captive mammals deprived of drinking water, including baboons *Papio hamadryas* (Mitchell et al., 2009), goats (Jessen et al., 1998) and sheep

(Fuller et al., 2007). To date, dehydration-induced hyperthermia in free-living mammals has only been observed in ungulates that experience severe water limitations, like Arabian oryx (Hetem et al., 2010; Ostrowski et al., 2003) and Arabian sand gazelle (Hetem et al., 2012a; Ostrowski and Williams, 2006) inhabiting the Arabian desert. Several experimental manipulations involving both desert and non-desert ungulates (e.g. dromedary camels *Camelus dromedarius* (Schmidt-Nielsen et al., 1956), Grant's gazelle, Thompson's gazelle, blue wildebeest, zebu steer, and African buffalo (Taylor, 1970), eland and hartebeest (Finch and Robertshaw, 1979)) suggest that dehydration hyperthermia may be a result of water stress rather than simply being an adaptation to desert environments. As temperatures continue to rise and water availability decreases in water-limited systems such as arid and semi-arid savannas, African ungulates, particularly those with higher water dependency, are likely to experience water stress more frequently.

Hotter and drier conditions will not only affect the hydration of large African ungulates but also challenge their energy balance as the abundance and quality of food decline and the spatiotemporal distribution of food changes. When endotherms experience energy deficits from inadequate food intake, they may not be able to maintain high metabolic rates and their ability to maintain a stable body temperature (i.e. homeothermy) becomes compromised, resulting in a lower minimum and mean body temperature (i.e. hypothermia) (Fuller et al., 2014; Hetem et al., 2016).

In northern temperate environments, low food availability coincides with cold winter months, making it difficult to distinguish the relative influence of low ambient temperature and food deficits on hypothermia. During cold and resource-poor winters, some large-bodied northern ungulates (e.g. moose *Alces alces* (Græsli et al., 2020), red deer *Cervus elaphus* (Arnold et al., 2004), Przewalski horse *Equus ferus przewalskii* (Arnold et al., 2006), Alpine ibex *Capra ibex ibex* (Signer et al., 2011), and llama *Lama glama* (Riek et al., 2019)) exhibit low minimum body temperatures suggested to be the result of an endogenous physiological mechanism employed to

reduce energy expenditure by reducing their metabolic rate (hypometabolism) to cope with limited energy supplies (e.g. food buried under snow) in freezing temperatures. However, food manipulation experiments involving captive Arabian oryx (Ostrowski et al., 2006), sheep *Ovis aries* (Maloney et al., 2013), Shetland ponies *Equus ferus caballus* (Brinkmann et al., 2012) and red deer (Turbill et al., 2011) have shown that when ambient temperatures are controlled, reduction in body temperature occurs with restricted food intake, suggesting energy limitation may drive hypothermia (i.e. starvation-induced hypothermia) in large ungulates. Further evidence for a mechanistic link between body temperature and energetic stress has been proposed for Cape buffalo *Syncerus caffer caffer* (Botha et al., 2023), where low minimum body temperatures were linked to poor body condition and low plasma leptin concentrations, associated with low energy reserves and depletion of fat stores.

Indeed, the lowering of minimum body temperature during seasonally dry periods when food resources were likely limited has been observed in free-living ungulates inhabiting warmer climates (Boyers et al., 2021, 2019; Hetem et al., 2012a, 2010; Shrestha et al., 2012). Blue wildebeest and gemsbok in the Kalahari (Boyers et al., 2019) and Arabian oryx in the Arabian desert (Hetem et al., 2010) displayed reductions in minimum 24-hour body temperatures in hot-dry seasons when forage quality and quantity was likely limited compared to the hot-wet season when food was likely abundant. Indeed, the reduction in the minimum body temperatures of blue wildebeest and gemsbok was directly linked to low vegetation greenness in the Kalahari (Boyers, 2018). Longer and more extreme dry seasons may have fitness consequences should inadequate energy intake impact adult survival, reproduction and juvenile survival.

Pregnancy and lactation are the most energetically expensive periods in a female's life (Gittleman and Thompson, 1988). The physiological consequences of reproduction can also manifest as perturbations to body temperature regulation in some mammal species. Reproduction requires increased food and water intake to meet the demands of gestation and lactation. During gestation,

some mammals (e.g. vervet monkeys *Chlorocebus pygerythrus* (McFarland et al., 2022), sheep (Laburn et al., 1992) and African lions *Panthera leo* (Trethowan et al., 2016) display a gradual decline in mean body temperature, termed gestational hypothermia (Laburn, 1996; Laburn et al., 1992). During foetal development, the metabolic heat production of foetal cells undergoing cell division typically results in foetal body temperature being higher than maternal body temperature (Laburn, 1996; Laburn et al., 1992). This temperature gradient (between the foetus and mother) allows for heat transfer from the foetus to the mother to protect the foetus from hyperthermia. However, to maintain this temperature gradient the mother must increasingly lower her body temperature which can be costly in terms of body water loss associated with evaporative cooling to maintain low body temperature, especially when ambient temperature is high (Hetem et al., 2016). Some animals display improved homeothermy during gestation (e.g. African lions (Trethowan et al., 2016) and brown bears *Ursus arctos* (Friebe et al., 2014), which likely encourages foetal development because cell division can take place under optimal thermal conditions (Trethowan et al., 2016). However, maintaining homeothermy is costly and requires sufficient food and water intake, which might be challenging in hot and dry environments (Hetem et al., 2016).

Lactation is energetically expensive because of the cost of milk production, and it requires sufficient water intake as water is a main component of milk. To maintain the increased metabolic cost of milk production, lactating mothers may increase their energy intake by increasing the quantity and/or quality of food intake. Lactating females may therefore experience increased body temperature during lactation because of the increased metabolic heat production associated with the production of milk and increased digestion (Speakman, 2007). Lactating mothers also face an increased demand for water to sustain milk production and aid in thermoregulation. Should lactating females need to prioritise the use of body water to produce milk rather than for evaporative cooling, they may experience increased body temperature (Hetem et al., 2016).

1.2 Research aim and objectives

My PhD research aimed to assess the variation in home range size, movement behaviours (movement patterns and behavioural states underlying movements), activity patterns, microclimate selection and body temperature rhythms of sable antelope in relation to prevailing environmental conditions.

I addressed the following objectives:

Objective 1: Quantify seasonal changes in total and core home ranges (Chapter 3).

Objective 2: Investigate whether 24-hour movement distances are influenced by vegetation greenness and 24-hour environmental heat load (Chapter 3).

Objective 3: Identify behavioural states underlying movements and assess whether the proportion of time spent in each behavioural state is influenced by vegetation greenness and 24-hour environmental heat load (Chapter 3).

Objective 4: Investigate whether 24-hour activity patterns are influenced by vegetation greenness and 24-hour environmental heat load Chapter 4).

Objective 5: Assess microclimate quality relative to available microclimates and in relation to vegetation greenness and 24-hour environmental heat load (Chapter 4).

Objective 6: Assess 24-hour body temperature rhythms in relation to prevailing environmental conditions, namely vegetation greenness and 24-hour environmental heat load, and behavioural states underlying movements (Chapter 5).

Objective 7: Describe perturbations in 24-hour body temperature rhythm related to gestation and lactation (Chapter 5).

1.3 Thesis outline

This thesis consists of an introduction chapter (Chapter 1), a general methods and materials chapter (Chapter 2), three data chapters (Chapters 3 – 5), a conclusion chapter (Chapter 6), one reference list, and appendices.

Since all my data chapters are based on data emanating from the same group of individuals in Bwabwata National Park, to avoid repetition, I have included a general methods and materials chapter that describes the study site and study species, details the data collection process, and describes how I calculated the environmental variables used in the data analysis of all three data chapters. Each data chapter includes a focused introduction, specific data analyses, results, and discussion. The conclusion chapter then integrates findings across the data chapters, with a conclusion highlighting my contribution to knowledge, future directions of research and conservation implications. To avoid repetitions of references, I have included a single complete reference list for the entire thesis, after the conclusion chapter. Appendices have been placed at the end of the thesis.

I have submitted a manuscript on the results presented in Chapter 3 to the Behavioural Ecology journal: Haylock, K., Parrini, F., Strauss, W.M., Beytell, P., Hetem, R., Vegetation greenness and heat load drives the movements of a water-dependent, selective grazer.

Some of my research findings have been presented at local and international conferences:

- Southern African Wildlife Management Association, Golden Gate National Park, South Africa, 10 – 15 September 2023 (awarded best overall presentation and best PhD presentation)
- Animal, Plant and Environmental Sciences Postgraduate Poster Event, University of the Witwatersrand, South Africa, October 2022
- 23rd International Congress of Zoology, Virtual, 21 – 26 November 2021
- Brain Function Research Group Research Day, University of the Witwatersrand, South Africa, 2019 (awarded best presentation) and 2017 (awarded second best presentation)
- Etosha 112 Symposium, 12 – 14 June, Etosha, Namibia, 12 – 14 June 2019
- 16th Annual Savanna Science Network Meeting, Kruger National Park, South Africa, 4 – 8 March 2018 (selected to present as part of a special Science-Management Interface session)
- 12th International Mammalogical Congress, Perth, Australia, 9 – 14 July 2017 (awarded a prestigious student travel award by the International Federation of Mammalogists)
- The Combined Congress of the Entomological Society of Southern Africa and the Zoological Society of Southern Africa, Pretoria, South Africa, 3 – 7 July 2017

CHAPTER 2

General methods and materials

2.1 Study area

This study took place within the Buffalo Core Area of Bwabwata National Park (17°57′S, 22°32′E), situated in the Zambezi regions of north-east Namibia (Figure 2.1). The Park is approximately 6334 km^2 in size, extending ~180 km from the Kavango River on its western boundary to the Kwando River on its eastern boundary, and ~32 km from its northern boundary with Angola to its southern boundary with Botswana. Bwabwata National Park lies in the centre of the Kavango–Zambezi Transfrontier Conservation Area (KaZa TFCA) and is therefore largely unfenced but maintains veterinary standard fences along its southern boundary with Botswana. The Park is situated in the Kalahari Basin within the broad leaf tree-shrub savanna biome of the miombo eco-region of southern Africa (Jones and Barnes, 2009). The largely flat landscape (~1000 meters above sea level) is characterised by major relic dunes stabilised by vegetation and old drainage lines and is dominated by dry, semi-arid to open woodlands (Le Roux et al., 2009). Soils are predominately composed of nutrient-poor Kalahari sands (Wang et al., 2007). The park is located within a summer rainfall region and receives approximately 550-600 mm of rainfall annually between November and March; while April to October is considered the dry season (Mayuni, 2012). The Buffalo Core Area includes the Kavango River at its western boundary and has one artificial water point which is poorly maintained.

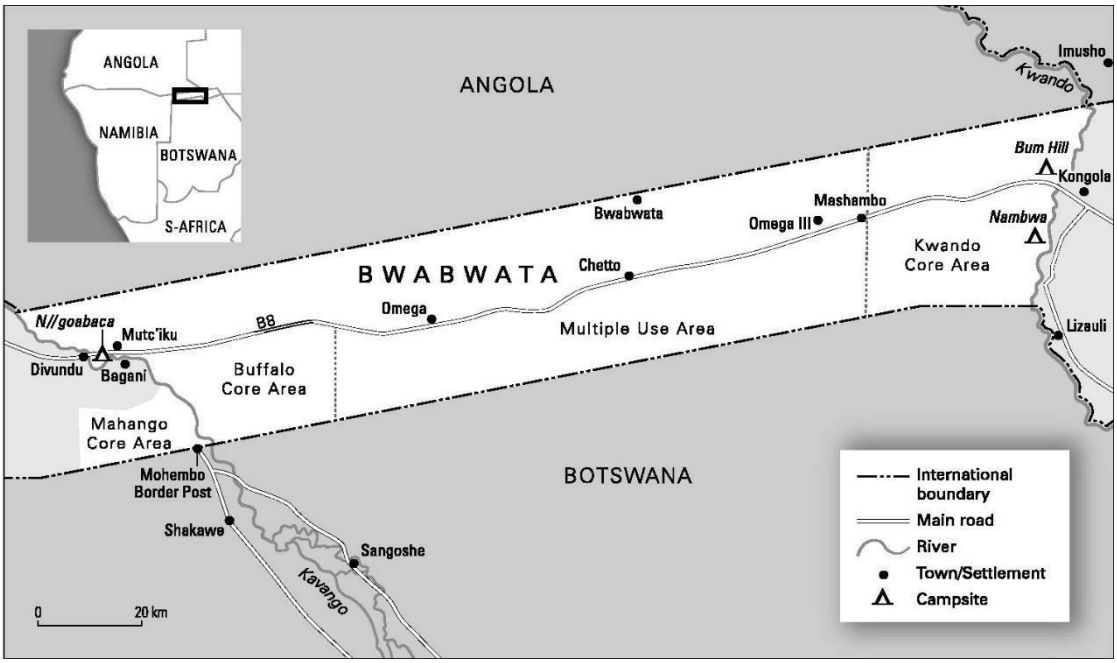

Figure 2.1 Map of Bwabwata National Park (17°57′S, 22°32′E), situated in the Zambezi Region of north-east Namibia. This study took place within the Buffalo Core Area, which includes the Kavango River at its western boundary. Map reproduced, with permission, from Koot (2019).

2.2 Study animals

The sable antelope is a large, gregarious antelope species found in the woodland-grassland ecotones of savannah woodlands of north-eastern southern Africa (Skinner and Chimimba, 2005). Sable antelope are principally selective grazers preferring fresh and green grasses of medium height (Grobler, 1981a). They are considered water-dependent, travelling to drinking water at 2 – 4 day intervals (Cain et al., 2012). Adult cows weigh 204 – 232 kg and live in female-juvenile herds with adult females, sub-adult males and youngsters forming breeding groups (Grobler, 1973). Gestation spans 8 – 9 months with calving occurring at the end of the wet season, typically February – March. They give birth to one calf which they hide in tall grass separate from the herd for ~2 weeks. Calves start grazing on grass ~30 days after birth but weaning takes place 6 – 8 months after birth (Grobler, 1973).

2.3 Data collection

2.3.1 Animal capture and surgical procedures

In April 2016, ten adult female sable antelopes from separate herds were collared and implanted with activity tags and body temperature loggers. Based on their social structure, each collared female was used as an individual representation of its herd's movement and activity patterns. At the time of capture eight out of ten individuals were lactating. Herd size ranged from 11 – 48 individuals.

The females were darted from a helicopter by an experienced veterinarian and fitted with species-specific satellite neck collars (Africa Wildlife Tracking, Pretoria, South Africa). Each dart contained a combination of thiafentanil oxalate (7mg, Thianil, Wildlife Pharmaceuticals (Pty) Ltd, White River, South Africa) or etorphine hydrochloride (7 mg, M99, Novartis, Johannesburg, South Africa) together with ketamine (80–100 mg, Anaket-V, Bayer Animal Health Pty, Isando, South Africa) and medetomidine (2 mg, Domitor, Novartis, Johannesburg, South Africa). Upon recumbency, each animal received an additional dose of ketamine (40–60 mg) and medetomidine (2 mg) to ensure sedation and was placed in sternal recumbency with their head elevated. Following endotracheal intubation, anaesthesia was maintained with 0–2% isoflurane (Aerrane, Astra Zeneca, Johannesburg, South Africa) administered in 100% oxygen. Respiratory rate, heart rate, blood pressure, arterial oxygen saturation and rectal temperature were monitored throughout the surgery which lasted approximately 30 minutes.

The incision site was shaved and sterilised with antiseptic (Hibitane, chlorohexidine 5%, Kryon Laboratories (Pty) Ltd, Johannesburg, South Africa and Hibicol, chlorohexidine gluconate 0.5% in spirit, Medicolab CC, Johannesburg, South Africa). Following administration of a local anaesthetic (6 ml, subcutaneous (SC), 2% lignocaine hydrochloride, Bayer Animal Health (Pty) Ltd, Isando, South Africa), a movement-sensitive activity tag (~70mm x 45mm x 30mm, mass of

~90g when covered in wax, Africa Wildlife Tracking, Pretoria, South Africa), coated in biologically and chemically inert wax (Sasol Wax, Hamburg, Germany) was implanted on the right flank via a paralumbar incision and tethered retro-peritoneally to the abdominal muscle wall using non-absorbable suture (Monofilament Nylon, USP 1 NY908, Gabler Medical (U.K.) Limited, United Kingdom) to ensure the activity tag remained in a fixed position for the duration of the study. A miniature temperature-sensitive data logger ("biologger") (46 mm x 15 mm diameter, mass of ~19 g, DST centi-T, Star Oddi, Iceland), coated in biologically and chemically inert wax (Sasol Wax GmbH, Hamburg, Germany), was also surgically implanted on the right flank of each sable antelope, between the second and third abdominal muscle layer to ensure the measurement of core body temperature and not subcutaneous temperature. Activity tags and body temperature loggers were sterilised in instant sterilant (F10 Sterilant with rust inhibitor, quaternary ammonium and biguandine compounds (0.058%), Health and Hygiene (Pty) Ltd, Johannesburg, South Africa) before implantation. The surgical incision site was sutured closed (absorbable polyglycolic acid coated Viamac, USP 2/0 VM514 (muscle suture), USP 2 VM410 (skin suture), Gabler Medical (U.K.) Limited, United Kingdom) and subsequently treated with a topical antiseptic spray (Necrospray, Centaur Labs, Johannesburg, South Africa) and topical tick repellent (tick grease, cypermethrin 0.025% m/m, Bayer Animal Health (Pty) Ltd, Isando, South Africa). Each animal received a long-acting antibiotic (0.04 ml/kg, intramuscular (IM), benzylpenicillin, Duplocillin, Intervet, Isando, South Africa) and an analgesic (0.05 mg/kg, IM, Meloxicam, Metacam 20, Ingelheim Pharmaceuticals (Pty) Ltd, Randburg, South Africa). Following surgery, inhalation anaesthesia was terminated and a GPS/VHF satellite neck collar (~1.2 kg, Africa Wildlife Tracking, Pretoria, South Africa) was fitted to the animal. Following the fitment of the collar, the effects of thiafentanil oxalate or etorphine were reversed with naltrexone hydrochloride (75–100 mg, Trexonil, Wildlife Pharmaceuticals (Pty) Ltd, White River, South Africa) and the effects of medetomidine were reversed with atipamezole hydrochloride (10–15 mg, Antisedan, Pfizer Laboratories (Pty) Ltd, Sandton, South Africa).

2.3.2 Collars and collar miniglobes

Each collar supported a VHF (Very High Frequency) tracking radio transmitter and GPS (Global Positioning System) unit recording locations at 1-hour intervals (Figure 2.2). Each collar also supported a miniature blackglobe thermometer ("miniglobe") which allowed for the dynamic measurement of the microclimate occupied by each animal (Hetem et al., 2007). Collar miniglobe temperature was measured hourly by a small temperature-sensitive chip (range: -10 – 85 ^{o}C, resolution: 0.0625 ^{o}C, calibrated accuracy: 0.5 ^{o}C, Africa Wildlife Tracking, Pretoria, South Africa) inserted into the centre of a miniature matte black hollow copper sphere (30 mm diameter) attached dorsally to the outer surface of the collar (Figure 2.2). The collar facilitated periodic data transmission (via satellite) to a data server to allow real-time downloads of the animal's location, miniglobe temperature and activity. The VHF tracking radio transmitter allowed for animals to be located to remove collars when the GPS communication system failed. One sable antelope collar stopped working seven months into my study period and another collar stopped working after 9 months. The remaining 8 collars started failing after 12 months, with 4 collars lasting 24 months.

Figure 2.2 Female sable antelope fitted with a neck collar supporting a GPS/VHF unit and a miniature black globe thermometer (attached dorsally) in Bwabwata National Park, Namibia.

2.3.3 Activity tags and body temperature loggers

Each activity tag supported an accelerometer which incremented the activity counter at every instance of acceleration above 4G, recording activity counts over 10-minute periods. Records of activity were logged on the tag and transmitted to the neck collar at hourly intervals. In addition to being limited by the lifespan of the collar, the lifespan of the activity tags varied between seven and 21 months with six individuals providing at least 12 months of activity measurements.

The body temperature logger recorded core body temperature (range: 5–45 ^{o}C, resolution: 0.032 ^{o}C, calibrated accuracy: ± 0.1 ^{o}C) at 10-minute intervals. Body temperature measurements were stored onboard the data logger. All body temperature data loggers were calibrated in an insulated water bath (range: 32–42 ^{o}C) against a high accuracy thermometer (Quat 100, Heraeus, Hanau, Germany). Premature battery failure of the GPS and VHF units on all the collars resulted in the recapture of nine out of the 10 individuals at the end of the study period and I was unable to retrieve two of the body temperature loggers. The lifespan of the remaining eight body

temperature loggers was 24 months for six individuals, 23 months for one individual and 17 months for one individual.

2.3.4 Weather measurements

A portable weather station (HOBO Weather Logger [H21-001], Onset Computer Corporation, Massachusetts, USA) was set up at the study site and programmed to record black globe temperature (150 mm diameter matte black hollow copper sphere) and dry-bulb air temperature at hourly intervals. Black globe temperature is a combined measure of air temperature, wind speed and solar radiation and therefore provides an index of environmental heat load experienced by animals (Hetem et al., 2007). Total monthly rainfall for May 2016 to April 2018 was obtained from the Namibian Ministry of Environment and Tourism from a rain gauge located within the Buffalo Core area of Bwabwata National Park.

To test whether sable antelope were selecting microclimates cooler than that of direct sun exposure, I placed free-standing reference miniature black globes (30 mm diameter matte black hollow copper sphere), identical to the miniglobe on the collars, within the study area where the sable antelopes were captured (i.e., Buffalo Core Area). These reference miniature black globes were erected 1m above the ground, in full sunlight and recorded black globe temperature hourly for comparison with the collar miniglobe temperatures. Four reference miniature black globes were erected initially but two went missing during the first year of the study. The two remaining miniature black globes provided me with temperature data from 1 May 2016 to 8 April 2017 and from 1 May 2016 to 28 April 2018.

The combined mass of each collar, activity tag, and body temperature data logger was less than 1% of the typical body mass of an adult female sable antelope (~220 kg). All experimental procedures were approved by the Animal Ethics Screening Committee of the University of the Witwatersrand (protocol no. 2015/06/24/C). A Namibian permit was issued by the National Commission on Research, Science and Technology NCRST permit no. 2044/2015).

2.4 General data analysis

2.4.1 Defining environmental variables

To interpret responses in movement, activity, microclimate selection and body temperature to key environmental factors, data were related to variation in i) vegetation greenness, as assessed by an EVI-related relative greenness index, and ii) mean and maximum 24-hour black globe temperature.

A relative greenness approach was used to quantify spatiotemporal variation in vegetation greenness (Relton et al., submitted) because it compensates for limitations associated with soil reflection and vegetation structure (e.g. trees and shrubs vs. grasses). Relative greenness was estimated using MODIS 13Q1.006 (250 m with 16-day composites) EVI time series satellite data obtained from Earth Data, Data Pool (https://lpdaac.usgs.gov/data_access/data_pool). The EVI value of each individual pixel was compared to its mean EVI value over the 24-month study period (May 2016 – April 2018). Relative greenness measures per pixel through time were subsequently classified into three greenness categories defined from the mean value and standard deviation (SD) for each pixel (i.e. brown = all values < mean - 0.5 SD, average = all values between mean - 0.5 SD and mean + 0.5 SD, green = all values > mean + 0.5 SD). To link measures of movement, activity, microclimate selection and body temperature to changes in vegetation greenness in time and space, I extracted the relative greenness category of each pixel containing a GPS location and used the count of GPS locations classified as “brown” to calculate the proportion of brown vegetation exposure, per individual for every 24-hour cycle of the study period. Mean and maximum 24-hour black globe (150 mm diameter) temperature was calculated from hourly black globe temperature recorded by the weather station on site. A 24-hour cycle was defined as the period occurring between consecutive sunrises. Sunrise and sunset times were obtained using the R (R Core Team, 2018) package Stream Metabolism (Sefick, 2023), which

uses sunrise/sunset functions based on the National Oceanic and Atmospheric Administration (NOAA) Solar Calculator.

CHAPTER 3

On the move: vegetation greenness and ambient temperature drive the movements of a water dependent, resource specialist antelope.

3.1 Introduction

Climate change is arguably the greatest threat to global biodiversity. Approximately 60% of the world's largest terrestrial herbivores (≥ 100 kg) are threatened with extinction and ~58% have decreasing populations (Ripple et al., 2015). Sub-Saharan Africa, where majority of the large herbivore diversity occurs (Ripple et al., 2016), has warmed more rapidly than the global average and is expected to experience high temperatures unprecedented in its recent history. As global mean temperature continues to rise Sub-Saharan Africa can expect an increase in the frequency, intensity, and duration of hot and dry events over the coming decades, particularly an increase in the annual number of days above 35oC and an increase in the occurrence of compound heatwaves and droughts (IPCC, 2023).

Increasingly hot and dry conditions will likely impact the spatiotemporal configuration, availability, and quality of key resources for large herbivores, particularly ungulates. Behavioural flexibility, specifically the ability to adjust movement patterns, increases the capacity of large herbivores to cope with spatiotemporal variability in food resources and surface water (Mueller and Fagan, 2008; Owen-Smith, 2014). However, meeting both food requirements, to prevent energy stress, and water requirements, for thermoregulation to prevent heat stress, becomes increasingly challenging as food and water availability decline. This means that ungulates may be forced to trade off meeting nutritional and water requirements during periods when increasingly high ambient temperature compounds resource limitations. The predicted increasingly hot and dry conditions therefore threaten to alter how ungulates navigate their landscapes of food, water, and shelter from thermal extremes. It is therefore crucial to integrate spatiotemporal heterogeneity in resource availability, ambient temperature, and ungulate movement to provide realistic foundations for management and conservation in the face of climate change.

The majority of studies concerned with the movement ecology of large ungulates have been conducted in higher latitude ecosystems, particularly northern temperate and arctic environments

(Frair et al., 2005; Fryxell et al., 2008; Merkle et al., 2016; Prima et al., 2022; Schmidt et al., 2016), which fail to capture important features of highly dynamic African dryland ecosystems, particularly high spatiotemporal heterogeneity in vegetation and climate and high diversity of mammalian herbivores. While advancements in animal tracking technology and remote sensing continue to improve our understanding of the influence of resource availability on the movements of African ungulates (see review by Owen-Smith et al., 2020), there is a growing need to establish the impact of compounding high ambient temperatures on the movement responses of African ungulates, particularly during periods of limited resource availability (Owen-Smith et al., 2020).

Grazing ungulates are likely to be most impacted by hotter and drier conditions given their reliance on seasonal grasses and surface water (Duncan et al., 2012). Species exhibiting greater water dependence and resource selectivity, narrow habitat requirements and low local densities are predicted to be most at risk of extirpation (Duncan et al., 2012) and have already shown population decline in various parts of their distribution (e.g. tsessebe *Damaliscus lunatus* and roan antelope *Hippotragus equinus* (Dunham et al., 2004, 2003; Harrington et al., 1999; Ogutu and Owen-Smith, 2003; Owen-Smith et al., 2005). Sable antelope is one such water dependent, resource specialist which in recent years have declined substantially across their southern African distribution range (Crosmary et al., 2015; Dunham, 2012; Ogutu and Owen-Smith, 2003), raising concerns that a multitude of different environmental and ecological factors, such as habitat deterioration, resource deficiencies and enhanced predation pressure, might constrain their performance across different landscapes (Asner et al., 2015; Owen-Smith et al., 2012a; Owen-Smith and Mills, 2006). While several studies have focused on different aspects of the movement ecology (Cain et al., 2012; Chirima et al., 2013; Hensman et al., 2014; Owen-Smith and Goodall, 2014; Rahimi and Owen-Smith, 2007) and foraging behaviour (Grobler, 1981a; Hensman et al., 2014b; Magome et al., 2008; Owen-Smith et al., 2013; Parrini and Owen-Smith, 2010) of sable

antelope, all these previous studies have overlooked the exacerbating compounding effect of thermal stress on resource constraints.

To overcome this knowledge gap, I recorded the hourly GPS locations of 10 sable antelope inhabiting Bwabwata National Park in Namibia and recorded hourly blackglobe temperature for a measure of dynamic environmental heat load over 24 months. To investigate the movement patterns of sable antelope in relation to prevailing environmental conditions I set out to i) identify seasonal home ranges, ii) investigate the relationship between 24-hour mean hourly displacement distance and vegetation greenness and heat load, and iii) determine the underlying behavioural states (e.g., resting, foraging, local movement, relocating) driving observed movement patterns and investigate the relationship between behavioural states and vegetation greenness and heat load. I expected sable antelopes to i) have larger home ranges during the dry season as they are forced to search more widely for distributed resources, ii) display longer 24-hour mean hourly displacement distances as vegetation greenness decreased and heat load increased, and iii) spend a greater proportion of time in behavioural states characterised by longer searching movements (e.g. local movement and relocating) when vegetation was brown and heat load high, at the expense of behavioural states characterised by shorter movements (e.g. foraging and resting).

3.2 Data and analysis

As described in Chapter 2, I fitted 10 free-living female sable antelope with neck collars, each supporting a GPS unit that recorded locations at 1-hour intervals, from May 2016 to April 2018. The lifespan of the collars varied between 9 and 24 months with 8 collars lasting 12 months and 4 collars lasting 24 months (see Chapter 2). To link measures of movement to vegetation greenness in time and space, I extracted the relative greenness category of each pixel associated with each GPS location recorded over the study period to calculate the proportion of brown vegetation

exposure, per individual for every 24-hour cycle (sunrise to consecutive sunrise) from May 2016 to April 2018 (as per Chapter 2). I calculated the mean and maximum 24-hour standard (150 mm diameter) black globe temperature, recorded on the weather station, for every 24-hour cycle (sunrise to consecutive sunrise) from May 2016 to April 2018 (as per Chapter 2).

Seasonal home ranges

To investigate seasonal changes in home range sizes, I delineated four seasons, namely early dry (May - July), late dry (August - October), early wet (November - January) and late wet (February - April), based on monthly changes in rainfall, EVI (Enhanced Vegetation Index) and black globe temperature and air temperature from May 2016 to April 2018. Seasonal changes in rainfall, EVI, black globe temperature and air temperature for year 1 of the study (May 2016 – April 2017) are shown in Table 3.1. Seasonal changes in rainfall, EVI, black globe temperature and air temperature for year 2 of the study (May 2017 – April 2018) are shown in Appendix 1. The average EVI of the study site was obtained through the Application for Extracting and Exploring Analysis Ready Samples (AppEEARS) interface (available: https://lpdaacsvc.cr.usgs.gov/appeears/), which provided area averaged EVI (MODIS 13Q1.006 product, 250 m resolution, 16-day composite) data for the total spatial area covered by all GPS locations throughout the study period. EVI provides a seasonal measure of vegetation greenness accounting for canopy background and atmospheric effects (Huete et al., 2002). EVI data values range from -1 to +1, where negative values indicate an absence of vegetation. These EVI data were averaged per month and then per season. To quantify heat loads, 24-hour mean, minimum and maximum black globe and dry-bulb air temperatures, recorded by the weather station, were averaged per month and then per season.

To investigate variation in large-scale movement patterns, sable antelope seasonal home and core ranges were estimated using the Adaptive Local Convex Hull (*a*-LoCoH) method in the R (R Core Team, 2020) package t-LoCoH (Getz et al., 2007). Seasonal home ranges were defined from

95% isopleths, and seasonal core ranges from 50% isopleths. The extent of seasonal home and core ranges were subsequently calculated in ArcGIS 10.3 (Esri, 2011). Seasonal home and core range extents were compared using Linear Mixed-effects Models (LMMs) with Tukey's multiple comparison test. The identity of individual sable antelope was included as a random effect in the model. LMMs were fitted by Laplace Approximation using the R packages lme4 (Bates et al., 2015) and lmerTest (Kuznetsova et al., 2017). Multiple comparison tests were performed using the R package emmeans (Lenth, 2021).

The figures accompanying the text highlight the home and core ranges of sable antelopes for the first year of the study period (May 2016 – April 2017). Home and core ranges for the second year of the study period (May 2017 – April 2018) are shown in Appendix 2.

Displacement distances in response to vegetation greenness and heat load

Fine-scale movement was calculated as the 24-hour mean hourly displacement distance. Only GPS locations separated by 1-hour intervals and 24-hour cycles (sunrise to consecutive sunrise) containing 20 or more hourly locations were used to calculate 24-hour mean hourly displacement distance. The straight-line distance between consecutive GPS locations was measured in ArcGIS 10.3. A Generalised Linear Mixed-effect Model (GLMM) with a gamma error distribution and log link function was used to quantify the influence of the proportion of brown vegetation exposure and 24-hour mean blackglobe temperature (predictor variables) on 24-hour mean hourly displacement distance (response variable). The identity of individual sable antelope was included as a random effect.

Behavioural states in response to vegetation greenness and heat load

To identify the potential underlying behavioural drivers of variation in hourly displacement distances, I used Hidden Markov Models (HMMs) to identify behavioural states from movement tracks of each sable antelope using the R package moveHMM (Michelot et al., 2016). Each Hidden Markov Model used the displacement distance between hourly GPS locations to define distinct states of movement by modelling the probability distributions of step lengths (straight-line distance between consecutive hourly locations). Two-, three- and four-state log-normal HMMs were considered and individually fitted for all ten individuals using full GPS datasets. The four-state model provided the best model fit for nine individuals based on Akaike information criterion (AIC) model selection. Classifying each identified state of movement as a behavioural state relied on subjective interpretation, combining insights from the state-dependent probability distributions and my understanding of the behavioural patterns of sable antelope. For this study, the four inferred behavioural states corresponded to resting (mostly stationary but may include very short movements), foraging (mixture of short movements and stationary bouts related to feeding), local movement (intermediate movements related to searching for or moving between resources) and relocating (longer, more directed movements to distant resources such as water sources or foraging areas). The four-state model was not biologically sensible for one individual based on the typical 24-hour behaviour profile of the antelope. The GPS dataset for this individual was highly irregular due to technological failures, suggesting this individual lacked sufficient data to support a fourth behavioural state. This individual was therefore excluded from further behavioural state analyses

For the other nine individuals, I calculated the proportion of time spent in each behavioural state (i.e. resting, foraging, local movement and relocating) per 24-hour cycle of the study period. Four binomial GLMMs were used to assess whether the proportion of brown vegetation exposure and 24-hour mean blackglobe temperature (predictor variables) influenced the proportion of time

spent in each of the four behavioural states (response variables). Each model included the identity of individual sable antelope as a random effect. An observation level random effect (OLRE) was included in each model to account for the presence of overdispersion (Harrison, 2015).

All the GLMMs were fitted using the R package lme4 (Bates et al., 2015). Using the R package AICcmodavg (Mazerolle, 2023), I used Akaike's Information Criterion corrected for small sample size (AICc) to identify which mixed models supported the data best (Burnham et al., 2011) (see Appendix 3). Model diagnostics appropriate for assessing model fit and adequacy were performed for every model using the R package DHARMa (Hartig, 2017) to ensure mixed model assumptions of normality, homogeneity of variance and independence were met.

For descriptive purposes, the figure accompanying the text highlights the movement responses of sable antelopes averaged per month for the first year of the study (May 2016 – April 2017), when the sample size was greatest.

3.3 Results

Seasonal ranges

Sable antelopes occupied adjacent seasonal home ranges in the western half of Bwabwata National Park towards the Kavango River (Figure 3.1a). Home range location, shape and size varied seasonally (Figure 3.1a). Home ranges were smallest during the early dry season (range: 5.8 – 19.8 km^2) (Figure 3.2a), when rainfall and ambient temperature was lowest and vegetation brown (Table 3.1). As conditions became hotter and browner with the progression of the dry season (Table 3.1), home ranges elongated towards the Kavango River (Figure 3.1a) and increased in size by ~50% from the early dry to the late dry season (range: late dry: 8.9 – 24.2 km^2) (Figure 3.2a). Following the onset of rainfall and a substantial increase in vegetation greenness in the early wet season (Table 3.1), home ranges retracted from the Kavango River

(Figure 3.1a) but remained large (Figure 3.2a). With conditions remaining wet and green with the progression of the wet season (Table 3.1), home ranges remained distant from the Kavango River (Figure 3.1a) but more than halved in size from the early wet (range: 10.5 – 33.5 km^2) to the late wet season (range: 6.8 – 19.4 km^2) (Figure 3.2a). The late wet season range extent was no different from the preceding early dry season range extent (Figure 3.2a). Like the seasonal changes in home range extent, core ranges were small during the early dry season (range: 1.0 – 2.8 km^2), increasing in size by ~50% during the late dry season (range: 1.5 – 4.7 km^2); and remained large into the early wet season (range: 2.1 – 5.9 km^2), halving in extent during the late wet season (range: 1.3 – 3.5 km^2) (Figure 3.2b).

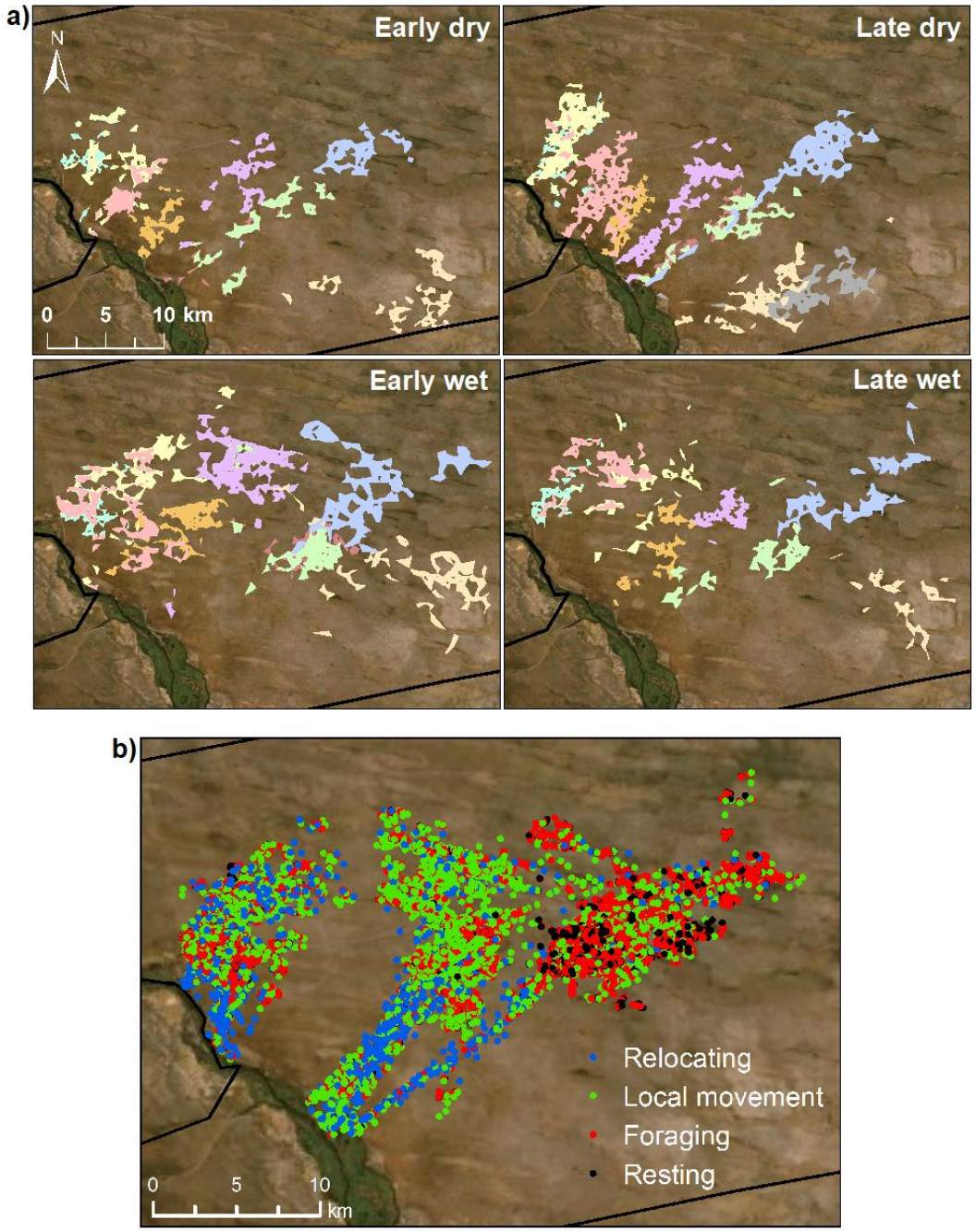

Figure 3.1. a) 95% LoCoH home ranges of ten free-ranging female sable antelopes in Bwabwata National Park, Namibia, during the early dry (May – July), late dry (August – October), early wet (November – January) and late wet (February – April) season of 2016/2017. b) Behavioural state allocation relative to GPS locations of three representative free-ranging female sable antelopes in Bwabwata National Park, Namibia, from May 2016 to April 2017. Four-state Hidden Markov Models (HMMs) were used to identify behavioural states from movement tracks with inferred states corresponding to resting, foraging, local movement and relocating. Long, relocating movements (blue) were mostly directed to and from the Kavango River.

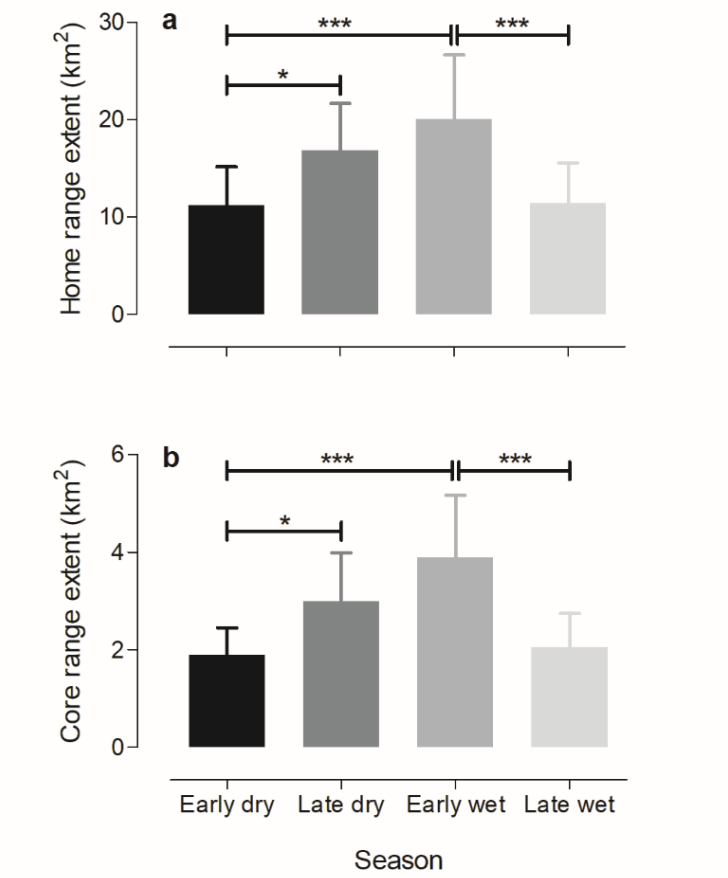

Figure 3.2. Mean (± SD) seasonal home (95% isopleth) and core (50% isopleth) range sizes of free-ranging female sable antelopes in Bwabwata National Park, Namibia, during the early dry (May – July), late dry (August – October), early wet (November – January) and late wet (February – April) seasons of 2016/2017. Linear Mixed-effects Models were significant for the influence of season on both the home range ($F[7, 39.98] = 10.861$, $p < 0.001$) and core range ($F[7, 38.97] = 10.691$, $p < 0.001$) sizes. Asterisks indicate statistically significant differences according to pairwise multiple comparisons using a Tukey adjustment (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$). Seasonal ranges were estimated using the *a*-LoCoH method.

Table 3.1. Prevailing environmental conditions (mean ± SD) during the early dry (May – July), late dry (August – October), early wet (November – January) and late wet (February – April) seasons from May 2016 – April 2017 during which sable antelopes were free-ranging within Bwabwata National Park, Namibia.

	Early dry	Late dry	Early wet	Late wet
Total rainfall (mm)	0	0	119	84
Area average EVI	0.25 ± 0.03	0.19 ± 0.01	0.32 ± 0.11	0.39 ± 0.05
Brown vegetation exposure (%)	47.6 ± 10.7	99.9 ± 0.1	37.3 ± 17.6	0.1 + 0.3
Dry-bulb air temperature (^{o}C)				
24-hour mean	18.2 ± 1.1	26.4 ± 5.0	26.1 ± 2.7	23.0 ± 1.3
24-hour minimum	7.1 ± 1.4	14.3 ± 5.7	19.9 ± 0.3	16.5 ± 3.4
24-hour maximum	30.5 ± 0.8	39.9 ± 4.4	35.5 ± 5.4	32.3 ± 0.4
Black globe temperature (^{o}C)				
24-hour mean	21.6 ± 1.4	29.4 ± 5.0	29.7 ± 2.3	27.4 ± 1.4
24-hour minimum	6.5 ± 1.5	13.7 ± 5.5	19.6 ± 0.3	16.2 ± 3.4
24-hour maximum	43.0 ± 1.5	50.0 ± 5.2	50.8 ± 3.0	49.6 ± 0.9

Area average EVI was obtained using the Application for Extracting and Exploring Analysis Ready Samples (AppEEARS) interface (https://lpdaacsvc.cr.usgs.gov/appeears/) which provided area averaged EVI (MODIS 13Q1.006, 250 m with 16-day composites) for the total spatial area covered by all GPS locations of free-ranging sable antelopes. Black globe temperature is indicative of environmental heat load.

Mean hourly displacement in response to vegetation greenness and heat load

Sable antelopes progressively increased the average distance moved per hour per day (Figure 3.3c) when they were increasingly exposed to high environmental heat load (Figure 3.3a) and brown vegetation (Figure 3.3b), with the progression of the dry season (May – October). Consequently, by the end of the late dry season, when conditions were hottest (Figure 3.3a) and brownest (Figure 3.3b), sable antelopes were moving ~50% further per hour per day (Figure 3.3c) compared to the start of the dry season. This observation, that sable antelopes walked greater distances when it was hot and dry, was confirmed by statistical analyses showing that the 24-hour mean hourly displacement distance of sable antelopes was positively associated with increased heat loads and increased exposure to brown vegetation (Table 3.2).

Table 3.2. Generalised Linear Mixed-effect Model results for the relationship between the average hourly distance moved by sable antelopes per 24 hours and environmental variables, namely the proportion of time exposed to brown vegetation and 24-hour mean black globe temperature, prevalent in Bwabwata National Park between May 2016 and April 2018. A 24-hour cycle was defined as the period between consecutive sunrises.

	β ± s.e.	*t*	*p*
The 24-hour mean hourly displacement distance			
Proportion of brown vegetation exposure	0.31 ± 0.02	13.984	< 0.0001
24-hour mean black globe temperature	0.02 ± 0.002	9.377	< 0.0001

Individual identity was included as a random factor. n = 10, N = 4063. Model: 24-hour mean hourly displacement distance ~ proportion of brown vegetation exposure + 24-hour mean blackglobe temperature+ (1 | individual identity).

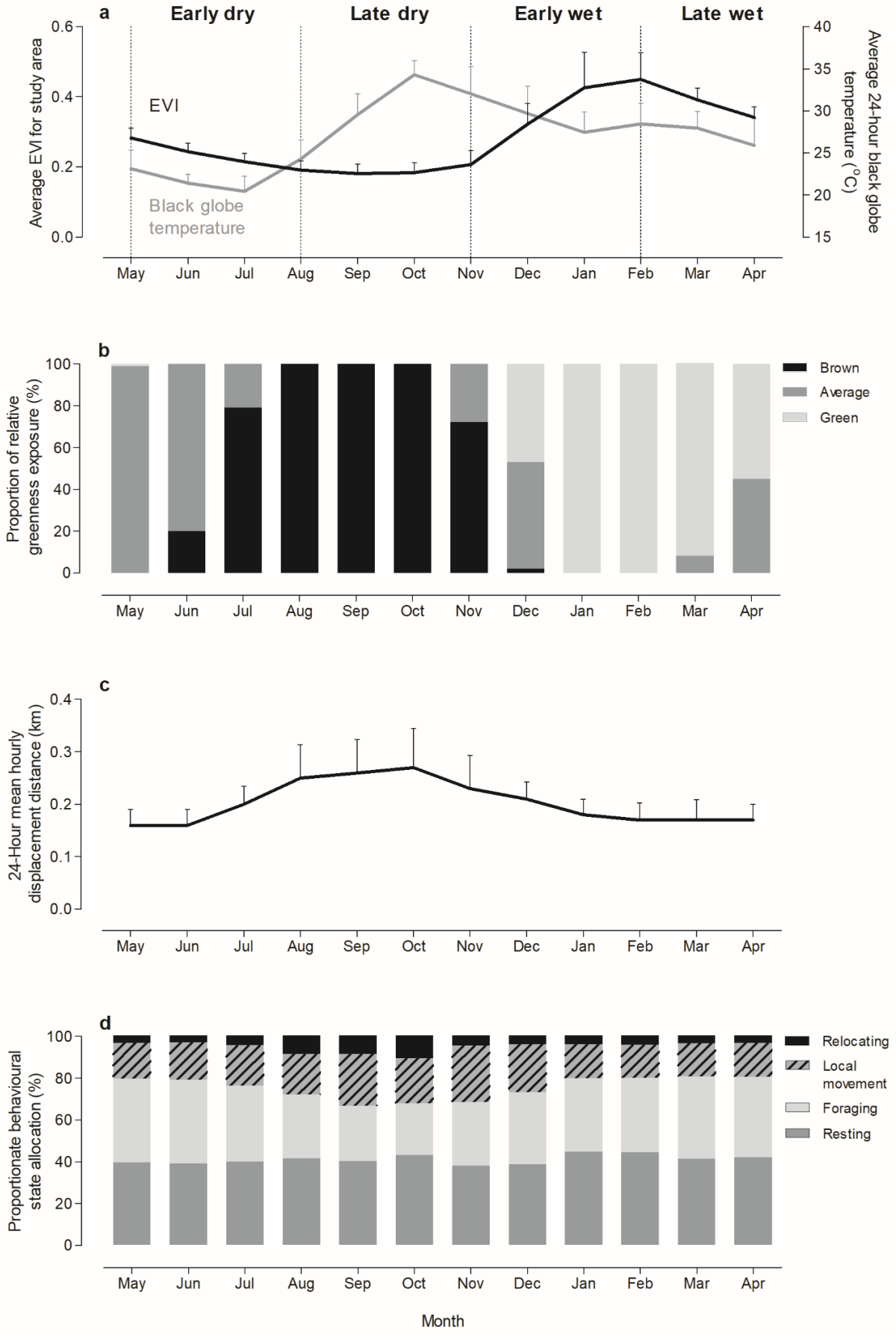

Figure 3.3. Monthly variation in a) mean (± SD) EVI (black trendline) and mean (± SD) 24-hour black globe temperature (grey trendline), b) average proportion of time spent in three relative greenness categories by sable antelopes, c) mean (± SD) hourly displacement distance per 24-hour period by sable antelopes, and d) average proportion of time per 24-hour period spent in behavioural states of resting, foraging, local movement and relocating by sable antelopes in Bwabwata National Park, Namibia, over one year (May 2016 – April 2017).

Behavioural states in response to vegetation greenness and heat load

As demonstrated for three representative individuals in Figure 3.1b, GPS locations classified as foraging behaviour were generally clustered while the GPS locations classified as relocating behaviour were mostly associated with widespread movements, particularly directed movements towards the Kavango River, but possibly also movements to other foraging areas. During the late dry season of the first year of my study, the sable antelope located furthest from the river travelled between 13 and 30 kms, every 4-5 days to access water from the river (Figure 3.1b). During the first year, as heat loads increased (Figure 3.3a) and exposure to brown vegetation increased (Figure 3.3b), sable antelopes increasingly spent more time per day in a relocating behavioural state, resulting in a ~four-fold increase in the time spent relocating per day by the end of the dry season (Figure 3.3d). Conversely, increased exposure to high heat load and brown vegetation resulted in sable antelopes spending ~38% less time foraging per day with the progression of the dry season (Figure 3.3d). This pattern was also evident in the second year, with GLMMs further highlighting an overall increase in relocating behaviour and a decrease in foraging behaviour associated with increased 24-hour mean black globe temperature and increased proportion of brown vegetation exposure (Table 3.3). Sable antelopes also displayed an increase in the proportion of time spent in local movement with increased exposure to brown vegetation and high 24-hour mean blackglobe temperature (Table 3.3), but a decrease in the proportion of time spent resting with an increase in the proportion of brown vegetation exposure. The proportion of time spent in a resting behavioural state was not affected by 24-hour mean blackglobe temperature (Table 3.3).

Table 3.3. Binomial Generalised Linear Mixed-effect Model results for the relationship between the proportion of time that sable antelopes spent in two behavioural states, namely relocating and foraging, and environmental variables, namely the proportion of time exposed to brown vegetation and 24-hour mean black globe temperature, prevalent in Bwabwata National Park between May 2016 and April 2018. A 24-hour cycle was defined as the period between consecutive sunrises.

Binomial generalised linear mixed model	β ± s.e.	*z*	*p*
Proportion of 24-hour cycle in relocating state			
Proportion of brown vegetation exposure	1.33 ± 0.12	10.961	< 0.0001
24-hour mean black globe temperature	0.08 ± 0.01	6.371	<0.0001
Proportion of 24-hour cycle in foraging state			
Proportion of brown vegetation exposure	-0.33 ± 0.02	-13.906	< 0.0001
24-hour mean black globe temperature	-0.03 ± 0.002	-13.802	< 0.0001
Proportion of 24-hour cycle in local movement			
Proportion of brown vegetation exposure	0.36 ± 0.03	11.27	< 0.0001
24-hour mean black globe temperature	0.02 ± 0.003	7.82	< 0.0001
Proportion of 24-hour cycle in resting state			
Proportion of brown vegetation exposure	-0.06 ± 0.02	-2.428	0.0152
24-hour mean black globe temperature	0.003 ± 0.002	1.425	0.1542

Individual identity was included as a random factor. An observation level random effect (OLRE) was included in the models to account for overdispersion. n = 9, N = 4660. Models: 1) proportion of 24-hour cycle spent in a foraging state ~ proportion of brown vegetation exposure + 24-hour mean black globe temperature + (1 | individual identity) + (1 | OLRE) and 2) proportion of 24-hour cycle spent in a relocating state ~ proportion of brown vegetation exposure + 24-hour mean black globe temperature + (1 | individual identity) + (1 | OLRE), 3) proportion of 24-hour cycle spent in a local movement state ~ proportion of brown vegetation exposure + 24-hour mean black globe temperature + (1 | individual identity) + (1 | OLRE), 4) proportion of 24-hour cycle spent in a resting state ~ proportion of brown vegetation exposure + 24-hour mean black globe temperature + (1 | individual identity) + (1 | OLRE).

3.4 Discussion

In this chapter, I aimed to improve our understanding of the behavioural capacity of resource specialist ungulates to cope with resource limitations under high heat load by evaluating the compounded effect of spatiotemporal changes in vegetation greenness and temporal variation in heat load on the movements of sable antelope. I have documented the longest directed movements to and from water within a single day by a non-migratory, water-dependent selective grazer with some sable antelopes covering an average round-trip distance of ~25km approximately every five days during the late dry season. These long, directed movements to the Kavango River, likely driven by the combination of high environmental heat load, decreased ephemeral surface water and low water content in browning forage, predominantly occurred during the late dry season when ambient temperature was high and sable antelopes likely experienced increased reliance on evaporative cooling in the hot and dry conditions. The additional time spent travelling to water however came at the expense of time spent foraging when grass quality was most limited. By evaluating the movement metrics in relation to prevailing vegetation greenness and ambient temperature, I was able to quantitatively confirm low vegetation greenness and high ambient temperature as significant drivers of movement in sable antelope.

Estimates of the total home range size of sable antelopes generally range from 7.5 km^2 to 118 km^2 (Cain et al., 2006; Henley, 2005; Hensman et al., 2014; Owen-Smith and Cain, 2007; Parrini, 2006; Rahimi and Owen-Smith, 2007; Wilson and Hirst, 1977) but have predominately been calculated using minimum convex polygons (MCP) which overestimate the home range size of sable antelope by 50 – 60% compared with methods like kernel density estimation (KDE) and LoCoH (Hensman et al., 2014; Owen-Smith and Cain, 2007). While the LoCoH home ranges of the ten sable antelope in my study (early dry: 5.8 – 19.8

km^2, late dry: 8.9 – 24.2 km^2, early wet: 10.5 – 33.5 km^2, late wet = 6.8 – 19.4 km^2) were mostly smaller than the KDE ranges of two adjacent sable antelope herds in northern Kruger National Park, South Africa (dry = 23.1 – 69.1 km^2, wet = 29.3 – 33.9 km^2) (Owen-Smith and Cain, 2007), they were generally congruent with the LoCoH ranges of three adjacent sable antelope herds in the Kwedi area of the Okavango Delta, Botswana (early dry: 11.3 – 12.5 km^2, late dry: 9.3 - 17.2 km^2, wet: 3.4 - 19.8 km^2) (Hensman et al., 2014). However, some of the sable antelopes in my study displayed home ranges larger than those of sable antelopes in the Okavango region. Since the home range patterns of sable antelope are largely influenced by habitat composition, food availability, surface water distribution and interspecific competition (Cain et al., 2012; Chirima et al., 2013; Hensman et al., 2014; Macandza et al., 2012b; Owen-Smith and Cain, 2007; Rahimi and Owen-Smith, 2007), it is evident that the home range occupation of sable is inherently dependent on the local ecological conditions experienced by individuals or herds (Owen-Smith et al., 2010). For instance, in northern Kruger National Park, when two sable antelope herds had year-round access to borehole-fed water points within their home ranges, one herd consistently occupied the same general area, displaying minimal seasonal variation in KDE home range size, while the adjacent herd utilized an area double the size of its wet season range during the dry season explained by the need to access a distant water point (Owen-Smith and Cain, 2007). In the Okavango, sable displayed little seasonal variation in LoCoH home range size but shifted the location of their ranges, utilizing the floodplain alongside permanent water during the wet season, and occupying ranges further upland from permanent water during the late dry season, a shift enabled by upland pools retaining water through the late dry season (Hensman et al., 2014).

Unlike the sable antelopes in the Okavango, sable antelope in my study occupied home ranges upland from the Kavango River and floodplain during the wet season. The especially large and widespread home ranges during the early wet season likely reflected sable maximizing their intake of high-quality grass (i.e. maximize crude protein intake), following post-rain grass green-up, to meet the nutritional requirements of late gestation to parturition (November – March). Sable maintained the upland location of their home ranges throughout the wet season as the presence of ephemeral surface water likely enabled sable to access water within their preferred range. However, as conditions became hotter and drier with the progression of the dry season, food and water seemingly became spatially segregated as home ranges elongated towards the Kavango River with the progression of the dry season.

Heightened inter-specific competition likely prevented the sable antelopes in my study from occupying home ranges adjacent to the river since interspecific and apparent competition from more abundant grazers often forces sable antelope to occupy home ranges further away from water resources, even during resource-limited periods (Cain et al., 2012; Macandza et al., 2012a, 2012b). These outlying areas located further away from surface water and the presence of more abundant grazers are typically sandy, nutrient-poor regions of open to semi-open woodland. However, the sandy soils often facilitate water filtration which supports the retention of green grass into the dry season while tree canopies in woodland patches support the retention of green leaf grass (Parrini, 2006) such as *Panicum maximum* which commonly grows in shaded areas and is a grass species highly favoured by sable antelope (Gureja and Owen, 2002; Magome et al., 2008; Parrini, 2006; Wilson and Hirst, 1977). Sable antelope are adept at concentrating their grazing on grass species that retain green leaves during the dry season (Hensman et al., 2014b; Macandza et al., 2012a; Owen-Smith et al., 2013), green grass flush in recently burned areas (Magome et al., 2008; Parrini and Owen-Smith, 2010) or green grass retained in vlei areas (Parrini and Owen-Smith, 2010). Selecting patches of green forage may

also enable sable to obtain pre-formed moisture from their diet during the dry season. However, as the dry season progresses, and conditions become drier and hotter, sable become increasingly dependent on surface water (Cain et al., 2012). While the narrowing of home ranges during the dry season may reflect the focused foraging efforts of sable in areas retaining green leaf forage (such as along the omurambas or within strips of woodland), the extensive elongation of home ranges towards the Kavango River suggests that sable made accommodations for accessing distant surface water, particularly as ambient temperature increased during the late dry season.

It appeared the sable antelopes in my study did not have access to upland ephemeral surface water during the dry season to maintain home ranges distant and separated from the river. Instead, they travelled to and from the river, often using the same route, and limiting the range overlap with adjacent herds, which has commonly been found in previous studies (Hensman et al., 2014; Owen-Smith and Cain, 2007). These directed and long-distance movements were distinct and classified as a relocating behavioural state in the 4-state HMMs. The frequency of these relocating movements increased with increasing heat load and were mostly associated with directed movements to and from the Kavango River at the end of the hot late dry season, highlighting that accessing free-standing surface water became increasingly important during the late dry season when sable antelopes would have faced increased water requirements under high heat load.

While browning vegetation was a significant driver of the increased movement distances of the sable antelopes in my study, travel to water rather than shifts between foraging patches has been shown to increase the daily distances travelled by sable antelope during the dry season (Owen-Smith and Cain, 2007; Rahimi and Owen-Smith, 2007). In northern Kruger National Park, Cain et al (2012) found that a remnant sable antelope herd travelled two to three times further on days when the movement to water occurred than on non-water

movement days during the dry season. This herd travelled approximately 5-9 kms to pools remaining in a seasonal river every 3-4 days, with the longest total round-trip covering ~22 km. On days when movement to water occurred this herd spent on average 4 fewer hours per day resting and 4.1 fewer hours per day foraging. The analysis and comparison of water movement versus non-water movement days was limited by GPS frequency (6-h) and to days where 1-h intervals were available during the late dry season (Cain et al., 2012). Owen-Smith and Goodall (2014) found that a sable herd inhabiting the drier northern region of KNP progressively increased foraging and travel time during the late dry season at the cost of time spent resting. However, in southern KNP, a sable antelope herd exposed to higher wet season rainfall and greater surface water availability within their range during the dry season displayed little change in foraging time with the progression of the dry season and no increase in travel time (Owen-Smith and Goodall, 2014). During the late dry season, the sable antelope located furthest from the river in my study travelled between 13 and 30 kms, every 4-5 days to access water from the river. The increased time spent travelling to and from the river significantly constrained the time available for foraging and resting. As ephemeral surface water progressively depleted and the increasing lack of green forage failed to mitigate water and food limitations under high heat load, sable antelope in my study were unable to save travel time by acquiring water close to foraging patches and were forced to travel to and from the Kavango River. Increased travel to water resources may however incur additional energy and time costs in an already energy-limited dry season. In the Makgadikgadi Pan region of Botswana, wildebeest *Connochaetes taurinus* drank only every 2-4 days and grazed 10-15 km from a river (Curtin et al., 2018). Despite efficient muscles (Curtin et al., 2018), long-distance movements to key resources may come at an energetic cost (Boyers et al., 2019). Thus, challenged with maintaining both energy and water balance during a period

where food is limited, and high heat load exacerbates water limitations, I question whether this trade-off is sustainable, especially in the face of a hotter and drier future.

As conditions become increasingly hotter and drier, and the availability and distribution of resources become more unpredictable in space and time, these specialist species may face increased risk of extirpation as it becomes increasingly difficult to trade-off key resource requirements (e.g. food and water) necessary for survival. Long-term movement studies can inform management decisions to improve conservation efforts by i) indicating when and where populations experience increasingly stressful conditions before or amid population decline, and ii) identifying important access routes to key resources (i.e. landscape features, habitats and corridors) to prioritise their preservation.

CHAPTER 4

Escaping the heat: a water-dependent, specialist antelope increases its nocturnal activity and seeks thermal refuge during hot and dry conditions.

4.1 Introduction

The current rate of climate change in sub-Saharan Africa requires large-bodied ungulates to respond relatively quickly and sufficiently to changes in environmental conditions to ensure their survival. Limited by their slow life history traits and consequential inability to adapt timeously through microevolution (Rosenheim and Tabashnik, 1991), and increasingly restricted from tracking suitable climatic envelopes as a result of habitat loss, habitat fragmentation and increased anthropogenic barriers (Thuiller et al., 2006), large African ungulates may need to rely on phenotypic flexibility, such as behavioural adjustments, to cope with hotter and drier conditions (Fuller et al., 2016; Hetem et al., 2014). A primary behavioural response to changing environmental conditions is adjusting and rescheduling daily activity patterns (McCain and King, 2014). The 24-hour activity pattern describes how ungulates distribute their activity, energy, and time while responding to changes in biotic (e.g. resource availability) and abiotic (e.g. temperature and photoperiod) factors. Assessing changes in activity patterns over long timescales can provide insight into the environmental constraints of activity such as seasonal changes in resource availability and climate, and how ungulates adjust their activity to meet resource requirements and cope with thermal challenges.

As food availability decreases with the progression of the dry season, ungulates may increase their activity by spending more time searching for remaining food (Owen-Smith et al., 2010). Alternatively, ungulates may prioritise energy conservation during resource scarcity and decrease activity to save energy. Indeed, blue wildebeest *Connochaetes taurinus* reduced their overall activity during the dry season when food availability was presumed to be low (Selebatso et al., 2017) and responded to increased exposure to brown vegetation during the dry season by reducing total 24-hour activity (Boyers, 2018). However, as temperatures start

to increase towards the late dry season, diurnal activity can be constrained by high heat load. To reduce diurnal heat loads, ungulates may reduce their diurnal activity, particularly during the heat of the day (Berry et al., 2023; Boyers et al., 2021, 2019), shift activity to cooler crepuscular periods such as dawn and dusk (Berry et al., 2023) or, depending on predation risk shift activity to the nocturnal period (Hetem et al., 2012b, 2012a). Historically, nocturnal observations of activity were limited by the need for direct observations however, advances in biologging technology now enable the continuous and unbiased measurement of fine-scale activity (seconds to minutes resolution), allowing for a better measure of nocturnal activity, overall activity, and identification of compensatory shifts in activity in response to prevailing environmental conditions (Rutz and Hays, 2009; Williams et al., 2020; Wilmers et al., 2015).

A reduction in diurnal activity during hot and dry conditions often results from decreased activity over the heat of the day (Berry et al., 2023; Boyers et al., 2019; Selebatso et al., 2017), which generally coincides with the use of cooler microclimates, with shade being particularly important for large ungulates (Fuller et al., 2016). Cool microclimates act as a thermal refuge, buffering the impacts of radiant heat exposure, allowing ungulates to reduce their heat load and evaporative water loss, particularly during hot periods when water is limited (Cain et al., 2006; Fuller et al., 2016, 2014). Indeed, the selection of cool microclimates with increasing environmental temperature has been shown in free-living African ungulates including kudu *Tragelaphus strepsiceros* (Hetem et al., 2008), Angora goats *Capra aegagrus hircus* (Hetem et al., 2011), eland *Tragelaphus oryx* (Shrestha, 2012) and blue wildebeest and gemsbok *Oryx gazella gazella* (Boyers et al., 2021, 2019), as well as free-living Arabian oryx *Oryx leucoryx* (Hetem et al., 2012b) and Arabian sand gazelle *Gazella subgutturosa marica* (Hetem et al., 2012a). Biologging can be used to quantify microclimate selection allowing us to measure the degree to which free-living animals exploit

environmental thermal heterogeneity by quantifying the selection of cool microclimates at high environmental heat loads (Hetem et al., 2007).

The continuous quantification of activity allows unique insights into trade-offs, for example, if individuals decrease their activity during the heat of the day, they may compensate by increasing nocturnal activity, as observed in eland (Berry et al., 2023), Arabian oryx (Hetem et al., 2012b), Arabian sand gazelle (Hetem et al., 2012a), and gemsbok (Boyers et al., 2019), or they may fail to compensate resulting in a reduction in total 24-hour activity, as observed in blue wildebeest (Boyers et al., 2019; Selebatso et al., 2017). Without efficient compensation, reducing activity during the heat of the day may compromise other important activities such as resource acquisition (e.g. food and water), which may be detrimental for water-dependent, specialist antelope species such as sable antelope, particularly in the face of hotter and drier conditions. Analysing fine-scale activity and microclimate selection in relation to key environmental factors such as vegetation greenness and black globe temperature, may provide important insight into behavioural strategies and capacity for behavioural flexibility in the face of climate change.

To investigate the variation in the activity patterns and microclimate selection of sable antelope in relation to prevailing environmental conditions I set out to i) investigate the relationship between total 24-hour activity and the timing of activity, and vegetation greenness and heat load, and ii) assess microclimate selection relative to reference miniglobes in open environments and in relation to vegetation greenness and 24-hour heat load. I expected sable antelopes to i) increase total 24-hour activity when exposed to brown vegetation and high heat load based on increased movement (Chapter 3), ii) decrease midday activity and increase nocturnal activity to reduce compounding effect of high metabolic activity in the heat as conditions become hotter and drier, iii) select cooler microclimates for

longer during the heat of midday to reduce heat loads and evaporative water loss in response to increasing exposure to brown vegetation and high heat load.

4.2 Data and analysis

As described in Chapter 2, together with my team, I collared 10 free-living female sable antelope and implanted each with a multi-axis accelerometer tag which recorded activity counts over 10-minute periods, from May 2016 – January 2018. Records of activity counts were logged on the tag and transmitted to the neck collar at hourly intervals, thus the lifespan of the activity tag was limited to the lifespan of the respective collar (see Chapter 2). After the data cleaning process, activity data varied between 7 and 21 months with six individuals providing at least 12 months of activity measurements. Each collar also had a miniature (30mm diameter) black globe thermometer (miniglobe) attached to it which recorded black globe temperature hourly.

To test whether sable antelope were selecting microclimates cooler than that of the open environment, I compared the collar miniglobe temperatures to the hourly black globe temperatures recorded by two reference miniature black globes (30 mm diameter) erected within the study area and exposed to sunlight throughout most of the day (see Chapter 2). When I plotted the 24-hour black globe temperature rhythms for each reference miniglobe, I identified slight differences in the 24-hour temperature rhythm between the two reference miniglobes. These slight differences were potentially caused by one reference miniglobe receiving shade in the early morning. Therefore, I 1) restricted microclimate and shade-seeking analyses to the heat of the day which occurred over the midday period (11:00-16:00), and 2) used the hourly temperature measurements of both reference miniglobes to calculate an average hourly reference miniglobe temperature, from 1 May 2016 to 8 April 2017,

hereafter referred to as the averaged reference miniglobe. The time frame of the averaged reference miniglobe temperature data was restricted to the shorter life span of one of the two reference miniglobes. While the lifespan of the collar miniglobe logger was limited to the lifespan of the respective collar (see Chapter 2), the analysis of microclimate selection was restricted to correspond with the availability of the averaged reference miniglobe data (i.e., 1 May 2016 – 8 April 2017).

To link measures of activity and microclimate selection to vegetation greenness in time and space, I extracted the relative greenness category of each pixel associated with each GPS location recorded over the study period to calculate the proportion of brown vegetation exposure, per individual for every 24-hour cycle (sunrise to consecutive sunrise) from May 2016 – January 2018 (as per Chapter 2). I calculated the mean and maximum 24-hour standard (150 mm diameter) black globe temperature, recorded on the weather station, for every 24-hour cycle (sunrise to consecutive sunrise) from May 2016 to January 2018 (as per Chapter 2).

Activity in relation to vegetation greenness and heat load

To identify variation in the timing of 24-hour activity, I calculated total 24-hour activity, proportion of diurnal activity, and proportion of nocturnal activity per individual for successive 24-hour cycles occurring between consecutive sunrise times from May 2016 to January 2018. Total 24-hour activity was calculated as the sum of activity counts per 24-hour cycle between consecutive sunrises. The 24-hour proportion of diurnal activity was calculated as the proportion of total 24-hour activity that occurred between sunrise and the consecutive sunset (i.e. daytime). The 24-hour proportion of nocturnal activity was calculated as the proportion of total 24-hour activity that occurred between sunset and the consecutive sunrise (i.e. night-time). To account for differences in the sensitivity of individual activity tags, each

activity record was expressed as a percentage of the maximum activity recorded by each tag over the study period. To be included in mixed model analysis, each total 24-hour activity measurement required a minimum of 19 hours of 10-minute recordings, and each diurnal and nocturnal measurement required a minimum of 9 hours of 10-minute recordings.

A Linear Mixed Model (LMM) was used to test for the influence of the proportion of brown vegetation exposure and mean 24-hour black globe temperature (predictor variables) on total 24-hour activity (response variable). The statistical distribution of the total 24-hour activity response variable was right skewed and therefore log transformed before mixed model analysis to meet mixed model assumptions of normality, homogeneity of variance and independence. A Generalised Linear Mixed Model (GLMM) with a beta error distribution and logit link function, was used to test for the influence of the proportion of brown vegetation exposure and mean 24-hour black globe temperature (predictor variables) on the response variables of 1) the 24-hour proportion of diurnal activity and 2) the 24-hour proportion of nocturnal activity. The beta error distribution with logit link provided a superior fit compared to the binomial distribution with logit link because the response variables were continuous proportions calculated from non-integer trial counts. To account for seasonal variation in day length, I included day length (i.e., diurnal photoperiod) in the 24-hour proportion of diurnal activity model. Similarly, to account for seasonal variation in the length of the nighttime, I included the length of the nighttime period (i.e., nocturnal period) in the 24-hour proportion of nocturnal activity model.

Microclimate selection and shade-seeking in relation to vegetation greenness and heat load

To quantify microclimate selection during the heat of the day, I calculated the hourly temperature difference between the collar miniglobe and the averaged reference miniglobe (i.e. collar miniglobe temperature minus averaged reference miniglobe temperature), per individual for every hour during the midday periods (11:00 –16:00) occurring from 1 May 2016 to 8 April 2017. I subsequently extracted the minimum value of these hourly temperature differences for every midday period that contained at least 4 out of the possible 6 hourly temperature difference measurements for that period. This minimum temperature difference was then used as an index of the quality of the microclimate selected by sable antelopes during the heat of the day, with more negative values indicating the selection of higher quality (i.e. cooler) microclimates. A LMM was used to assess the influence of the proportion of brown vegetation exposure and maximum 24-hour black globe temperature (predictor variables) on the quality of the midday microclimate selected (response variable).

To quantify the degree of shade-seeking during the heat of the day, I extracted the count of hourly miniglobe temperature differences that were less than -0.5 ^{o}C (i.e. collar miniglobe temperature was at least 0.5 ^{o}C cooler than the averaged reference miniglobe temperature) and calculated the proportion of time spent in shade during the heat of the day (11:00 –16:00) per individual for successive midday periods from 1 May 2016 to 8 April 2017. When calculating the proportion of time spent in the shade during the heat of midday, I only considered midday periods that contained at least 4 out of the possible 6 hourly miniglobe temperature difference measurements. A GLMM with a binomial error distribution and logit link function was then used to assess the influence of the proportion of brown vegetation exposure and maximum 24-hour black globe temperature (predictor variables) on the proportion of time spent in shade during the heat of the day (response variable). An

observation level random effect (OLRE) was included in the model to correct for the presence of overdispersion (Harrison, 2015) and meet mixed model assumptions.

Midday activity in relation to shade-seeking, vegetation greenness and heat load

The 24-hour proportion of midday activity was calculated as the proportion of total 24-hour activity that occurred during the heat of the day (i.e. 11:00–16:00). Each 24-hour proportion of midday measurement required at least 4 hours of 10-minute recordings to be included in mixed model analysis. A Generalised Linear Mixed Model (GLMM) with a beta error distribution and logit link function, was used to assess the influence of the proportion of brown vegetation exposure, mean 24-hour black globe temperature and the proportion of time spent in shade during the heat of the day (predictor variables) on the 24-hour proportion of midday activity (response variable). The beta error distribution with logit link provided a superior fit compared to the binomial distribution with logit link because the response variable was a continuous proportion calculated from non-integer trial counts. The analysis of the 24-hour proportion of midday activity was restricted to correspond with the availability of the averaged reference miniglobe data used to calculate the proportion of time in shade predictor variable (i.e., 1 May 2016 – 8 April 2017).

All mixed models were fitted using the R (R Core Team, 2023) packages lme4 (Bates et al., 2015) and glmmTMB (Brooks et al., 2017). The identity of individual sable antelopes was included as a random effect in all mixed models. All LMMs were fitted using restricted maximum likelihood (REML). Using the R package AICcmodavg (Mazerolle, 2023), I used Akaike's Information Criterion corrected for small sample size (AICc) to identify which mixed models supported the data best (Burnham et al., 2011) (see Appendix 4). Model diagnostics appropriate for assessing model fit and adequacy were performed using the R

package Dharma (Hartig, 2017). Figures show data for the first year of the study (May 2016 – April 2017) when sample sizes were larger.

4.3 Results

There was distinct variation in mean and maximum 24-hour black globe temperature, and the mean proportion of brown vegetation exposure experienced by sable antelopes across months (Figure 4.1). May to July was characteristic of the early cool dry season with mean and maximum 24-hour black globe temperature progressively decreasing to its lowest in July (mean: 20.4 ± 1.6 ^{o}C; maximum: 42.0 ± 2.9 ^{o}C) while the proportion of brown vegetation exposure progressively increased. August to October was hot and dry, characteristic of the late dry season, with mean and maximum 24-hour black globe temperature increasing to its maximum in October (mean: 34.3 ± 1.5 ^{o}C; maximum: 55.1 ± 3.1 ^{o}C) during which time sable antelope experienced maximal exposure to brown vegetation (100%). Following rainfall in November, sable antelope increasingly selected green patches so that the proportion of brown vegetation exposure decreased to 0% in January and mean 24-hour black globe temperature gradually decreased by ~7 ^{o}C, reaching 27.5 ± 2.3 ^{o}C by January (maximum 47.8 ± 4.8 ^{o}C). February to April remained warm and wet during which time mean and maximum 24-hour black globe temperature averaged 27.4 ± 1.5 ^{o}C and 49.6 ± 0.9 ^{o}C respectively and the proportion of brown vegetation exposure remained 0%.

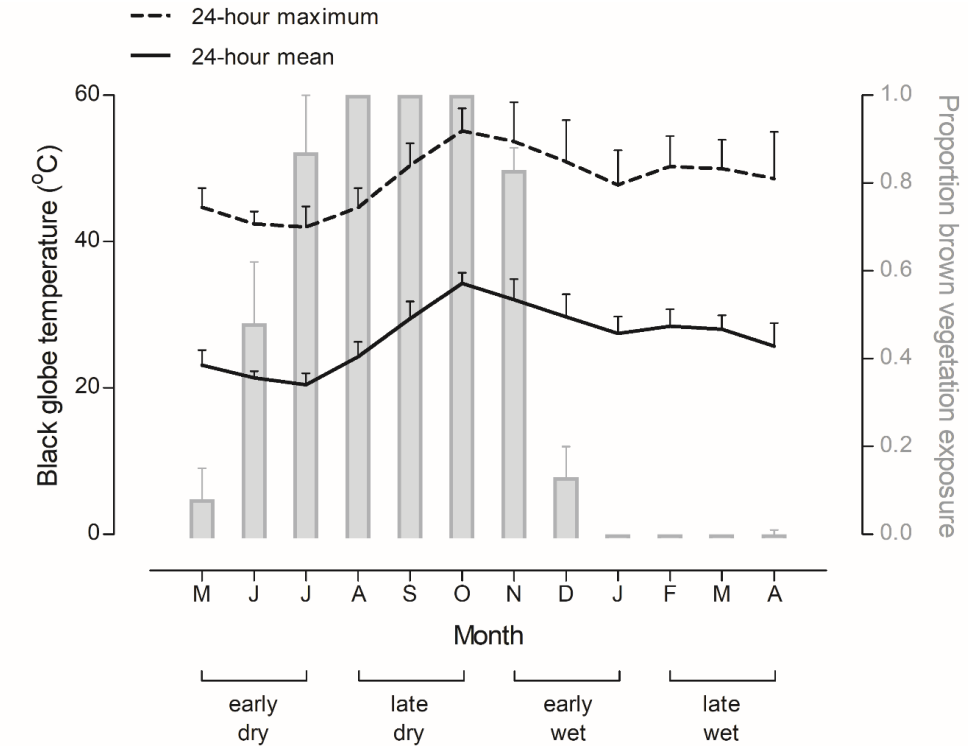

Figure 4.1. Average (mean± SD) mean and maximum 24-hour standard (150mm) black globe temperature (black trendlines, left y-axis), and the average (mean ± SD) daily proportion of brown vegetation exposure (grey bars, right y-axis) experienced by 10 free-ranging female sable antelopes in Bwabwata National Park, Namibia, from May 2016 to April 2017.

Sable antelopes were consistently more active during the daytime than at night-time (Figure 4.2), however, their total 24-hour activity and diurnal and nocturnal proportion of total 24-hour activity varied in response to changes in exposure to vegetation greenness and environmental heat load (Table 4.1). Sable antelopes displayed a reduction in their total 24-hour activity in response to an increasing proportion of brown vegetation exposure and rising mean 24-hour black globe temperature (Table 4.1), such that total 24-hour activity was ~38% lower when conditions were hottest and driest at the end of the late dry season (October) compared to when conditions were warm and greenest at the height of the wet season (January – March). After controlling for variation in day length, sable antelopes displayed a reduction in their proportion of diurnal activity in response to increasing exposure to brown

vegetation and rising black globe temperature. To accommodate for the reduced diurnal activity, sable antelope increased their 24-hour proportion of nocturnal activity in response to increasing exposure to brown vegetation and rising black globe temperature (Table 4.1). By October when conditions were hottest and driest sable antelopes neared equal proportions of diurnal and nocturnal activity (Figure 4.2).

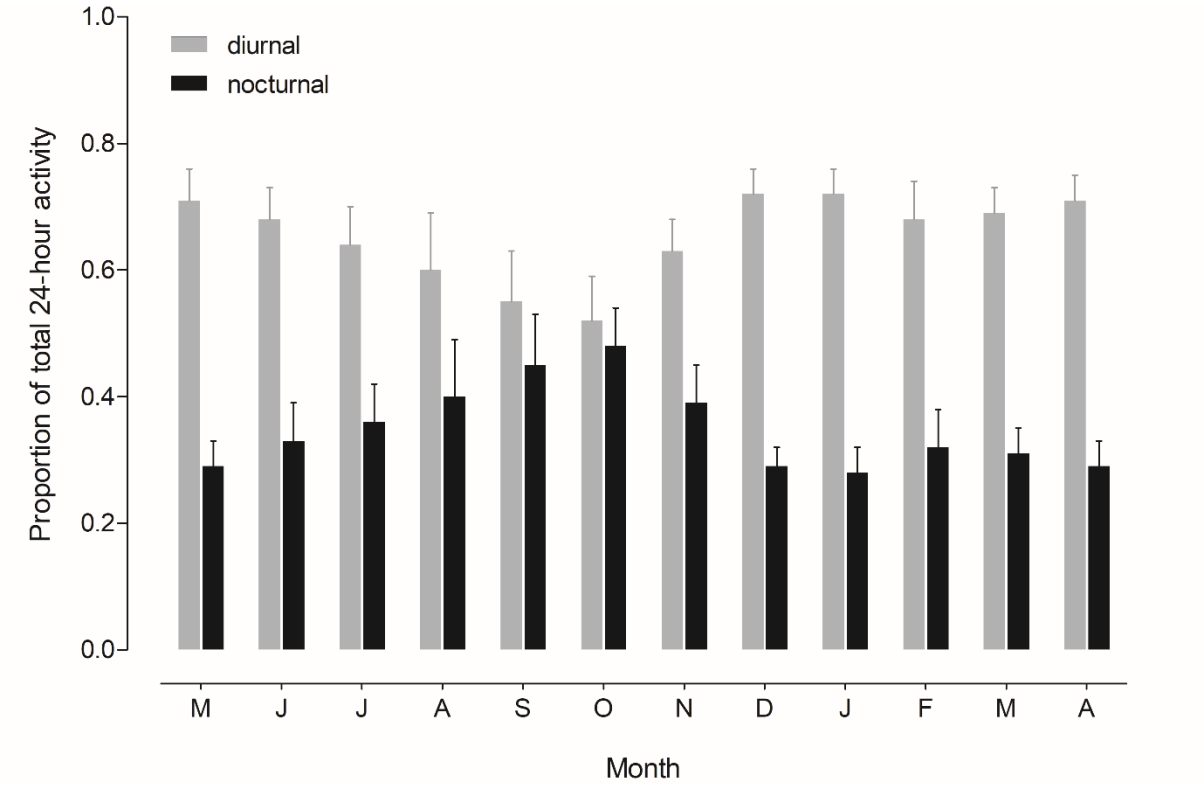

Figure 4.2. The average (mean ± SD) diurnal and nocturnal proportion of total 24-hour activity of 10 free-ranging female sable antelope in Bwabwata National Park, Namibia, from May 2016 to April 2017. Diurnal activity occurred between sunrise and the consecutive sunset time. Nocturnal activity occurred between sunset and the consecutive sunrise time.

Table 4.1. Mixed model results for the relationship between total 24-hour activity, 24-hour proportion of diurnal activity and 24-hour proportion of nocturnal activity of 10 sable antelope and prevailing environmental conditions in Bwabwata National Park, Namibia, from May 2016 to January 2018.

Linear mixed model	β ± s.e.	*t*	*p*
a) Total 24-hour activity			
Proportion of brown vegetation exposure	-0.45 ± 0.02	-19.624	< 0.0001
Mean 24-hour black globe temperature	-0.009 ± 0.002	-4.287	< 0.0001
Beta generalised linear mixed model	**β ± s.e.**	***z***	***p***
b) 24-hour proportion of diurnal activity			
Proportion of brown vegetation exposure	-0.42 ± 0.03	-14.530	< 0.0001
Mean 24-hour black globe temperature	-0.03 ± 0.004	-7.314	< 0.0001
Diurnal photoperiod	0.09 ± 0.03	3.496	0.0005
c) 24-hour proportion of nocturnal activity			
Proportion of brown vegetation exposure	0.41 ± 0.03	14.656	< 0.0001
Mean 24-hour black globe temperature	0.03 ± 0.004	7.074	< 0.0001
Nocturnal period	0.09 ± 0.03	3.230	0.0012

Models: a) total 24-hour activity ~ proportion of brown vegetation exposure + mean 24-hour black globe temperature + (1 | individual identity), n = 10, N = 3708. Total 24-hour activity response variable was log-transformed; b) 24-hour proportion of diurnal activity ~ proportion of brown vegetation exposure + mean 24-hour black globe temperature + diurnal photoperiod + (1 | individual identity), n = 10, N = 3685; c) 24-hour proportion of nocturnal activity ~ proportion of brown vegetation exposure + 24-hour mean black globe temperature + nocturnal period + (1 | individual identity), n = 10, N = 3647. Diurnal and nocturnal periods were calculated using sunrise and sunset times. Individual identity was included as a random factor in all models.

Sable antelopes displayed crepuscular peaks of activity, with activity peaking from dawn through the early morning and from late afternoon into the early evening, attenuating during the heat of the day (11:00 – 16:00) when 24-hour black globe temperature was highest (Figure 4.3). As conditions became hotter and drier with progression of the dry season sable antelopes halved their midday activity (Figure 4.4a) and spent ~50% more time in the shade (i.e. where collar miniglobe temperature minus averaged reference globe temperature was less than -0.5^{o}C) during the heat of the day (Figure 4.4b). The reduction in midday activity

was associated with increased exposure to brown vegetation, high 24-hour mean blackglobe temperature and an increased proportion of time spent in the shade (Table 4.2). Sable antelopes spent an increasing proportion of time in the shade in response to high 24-hour maximum black globe temperature and increased exposure to brown vegetation (Table 4.2). They also selected higher quality microclimates (i.e. cooler microclimates) when increasingly exposed to brown vegetation and high 24-hour maximum black globe temperature (Table 4.2). At the height of the hot late dry season sable antelopes selected microclimates that were on average 6.7 ± 0.2 ^{o}C cooler than the reference miniglobe in the sun (Figure 4.5a), with selected microclimates averaging 10.7 ± 1.3 ^{o}C cooler during October. On occasion, two sable antelopes selected microclimates that were 12.4 ^{o}C and 12.9 ^{o}C cooler than the open environment when conditions were hottest and driest during October.

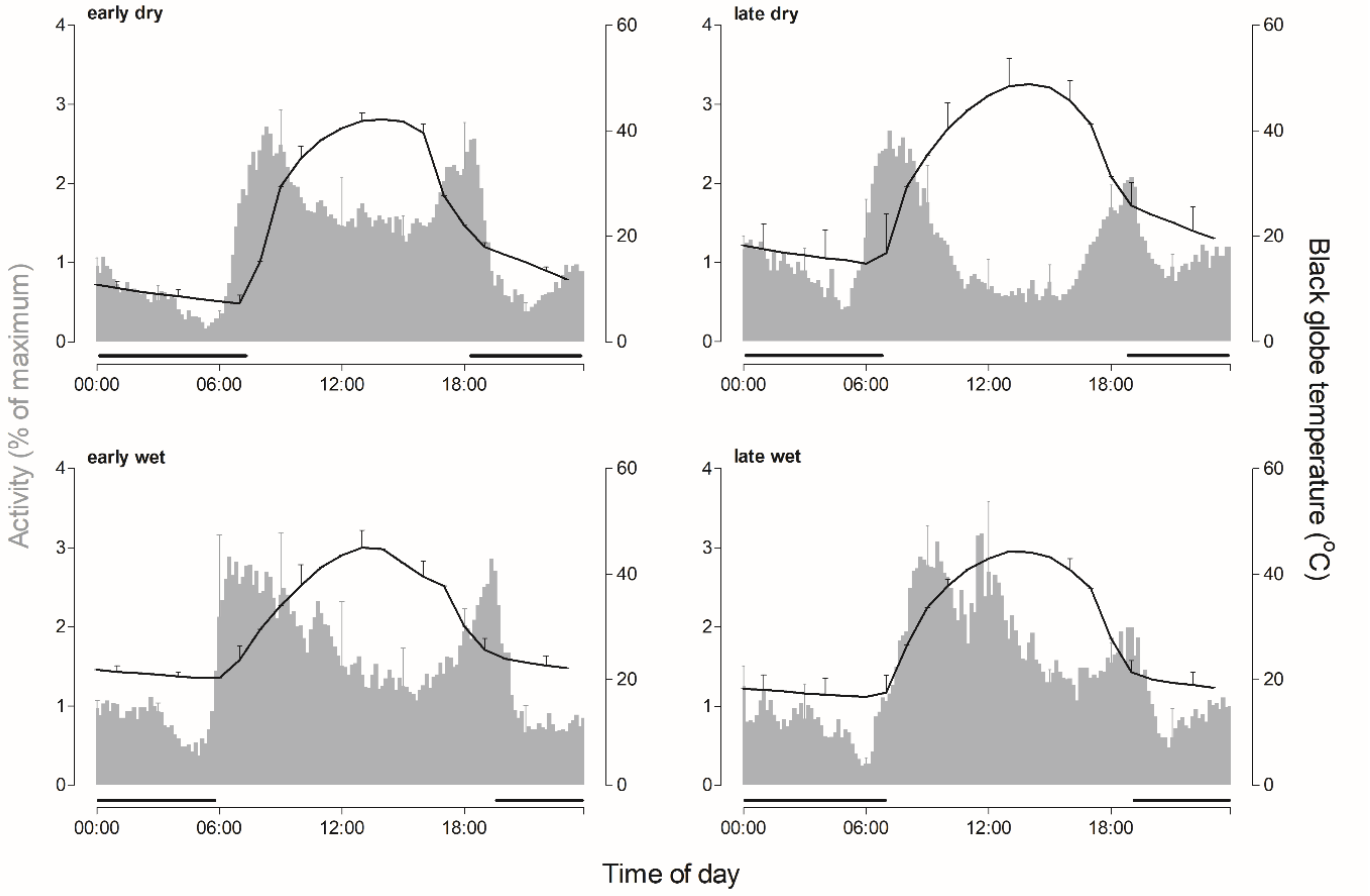

Figure 4.3. The average (mean ± SD) 24-hour activity pattern of 10 free-ranging sable antelope (grey bars, left axis) and average (mean ± SD) 24-hour black globe temperature (black line, right axis) during the early dry (May - July), late dry (August - October), early wet (November - January) and late wet (February - April) periods occurring from May 2016 to April 2017 in Bwabwata National Park, Namibia. Horizontal black bars indicate night-time.

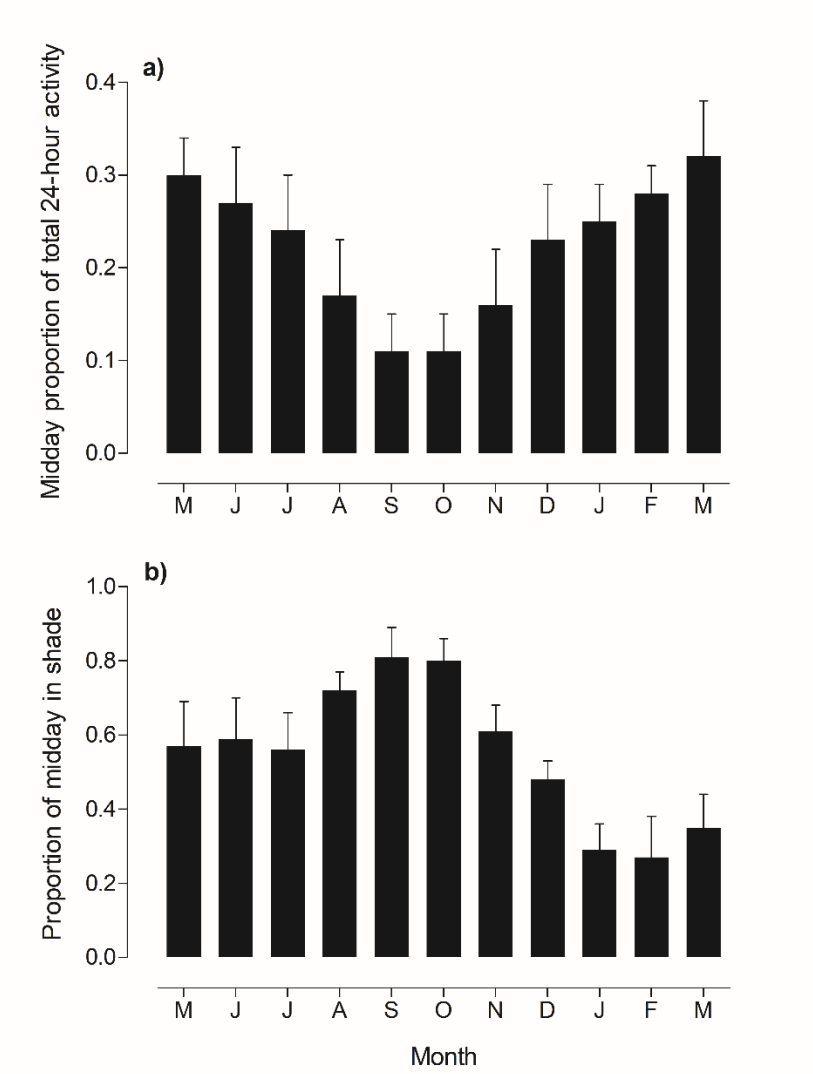

Figure 4.4. a) The average (mean ±SD) midday proportion (11:00 – 16:00) of total 24-hour activity of 10 free-ranging female sable antelopes in Bwabwata National Park, Namibia, from May 2016 – March 2017, and b) the average (mean ±SD) proportion of midday spent in the shade by 10 free-ranging female sable antelopes from May 2016 to March 2017.

Table 4.2. Mixed model results for the relationship between a) the proportion of time sable antelope spent in the shade during the heat of the day (11:00 – 16:00), b) the quality of the microclimate selected by sable antelope during the heat of the day and c) the proportion of midday activity of sable antelope in relation to the proportion of time spent in the shade and prevailing environmental conditions in Bwabwata National Park, Namibia. The quality of the microclimate selection was calculated by subtracting the reference miniglobe temperature from the collar miniglobe temperature, where more negative differences indicated cooler/better-quality microclimates.

Binomial generalised linear mixed model	β ± s.e.	*z*	*p*
a) Proportion of time spent in shade			
Proportion of brown vegetation exposure	1.33 ± 0.04	37.69	< 0.0001
Maximum 24-hour black globe temperature	0.09 ± 0.003	25.71	< 0.0001
Linear mixed model	β ± s.e.	*t*	*p*
b) Quality of microclimate selected			
Proportion of brown vegetation exposure	-1.31 ± 0.12	-10.63	< 0.0001
Maximum 24-hour black globe temperature	-0.13 ± 0.01	-12.73	< 0.0001
Beta generalised linear mixed model	β ± s.e.	*z*	*p*
c) 24-hour proportion of midday activity			
Proportion of brown vegetation exposure	-0.56 ± 0.04	-15.83	< 0.0001
Mean 24-hour black globe temperature	-0.04 ± 0.003	-14.15	< 0.0001
Proportion of time spent in shade	-0.29 ± 0.06	-5.16	< 0.0001

Models: a) proportion of midday spent in shade ~ proportion of brown vegetation exposure + maximum 24-hour black globe temperature + (1 | individual identity) + (1 | OLRE), n = 10, N = 3023. An observation level random effect (OLRE) was included in the model to correct for overdispersion; b) quality of midday microclimate selected ~ proportion of brown vegetation exposure + maximum 24-hour black globe temperature + (1 | individual identity), n = 10, N = 3168; c) 24-hour proportion of midday activity ~ proportion of brown vegetation exposure + mean 24-hour black globe temperature + proportion of midday spent in shade + (1 | individual identity), n = 10, N = 2616. Individual identity was included as a random factor in all models.

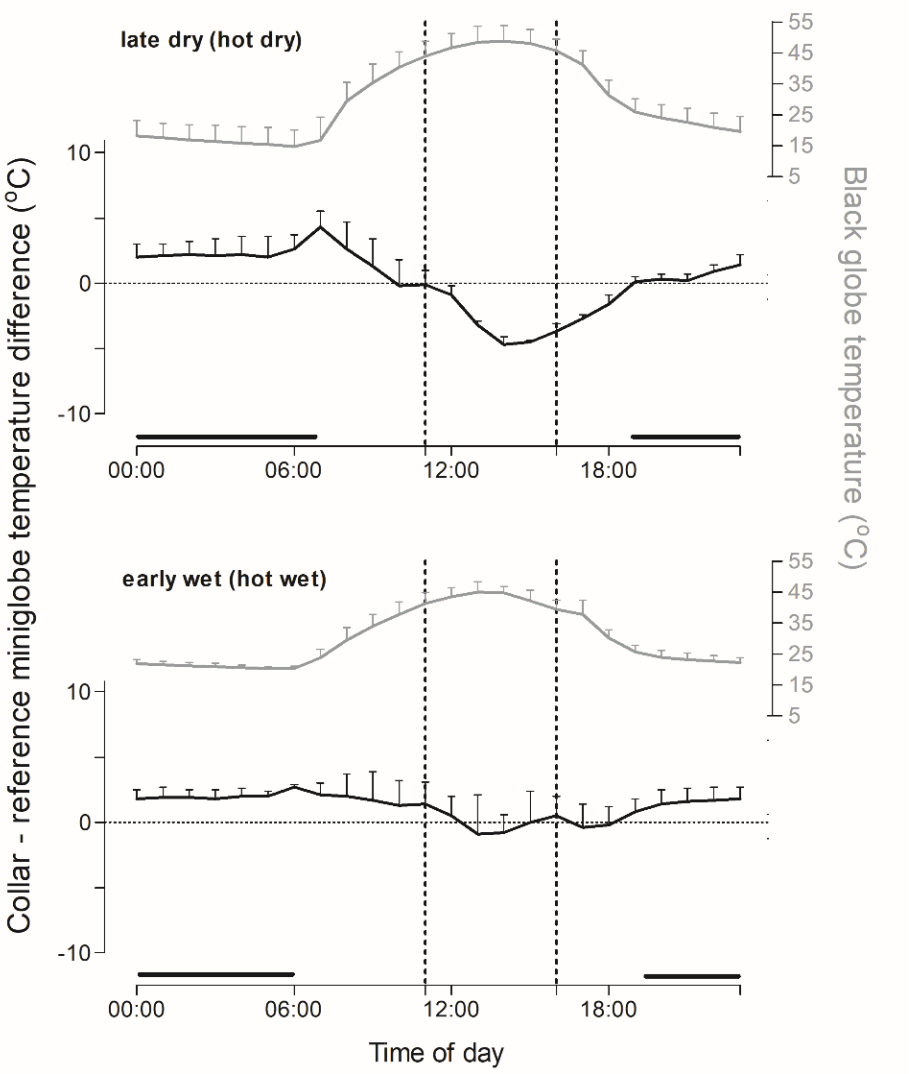

Figure 4.5. The average (mean ±SD) quality of microclimate selected by 10 female sable antelopes during the hot, late dry season (August – October 2016) and the hot, early wet season (November 2016 – January 2017) in Bwabwata National Park, Namibia. Quality of microclimate is expressed as the minimum temperature difference between the miniglobe on the collar of the animal and the reference miniglobe on site, where temperature differences <0 indicate the selection of cool microclimates, with more negative values representing better quality shade.

4.4 Discussion

In this chapter, I investigated the behavioural flexibility of sable antelope in response to resource limitations under high heat load by evaluating the compounding effects of spatiotemporal changes in vegetation greenness and temporal variation in heat load on the activity patterns and microclimate selection of sable antelope. My results show that spatial and temporal variations in vegetation greenness and environmental heat load are significant drivers of adjustments in activity patterns and microclimate selection in sable antelope. Under increasingly hot and dry conditions, typical of the late dry season, sable antelope not only selected increasingly cooler microclimates during the midday heat but spent an increasing proportion of time in these cooler shaded areas, likely to conserve body water during a hot, water-limited period. This increased duration of shade-seeking also coincided with a substantial reduction in activity during the heat of the day. While high thermal load constrained diurnal activity when resources were most limited, sable antelope increased their nocturnal activity under hot and dry conditions. However, sable antelope displayed an overall reduction in total 24-hour activity when conditions were hot and dry, implying that they could not completely compensate for reduced diurnal activity by increasing their nocturnal activity.

While the premature failure of the collars reduced the sample size in the second year of my study, the current data set provides the most comprehensive assessment of sable antelope activity, at a finer resolution (10-minute intervals) than has been achieved previously through hourly GPS locations (Owen-Smith and Goodall, 2014). Although my analysis of microclimate selection was limited to the first year of my study, due to technical complications with the reference miniglobes, my study provides the first quantification of microclimate selection and shade use in sable antelope.

Sable antelopes in my study decreased their midday activity and sought microclimates that were up to 12.9 ^{o}C cooler than the surrounding open environment in response to high heat loads and reduced vegetation greenness. Sable antelope favour woodland habitats (Macandza et al., 2012a) with high tree cover (Asner et al., 2015; Le Roux, 2010) which not only enhances their access to beneath-canopy grass with high nutrient content (Treydte et al., 2008) but may also reduce their exposure to high heat loads during the heat of the day. Similar patterns of shade-seeking have been quantified in other ungulates (e.g. blue wildebeest and impala *Aepyceros melampus* (Hetem et al., 2007), and the greater kudu (Hetem et al., 2008)). Similar to the sable antelope in my study, blue wildebeest and gemsbok in the semi-arid Kalahari (Boyers et al., 2021, 2019), and Arabian sand gazelle (Hetem et al., 2012a) and Arabian oryx (Hetem et al., 2012b) in the more extreme Arabian desert, enhanced both the quality and frequency of time spent shade-seeking during water-limited dry periods, with Arabian oryx selecting microclimates up to 12 ^{o}C cooler than the open desert environment and blue wildebeest and gemsbok selecting microclimates ~10 ^{o}C cooler than in the Kalahari sun. Increased shade-seeking would reduce the heat loads experienced, thereby reducing evaporative cooling requirements and saving body water in hot and dry conditions (Cain et al., 2006; Fuller et al., 2016), but it may come at a cost of reduced diurnal activity (Hetem et al., 2014).

Indeed, the sable antelopes in my study displayed decreased diurnal activity in response to high heat loads and reduced vegetation greenness. My results however contradict previous studies in which sable antelope increased time spent foraging, quantified through traditional diurnal behavioural observations (Grobler, 1981a) and foraging activity assessed through GPS-derived activity states (Owen-Smith and Goodall, 2014), during the dry season compared to the wet season. In both these studies, sable antelope displayed increased foraging around midday in the hot, late dry season, which may have been associated with

daily drinking (Grobler, 1981a). Unlike the sable antelopes in my study, these sable antelopes were drinking water daily (Grobler, 1981a) or every 2-4 days (Owen-Smith and Goodall, 2014) during the late dry season. Greater access to water might have allowed a greater reliance on evaporative cooling to mitigate heat stress and enabled sable antelopes in Rhodes Matopos National Park, Zimbabwe (Grobler, 1981a) and Kruger National Park, South Africa (Owen-Smith and Goodall, 2014) to be active throughout the heat of the day. However, in more water-limited regions, like Bwabwata National Park, sable antelope may be forced to seek shade and reduce diurnal activity, particularly during the heat of the day, to conserve body water during the late dry season.

Sable antelopes in my study attempted to compensate for the reduced diurnal activity by increasing their nocturnal activity in response to high heat loads and low exposure to green vegetation. Similarly, sable antelope in the arid northern region of Kruger National Park displayed increased GPS movement rates and a greater shift to nocturnal activity in the late dry season than those inhabiting the more mesic southern region (Owen-Smith and Goodall, 2014). With activity biologgers allowing for continuous quantification of 24-hour activity, a number of studies have shown increased nocturnal activity of ungulates when conditions are hot and dry (Berry et al., 2023; Boyers et al., 2021, 2019; Shrestha et al., 2014). In more extreme environments, such as the Arabian Desert, Arabian sand gazelle and Arabian oryx shifted to being completely nocturnal (Hetem et al., 2012b, 2012a) during hot and dry conditions. The switch to nocturnal activity in Arabian ungulates allowed them to completely compensate for reduced diurnal activity, such that their total 24-hour activity did not change seasonally (Hetem et al., 2012a). While there were no predators in the Arabian Desert to limit shifts in the timing of activity, in African ecosystems, high predation pressures at night may increase risks associated with increased nocturnal activity (Owen-Smith, 2019). In the arid Etosha National Park in Namibia, kudu displayed little difference in both total 24-hour

activity and the timing of activity between hot and cool days during the late dry season, whereas larger eland (with few predators) increased their nocturnal activity on hot days while maintaining total 24-hour activity (Berry et al., 2023). In the Kalahari, gemsbok maintained total 24-hour activity during the hot dry season but became proportionately more active at night, while wildebeest (highly susceptible to predation) showed little change in the timing of activity but total 24-hour activity decreased (Boyers et al., 2019). Despite an increase in nocturnal activity, sable antelopes in my study were not able to completely compensate for the reduced diurnal activity when conditions were hot and dry, as highlighted by the reduction in total 24-hour activity. Sable antelope are sensitive to predation (Owen-Smith et al., 2012a; Owen-Smith and Mills, 2006) which may have limited sufficient large temporal shifts in activity by the sable antelopes in my study.

The 24-hour activity data presented in this chapter provided an integrated measure of whole-body movement and did not differentiate between non-foraging movement states and foraging movement states. Yet, the reduction in total 24-hour activity in the late dry season occurred at a time when relocating movement was highest (see Chapter 3). The increased nocturnal activity of sable antelopes in my study may have been associated with increased travel to water, like sable antelope in Kruger National Park which often initiated movements to water before sunrise with sable antelope returning to their home ranges after sunset (Cain et al., 2012). If the increased nocturnal activity of sable antelope in my study was associated with increased travel to water, their foraging time would have been further compromised. Indeed, sable antelopes in my study displayed a reduction in foraging movements during the dry season (Chapter 3). This reduction in total 24-hour activity may highlight the degree of resource scarcity and thermal stress faced by these sable antelopes in Bwabwata National Park i.e., unnecessary expenditure of energy to increase activity in search of food for little reward when energy is needed to travel long distances to drink water. Indeed, during a

drought year in the Kalahari, blue wildebeest increased their travel to water but reduced their total 24-hour activity potentially conserving energy during a period of extreme aridity when the quality and quantity of vegetation was poor (Boyers et al., 2021).

While sable antelopes displayed flexibility in their behavioural responses to dry season stressors, whether these behavioural adjustments buffer the restricted resource availability requires a physiological measure of performance or well-being. Rising temperatures and increasingly unpredictable rainfall may result in longer and more extreme dry seasons. My findings highlight the challenges presented by resource scarcity under high heat load for a water-dependent, specialist grazer, particularly, the anticipated conflict between resource acquisition and thermal refuge, which will worsen in hotter and drier conditions.

CHAPTER 5

Feeling the heat: changes in movement and body temperature regulation in a resource-stressed specialist antelope.

5.1 Introduction

Warm and dry regions of southern Africa are warming at approximately double the average global rate (IPCC, 2023). A warming climate is particularly concerning for large, free-living ungulates because of the direct effects of heat on physiological performance and the indirect effects of heat and aridity on resource availability (Hetem et al., 2014). African savannas are already highly seasonal environments where dry periods of reduced resource availability are compounded by thermal extremes (du Toit et al., 2003). The dry season generally occurs during the cool winter months; however, reduced precipitation and increased transpiration are extending the dry season, increasingly exposing ungulates to high ambient temperatures combined with food and water shortages. The predicted increase in the duration and intensity of dry seasons therefore threatens the persistence of large African ungulates. If ungulates are to survive a hotter and drier future, they may need to rely on phenotypic flexibility, that is, their behavioural and physiological capacity to buffer the consequences of climate change (Boutin and Lane, 2014; Fuller et al., 2016, 2010; Hetem et al., 2014). Behavioural changes are often the first response to changes in environmental conditions. However, it is uncertain whether behavioural flexibility can completely buffer the impact of the anticipated increased thermal, water and energy stress. If the environmental change is sufficiently extreme or rapid, as predicted for climate change, ungulates may need to adjust their physiology, but that may come at a cost of energy and water.

Concurrently assessing behavioural and physiological responses gives insight into the capacity of behavioural flexibility to buffer environmental changes. Biologging body temperature provides a remote and continuous measurement of physiological well-being in free-living ungulates (Fuller et al., 2016; Hetem et al., 2016). Free-living ungulates with an adequate supply of food and water appear to maintain their body temperature within a narrow

range (i.e. homeothermy, Hetem et al., 2016). Fluctuations in the core body temperature (i.e. heterothermy) are a good indication of the physiological impact of changes in resource availability and thermal load, enabling the identification of periods when behavioural adjustments are unable to buffer energy and water stress (Botha et al., 2023; Boyers et al., 2019; Hetem et al., 2016, 2012a, 2010; Ostrowski et al., 2003).

Maintaining homeothermy has an energetic cost, particularly when ambient temperatures are low (Tattersall et al., 2012). Using metabolic heat production to keep warm requires adequate food energy, which becomes increasingly difficult to obtain during the dry season when forage available for ungulates is low. An energy deficit because of a reduction in food quality or intake may manifest as a reduction in minimum 24-hour body temperature as has been shown in experimental manipulations with sheep *Ovis aries* (Maloney et al., 2013). Similar reductions in body temperature have been observed in free-living northern hemisphere ungulates, such as red deer *Cervus elaphus* (Turbill et al., 2011), and free-living Arabian ungulates, including Arabian oryx *Oryx leucoryx* and Arabian sand gazelle *Gazella subgutturosa marica* (Hetem et al., 2012a), and free-living African ungulates, such as Cape buffalo *Syncerus caffer caffer* (Botha et al., 2023), blue wildebeest *Connochaetes taurinus* (Boyers et al., 2019; Shrestha et al., 2012) and gemsbok *Oryx gazella gazella* (Boyers et al., 2019).

Maintaining homeothermy also costs body water. When ambient temperatures rise above core body temperature, evaporative cooling such as panting and sweating, is the only way ungulates can dissipate heat gained from the environment and metabolic activity (Tattersall et al., 2012). However, evaporative cooling may be limited when an individual is faced with high air temperatures and concurrent water shortages. When evaporative cooling is limited, maximum 24-hour body temperatures increase. The elevation of maximum 24-hour body temperature during periods of water scarcity and high heat load has been shown in

experimental manipulations with desert ungulates, including dromedary camel *Camelus dromedarius* (Schmidt-Nielsen et al., 1956), Grant's gazelle *Gazella granti* and oryx *Oryx beisa* (Taylor, 1970), and non-desert ungulates such as Thompson's gazelle *Gazella thomsonii*, blue wildebeest, zebu steer *Bos indicus* and African buffalo *Syncerus caffer* (Taylor, 1970), eland *Taurotragus oryx* and hartebeest *Alcelaphus buselaphus cokii* (Finch and Robertshaw, 1979), as well as in free-living Arabian oryx (Hetem et al., 2010; Ostrowski et al., 2003) and Arabian sand gazelle (Hetem et al., 2012a; Ostrowski and Williams, 2006) in the Arabian Desert. Although dehydration hyperthermia has only been shown in free-living ungulates in extreme desert conditions, these aforementioned experimental manipulations conducted with non-desert ungulates show that dehydration hyperthermia may represent water stress, rather than just being an adaptation to desert environments (Mitchell et al., 2002). As conditions become hotter and drier across water-limited systems, such as arid and semi-arid savannas, African ungulates will likely experience water stress, particularly species with higher water dependency.

The sable antelope in my study likely experienced thermal and resource stress based on their behavioural adjustments during the hot, late dry season (Chapters 3 and 4). In response to increasingly hotter and drier conditions, sable antelopes spent more time travelling to water at the expense of time spent foraging (Chapter 3), decreased total 24-hour activity, became proportionately more active at night and enhanced both the quality and frequency of time spent shade-seeking during the heat of the day (Chapter 4). Simultaneously monitoring changes in the behaviour and body temperature of these sable antelope can provide insight into these observed trade-offs and inform us about the capacity of their behavioural adjustments to buffer the physiological consequences of high heat load and resource stress.

In this chapter I set out to, i) explore perturbations to the 24-hour body temperature rhythm of sable antelopes, ii) assess 24-hour body temperature in relation to vegetation greenness and

environmental heat load, and iii) investigate the association between body temperature and movements to water during the late dry season. I expected sable antelopes to display lower minimum 24-hour body temperatures when exposed to browning vegetation and low heat loads. I expected the maximum 24-hour body temperature of sable antelopes to be highest when exposed to brown vegetation and high heat loads. Furthermore, I expected high maximum 24-hour body temperatures to be related to movements to water during the hot, late dry season.

5.2 Data and analysis

As detailed in Chapter 2, I collared 10 free-living female sable antelope and implanted each with a body temperature logger which recorded core body temperature every 10 minutes from May 2016 until April 2018. I could not retrieve two of the body temperature loggers because of premature battery failure of the GPS and VHF units on the collars (see Chapter 2). The lifespan of the remaining eight body temperature loggers was 24 months for six individuals, 23 months for one individual and 17 months for one individual.

To link measures of body temperature to vegetation greenness variation in time and space, I extracted the relative greenness category (see Chapter 2 for details) of each pixel associated with each GPS location recorded over the study period to calculate the proportion of brown vegetation exposure per individual, for every 24-hour cycle (sunrise to consecutive sunrise) between May 2016 and April 2018. Mean and maximum 24-hour black globe temperature was calculated for every 24-hour cycle (sunrise to consecutive sunrise) between May 2016 and April 2018 (as per Chapter 2).

Body temperature rhythm and parameters

To describe perturbations to the 24-hour body temperature rhythm of sable antelopes, I plotted the raw 10-minute data of each individual from May 2016 –to April 2018. Fevers, defined as a 24-hour mean body temperature >0.5 ^{o}C above normal lasting for two or more consecutive days (Kamerman et al., 2001), were removed from the dataset. I calculated the maximum and minimum body temperature of each sable antelope (n=8) for successive 24-hour days (i.e. the 24 hours between consecutive sunrise times) from May 2016 to April 2018.

Body temperature parameters in response to vegetation greenness and heat load

To assess variation in the 24-hour body temperature rhythm of sable antelope in response to variation in prevailing environmental conditions, maximum 24-hour body temperature and minimum 24-hour body temperature (response variables) were related to variation in mean 24-hour black globe temperature and the proportion of brown vegetation exposure (predictor variables) in a series of LMMs. For illustrative purposes, I plotted the mean 24-hour body temperature rhythm of all eight sable antelopes over four seasonal periods, namely early dry (May – July), late dry (August – October), early wet (November – January) and late wet (February – April), for the first year of the study (May 2017 – April 2018; see Appendix 5 for year 2). Seasons were defined using monthly changes in rainfall, 24-hour black globe temperature and the proportion of brown vegetation exposure (as per Chapter 3).

Maximum 24-hour body temperature and movement to water

To explore the relationship between the maximum 24-hour body temperature of sable antelopes and their movement to water, I used the relocating behavioural state identified with Hidden Markov Models to identify the proportion of time sable antelope spent in the relocating state per day, likely reflecting travel to water (as per Chapter 3). To test whether sable antelopes were more likely to travel to water when maximum 24-hour body temperature was high (indicative of dehydration-induced hyperthermia), I ran a GLMM with a binomial error distribution and logit link function to assess the relationship between the proportion of time spent travelling to water (response variable) and the maximum 24-hour body temperature of sable antelope the previous day (predictor variable). To test whether sable antelope maximum body temperatures decreased following a directed movement to water, I ran a LMM to relate the maximum 24-hour body temperature of sable antelope (response variable), to the proportion of time spent travelling to water the previous day (predictor variable).

All mixed models were fitted using the package lme4 (Bates et al., 2015) in R (R Core Team, 2023). The identity of individual sable antelope was included as a random effect in all the mixed models. An observation level random effect (OLRE) was included in the binomial GLMM to account for the presence of overdispersion (Harrison, 2015). I used Akaike's Information Criterion corrected for small sample size (AICc) to identify which mixed models supported the data best (Burnham et al., 2011), using the R package AICcmodavg (Mazerolle, 2023) (see Appendix 6). All models were validated by assessing mixed model fit in terms of assumptions of normality, homogeneity of variance and independence using the R package DHARMa (Hartig, 2017).

5.3 Results

Fluctuations in 24-hour body temperature increased during the dry season (May – October). This increased amplitude was initially linked to a reduction in minimum 24-hour body temperature when low ambient temperature was coupled with brown vegetation (Figure 5.1). As black globe temperatures increased toward the end of the dry season (Figure 5.1), maximum 24-hour body temperature also increased. Following the commencement of the wet season, the body temperature rhythm narrowed (i.e. the amplitude decreased) as minimum body temperatures increased, and maximum body temperatures decreased (Figure 5.2). While all individuals displayed larger fluctuations in 24-hour body temperature during the dry season, the magnitude of these fluctuations varied among individuals, as shown in Figure 5.2. For example, one female (Figure 5.2a) consistently maintained a narrower rhythm of body temperature (average amplitude of body temperature rhythm – dry period: 2.4 ± 0.3 ^{o}C; wet period: 1.9 ± 0.1 ^{o}C), while another female (Figure 5.2b) displayed wider fluctuations in body temperature (average amplitude of body temperature rhythm – dry period: 3.3 ± 0.2 ^{o}C; wet period: 2.8 ± 0.1 ^{o}C). On occasion, females displayed minimum body temperatures below 36 ^{o}C, maximum body temperatures above 40 ^{o}C, with maximum amplitudes of body temperature rhythm of >5 ^{o}C within a single day during the late dry season (August – October) (Figure 5.2).

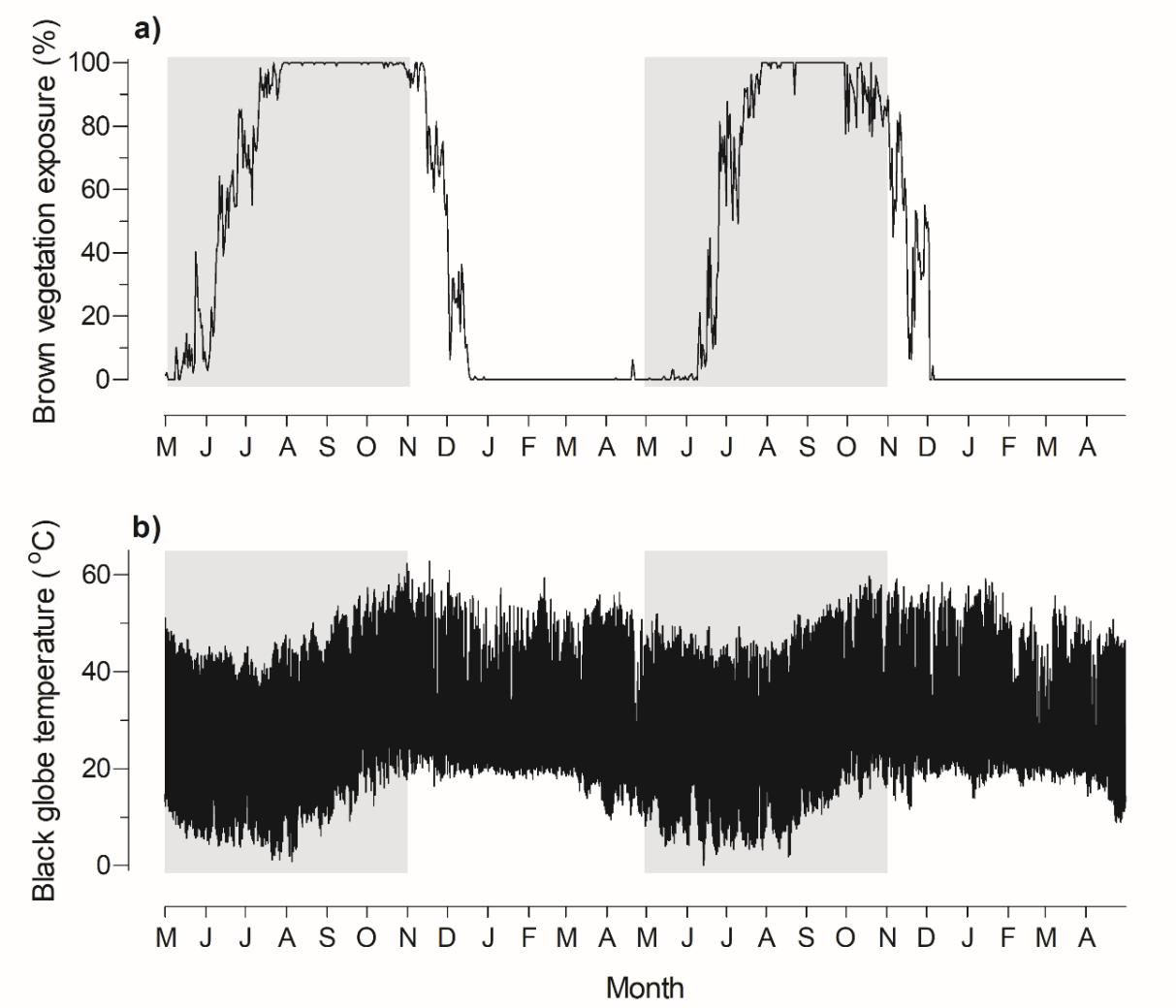

Figure 5.1. a) The average 24-hour exposure to brown vegetation encountered by eight free-living female sable antelopes in Bwabwata National Park, Namibia, and b) the hourly environmental black globe (150mm) temperature over 24 months (May 2016 – April 2018).

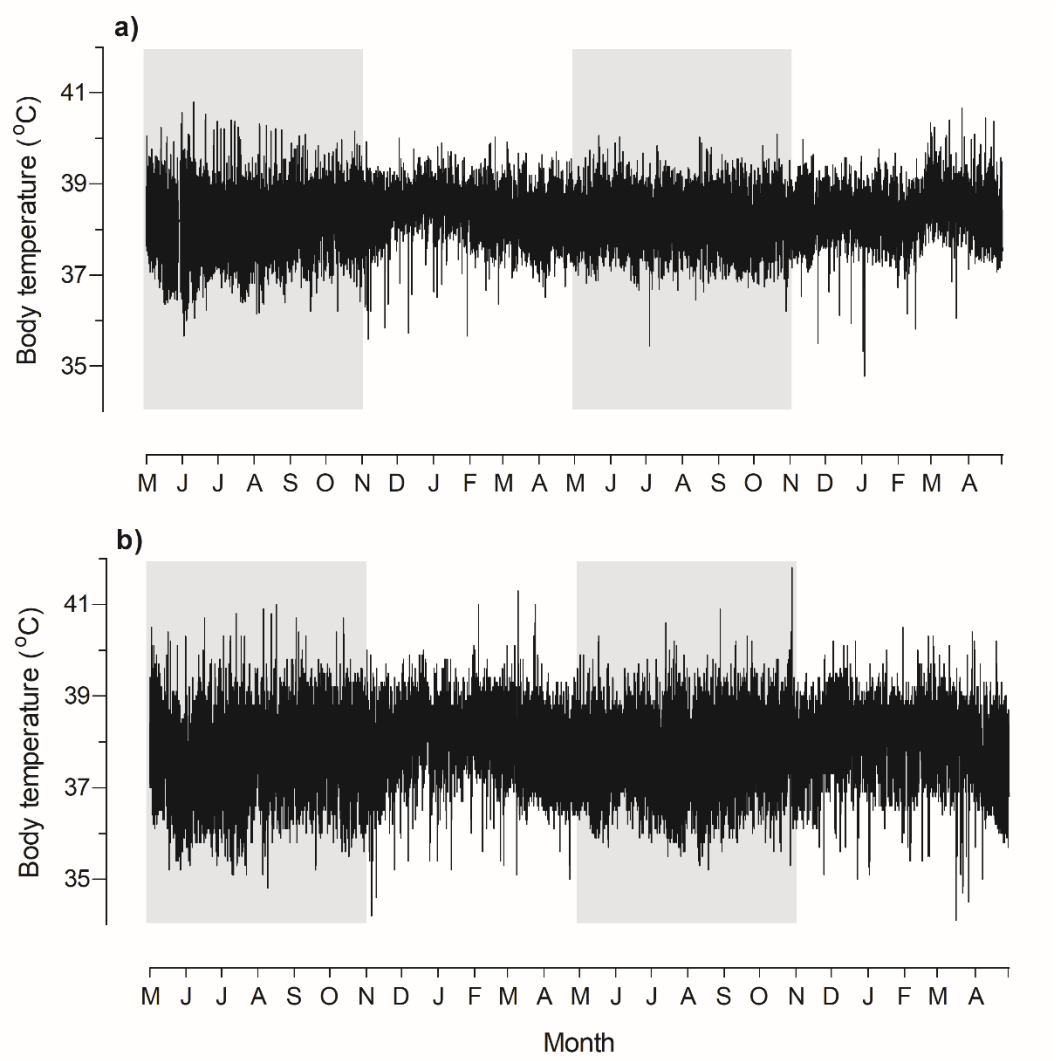

Figure 5.2. The original 10-minute body temperature recordings of two representative free-living female sable antelopes over 24 months (May 2016 – April 2018) in Bwabwata National Park, Namibia. The grey-shaded panels highlight the dry period (May – October). Note the variability in body temperature amplitude between individuals.

To highlight the changes in 24-hour body temperature, I plotted the average 24-hour body temperature rhythm (Figure 5.3) across the four seasonal periods (defined in Chapter 3) during the first year of the study (May 2016 – April 2017). Similar patterns were evident in the average 24-hour body temperature rhythm in the second year of the study (see Appendix 5). A decrease in minimum 24-hour body temperature (37.0 ± 0.2 ^{o}C), was evident during the early dry season when low black globe temperatures were coupled with reduced resource availability. A rise in maximum 24-hour body temperature (39.1 ± 0.1 ^{o}C), was also evident

during the late dry season when high black globe temperatures were coupled with resource scarcity. When resources were available during the early and late wet seasons, the 24-hour body temperature rhythm narrowed. Resultantly, amplitudes in body temperature were, on average, twice as large during the dry seasonal periods compared to the wet seasonal periods.

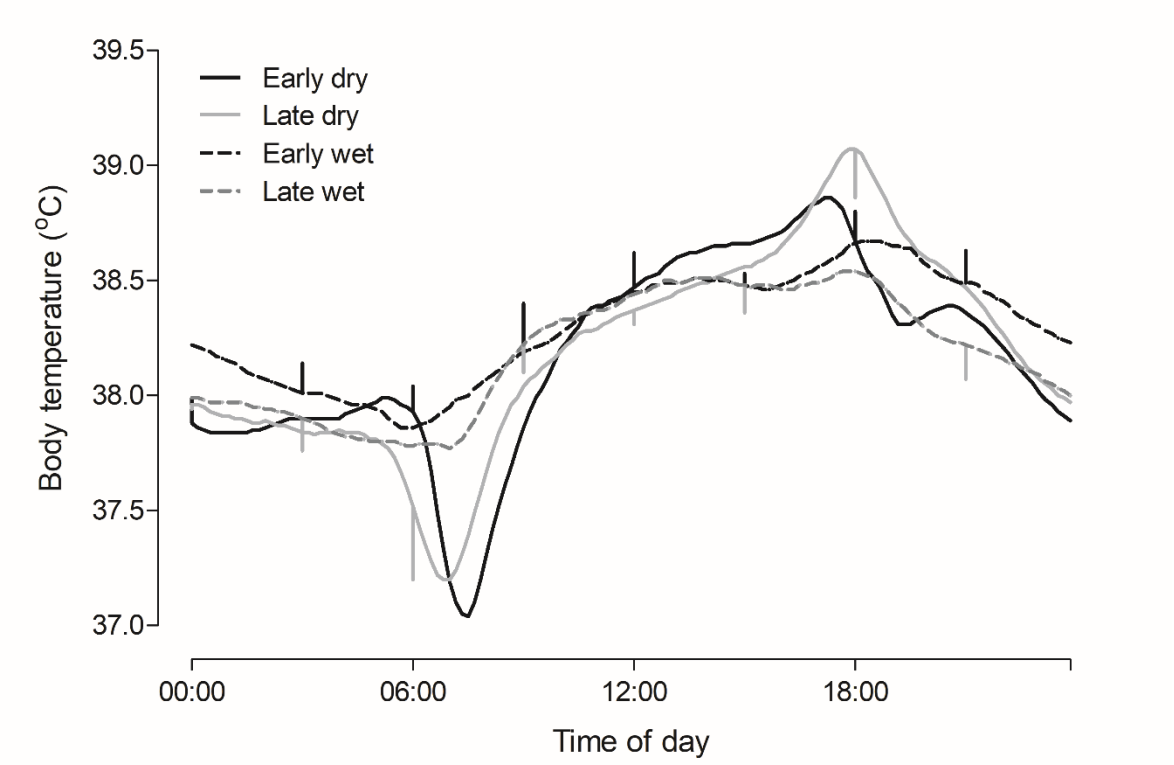

Figure 5.3. The mean **(**± SD) 24-hour body temperature rhythm of eight free-living female sable antelopes in Bwabwata National Park, Namibia, over four seasonal periods occurring between May 2016 and April 2017.

To test for the drivers of these changes in body temperature, I ran a series of LMMs relating minimum and maximum 24-hour body temperature to brown vegetation exposure and black globe temperature. Low minimum 24-hour body temperatures were associated with low mean 24-hour black globe temperature and increased exposure to brown vegetation (Table 5.1a). High maximum 24-hour body temperatures were associated with high mean 24-hour black globe temperature and increased exposure to brown vegetation (Table 5.1b).

Table 5.1. Linear mixed-effects model results for the association between a) the minimum 24-hour body temperature of sable antelopes and b) the maximum 24-hour body temperature of sable antelopes, and prevailing environmental variables, namely the proportion of brown vegetation exposure per individual and mean 24-hour black globe temperature in Bwabwata National Park, Namibia, from May 2016 to April 2018.

Linear mixed model	β ± s.e.	*t*	*P*
a) Minimum 24-hour body temperature (°C)			
Proportion of brown vegetation exposure	-0.38 ± 0.01	-27.09	< 0.0001
Mean 24-hour black globe temperature	0.03 ± 0.001	18.55	< 0.0001
b) Maximum 24-hour body temperature (°C)			
Proportion of brown vegetation exposure	0.11 ± 0.01	8.63	< 0.0001
Maximum 24-hour black globe temperature	0.007 ± 0.001	6.57	< 0.0001

*Individual identity was included as a random factor. Models: a) minimum 24-hour body temperature ~ proportion of brown vegetation exposure + mean 24-hour black globe temperature + (1 | individual identity), n = 8, N = 4109 and b) maximum 24-hour body temperature ~ proportion of brown vegetation exposure + maximum 24-hour black globe temperature + (1 | individual identity), n = 8, N = 4109.

In the late dry season, as ambient black globe temperate started to increase, some sable antelope travelled 13-30 kms, every 4-5 days to access water from the Kavango River (see Chapter 3). The proportion of time spent travelling to water (identified from the relocating behavioural state calculated in Chapter 3) was associated with the maximum 24-hour body temperature experienced the previous day (Table 5.2a), implying that if sable antelope were dehydrated (indicated by a high maximum 24-hour body temperature), they were more likely to travel to water. Following days on which sable antelopes spent more time in the relocating behavioural state, likely reflecting a trip to the Kavango River (see Figure 3.1, Chapter 3), maximum 24-hour body temperatures decreased (Table 5.2b). This pattern of a progressive increase in maximum 24-hour body temperature before a possible journey to the Kavango River and lowering of maximum 24-hour body temperature following a journey to water is visualized in the 52-day time series plot (Figure 5.4) showing changes in maximum 24-hour

body temperature relative to the proportion of time spent in the relocating state per day during the late dry season for a representative individual.

Table 5.2. a) Binomial generalised linear mixed-effects model results for the association between the proportion of time sable antelopes spent travelling to water and their maximum 24-hour body temperature the previous day, and b) linear mixed-effects model results for the association between the maximum 24-hour body temperature of sable antelopes and the proportion of time spent travelling to water the previous day, in Bwabwata National Park, Namibia, from May 2016 to April 2018.

Binomial generalised linear mixed model	β ± s.e.	z	*P*
a) Proportion of time spent travelling to water			
Maximum 24-hour body temperature the previous day	0.47 ± 0.18	2.64	0.0084
Linear mixed model	β ± s.e.	t	*P*
b) Maximum 24-hour body temperature			
Proportion of time spent travelling to water the previous day	-0.15 ± 0.05	-2.83	0.0046

*Day was defined as the 24-hour period between consecutive sunrises. Individual identity was included as a random factor. An observation level random effect (OLRE) was included to correct for overdispersion present in the binomial GLMM. Models: a) maximum 24-hour body temperature ~ proportion of time spent travelling to water the previous solar day + (1 | individual identity), n = 7, N = 3559 and b) proportion of time spent travelling to water ~ maximum 24-hour body temperature the previous solar day + (1 | individual identity) + (1 | OLRE), n = 7, N = 3553.

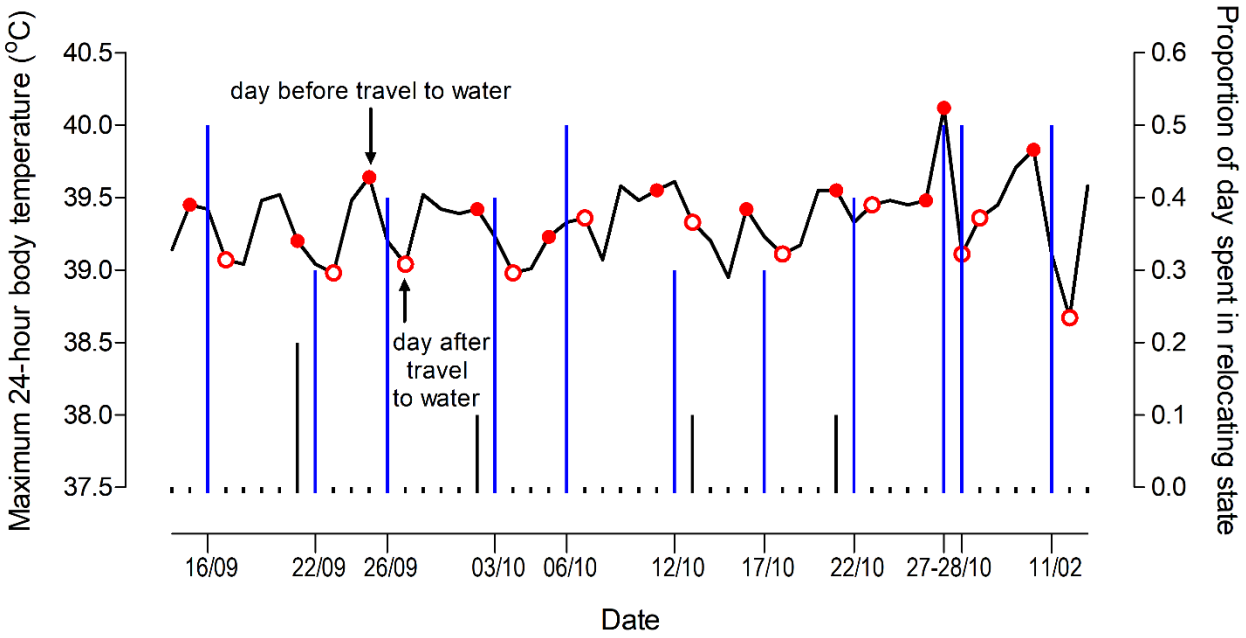

Figure 5.4. The maximum 24-hour body temperature recordings (black trendline) of a representative free-living female sable antelope in Bwabwata National Park, Namibia, and the daily proportion of time spent in a relocating behavioural state (vertical bars). This 52-day time series from the late dry season in 2016 shows the maximum 24-hour body temperature the day before (solid red dot) and the day after (open red dot) the individual travelled to the Kavango River (dated, blue vertical bars). On occasion, the sable antelope may have started the relocation the day prior or continued the subsequent day (highlighted by the black vertical bars). This individual travelled a round-trip distance of ~25 kms every 4-5 days, presumably to access a scarce resource (water) during the late dry season.

On occasion, there were perturbations in the body temperature rhythm of some sable antelope that were unrelated to vegetation greenness, black globe temperatures, or movements to water; but possibly related to pregnancy and lactation. In four of the female sable antelopes (two in 2017 and 2018 and two only in 2018), there was a notable decline in the body temperature rhythm in January/February (possibly gestational hypothermia) followed by an abrupt increase in the body temperature rhythm in February/March (potential birth event), whereafter the body temperature rhythm narrowed and increased for approximately six to eight weeks (possibly related to lactation) (Figure 5.5).

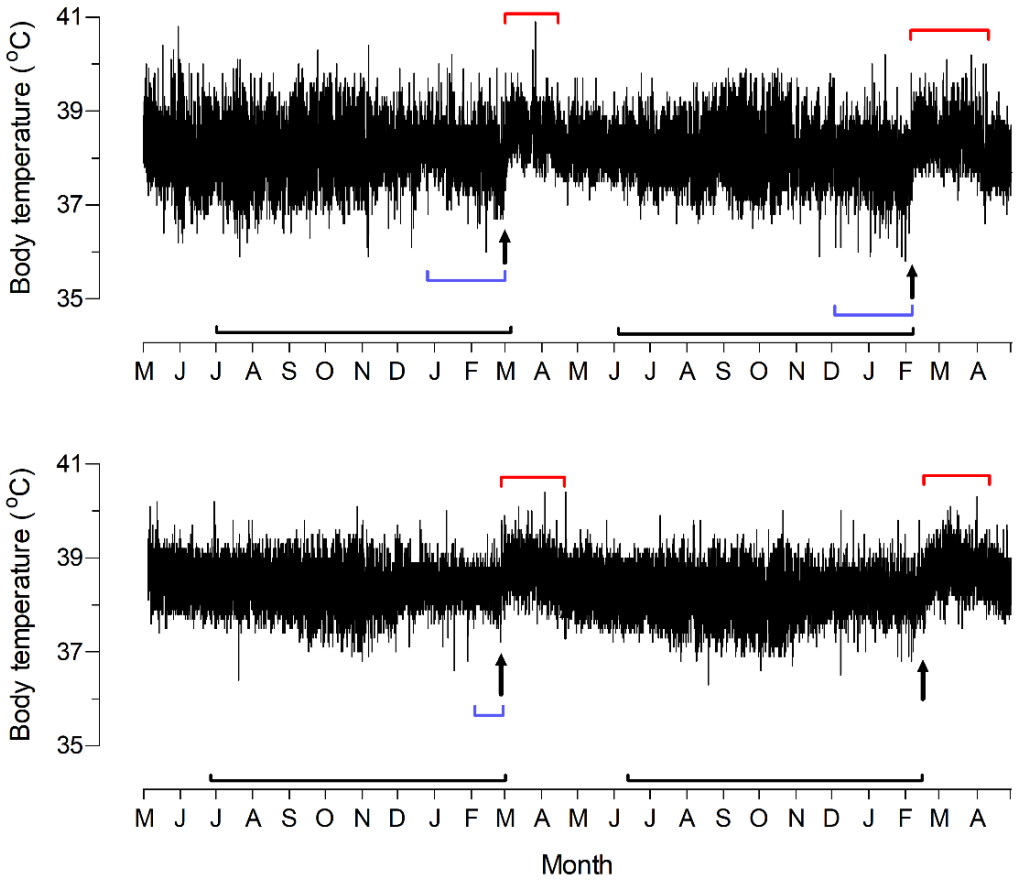

Figure 5.5. The original 10-minute body temperature recordings of two free-living female sable antelope over 24 months (May 2016 – April 2018) in Bwabwata National Park, Namibia, showing perturbations in body temperature regulation possibly related to pregnancy and lactation. The horizontal black lines show the estimated gestation period which generally spans 8–9 months with calving occurring at the end of the rainy season, February to March. The black arrows indicate the approximate time of assumed parturition (birth event). The horizontal blue lines show a progressive decline in body temperature towards the end of gestation, typically associated with gestational hypothermia. The horizontal red lines show an elevation and narrowing of body temperature following parturition, potentially related to lactation.

5.4 Discussion

In this chapter, I integrated a physiological response (body temperature) to enhance my interpretation of behavioural observations from the previous chapters to investigate whether sable antelopes were physiologically stressed during the dry season despite displaying behavioural flexibility to try to meet resource requirements under thermal constraints. When food and water were not limited during the wet season, sable antelopes maintained narrow body temperature rhythms (i.e. homeothermy) despite black globe temperatures frequently exceeding 50 ^{o}C and dropping below 10 ^{o}C. However, when low black globe temperatures were compounded by increased exposure to brown vegetation, sable antelopes exhibited a lowering of minimum 24-hour body temperature, likely reflecting energy deprivation. As the dry season progressed and black globe temperatures increased, maximum 24-hour body temperature was elevated, reaching 40.8^{o}C on one occasion. High maximum body temperatures, potentially indicative of dehydration-induced hyperthermia, increased the likelihood of long, directed movements to water, which were associated with a subsequent decline in maximum 24-hour body temperatures.

While I did not directly measure hydration state or energy expenditure in the field (techniques that until recently have remained elusive for field biologists e.g., stable isotope analysis, heart rate loggers and fine-scale accelerometery), I was able to quantify body temperature fluctuations (high and low) in response to environmental heat load and landscape features experienced by individual antelope (i.e. vegetation greenness and a water resource), allowing me to better account for individual variability in responses than simply investigating seasonal responses. Only one other study has linked vegetation greenness experienced by free-living individual ungulates to low minimum body temperatures during the resource-poor dry season (Boyers, 2018).

During cold and resource-poor winters, a reduction in minimum body temperature associated with reduced energy expenditure (as indexed by heart rate) is frequently observed in temperate ungulates such as moose *Alces alces* (Græsli et al., 2020), red deer (Arnold et al., 2004), Przewalski horse (Arnold et al., 2006), and Alpine ibex *Capra ibex ibex* (Signer et al., 2011) as an endogenous response to annual seasonal change where individuals are exposed to freezing temperatures and food resources buried under snow in winter. Most of these studies hypothesised the reduction in body temperature to be an endogenous physiological mechanism employed to reduce energy expenditure by reducing heart rate (hypometabolism) to cope with limited energy supplies in colder climates. However, following food restriction experiments with red deer during winter, Turbill et al. (2011) suggested that energy limitation was rather the main driver of a reduction in body temperature, and hence hypometabolism.

Indeed, the lowering of minimum body temperature during seasonally dry periods when food resources are usually limited has been observed in free-living ungulates inhabiting warmer climates (Boyers et al., 2019; Hetem et al., 2012a, 2010; Shrestha et al., 2012). In these cases, the lowering of minimum body temperature was suggested to be the consequence of energy deprivation whereby ungulates lacked sufficient energy to maintain body temperature (Hetem et al., 2016; Turbill et al., 2011). Indeed, blue wildebeest and gemsbok in the Kalahari (Boyers et al., 2019) and Arabian oryx in the Arabian desert (Hetem et al., 2010) displayed reductions in minimum 24-hour body temperatures in hot-dry seasons when food availability was presumed to be low compared to the hot-wet season when food resources were presumed abundant (Boyers et al., 2019). While both studies inferred the resource links to body temperature through presumed seasonal changes in resource availability, my study showed that a reduction in minimum body temperature was directly linked to low vegetation greenness, as has also been shown to be the case for blue wildebeest and gemsbok in the Kalahari (Boyers, 2018). Further evidence for a mechanistic link between body temperature

and energetic stress has recently been proposed for Cape buffalo (Botha et al., 2023) in which case low minimum body temperatures have been linked to low leptin levels (i.e. low satiety and signal of starvation) and poor body condition during drought conditions. Indeed, free-living wildebeest, kudu *Tragelaphus strepsiceros* and red hartebeest *Alcelaphus buselaphus* displayed a reduction in body mass associated with decreased NDVI (proxy for food availability) during the dry season (Fuentes-Allende et al., 2023).

The most energetically expensive periods during a mammal's lifetime are gestation and lactation (Gittleman and Thompson, 1988), the physiological consequences of which can present as perturbations to body temperature regulation in some mammal species. I observed a progressive decline in the minimum body temperatures of some sable antelopes during February and March, a time of the year that coincides with the general calving season of sable antelope (Grobler, 1981b), possibly reflecting gestational hypothermia. Gestational hypothermia is a progressive and regulated decline in mean body temperature during gestation proposed to protect the foetus from thermal stress by maintaining a gradient for heat loss from the foetus to the mother (Laburn, 1996) as observed in sheep (Laburn et al., 1992), vervet monkeys *Chlorocebus pygerythrus* (McFarland et al., 2022) and African lions *Panthera leo* (Trethowan et al., 2016). However, to maintain this temperature gradient the mother must continually lower her body temperature which can be costly in terms of body water loss associated with evaporative cooling, especially when ambient temperatures are high. Following presumed parturition (birth), body temperature increased abruptly and remained elevated for approximately two weeks, possibly reflecting early lactation. Indeed, some small mammal species experience increased body temperatures during lactation associated with the metabolic heat production of milk and increased foraging (Gamo et al., 2013; Speakman, 2007). Lactating females may however experience elevated body temperatures when body water is prioritised for milk production rather than heat dissipation

via evaporative cooling (Fuller et al., 2021). Interestingly, I noted that the distinctive perturbations in body temperature, suggestive of gestational hypothermia and lactation hyperthermia, were evident in females that maintained a narrower rhythm of body temperature (indicative of physiological well-being) compared to females that did not display these distinctive perturbations in body temperature. A similar pattern has been observed in African lions (Trethowan et al., 2016) and brown bears *Ursus arctos* (Friebe et al., 2014) which displayed improved homeothermy during gestation, possibly linked to healthier offspring. The occurrence of gestational hypothermia and early lactation hyperthermia also doubled during the second year of study following a shorter dry and longer wet season, further suggesting maternal nutrition and hydration were important for successful reproduction (Gittleman and Thompson, 1988). Indeed, in Kruger National Park, the juvenile survival of several ungulate species, including sable antelope, was correlated with dry season rainfall (promotes retention of green grass) before birth, implying the nutritional status of the mother during gestation influenced juvenile birth weight and survival (Owen-Smith et al., 2005). My study provides the first record of perturbations in body temperature likely related to gestation and lactation in a free-living antelope.

Longer and more extreme dry seasons will not only reduce fitness through reduced fecundity and reproductive success (Bronson, 2009) but will also impact the physiological well-being of individual animals through heat stress (Hetem et al., 2016). My study is the first to show increased maximum body temperature in an African ungulate during the hot, late dry season likely resulting from a combination of high ambient temperature and water deprivation. Indeed, large ungulates facing water shortage may reduce evaporative water loss, prioritising osmoregulation over thermoregulation to maintain constant body temperature (Hetem et al., 2016). As temperatures started to increase in the late dry season, some sable antelopes in my study walked 13-30 kms every 4-5 days to access drinking water (see Chapter 3). By linking

body temperature to landscape features, I am the first to demonstrate a direct link between access to a water resource and maximum body temperature in a free-living antelope. This link between body temperature and access to water concurs with experimental studies on captive desert and non-desert ungulates (Finch and Robertshaw, 1979; Schmidt-Nielsen et al., 1956; Taylor, 1970) and has been inferred (based on seasonal patterns) for free-living desert ungulates (Hetem et al., 2012a, 2010; Ostrowski et al., 2003; Ostrowski and Williams, 2006). By confirming that maximum body temperature was likely linked to hydration state in the free-living sable antelopes of my study, I was able to demonstrate that elevated maximum body temperature (i.e. dehydration-induced hyperthermia) may be driving their movements to water and that these movements to water were likely associated with drinking because of a reduction in maximum body temperature the day following journeys to water. Indeed, captive baboon *Papio hamadryas* (Mitchell et al., 2009) and sheep (Fuller et al., 2007) displayed a reduction in 24-hour maximum core body temperature with rehydration. However, travelling to water likely came at an energetic and time cost during a time when sable antelopes in my study were unable to compensate for the losses, as indicated by the low minimum 24-hour body temperatures during the late dry season.

My study has recorded the largest body temperature fluctuations to date for any free-living antelope species in Africa. While these fluctuations in body temperature were less extreme (amplitude of 5 ^{o}C vs 7 ^{o}C for Arabian oryx), they may be analogous to Arabian antelope inhabiting a more extreme desert environment (Hetem et al., 2010), highlighting the sensitivity of a water-dependent, selective grazing antelope to resource limitations. My findings show that behavioural flexibility failed to completely buffer reduced resource availability as sable antelopes experienced fluctuations in body temperature indicative of nutritional and water stress, which is likely to become more prevalent and exaggerated among water-dependent, selective grazers with future climate change.

CHAPTER 6

Conclusion

6.1 Synopsis

My thesis aimed to contribute towards an improved understanding of the behavioural and physiological responses of a water-dependent, specialist antelope species to key environmental stressors in the face of a hotter and drier future. Using an interdisciplinary approach, combining spatial ecology, behavioural ecology, and conservation physiology, I show that spatiotemporal changes in vegetation greenness and environmental heat load are significant drivers of variation in the movement patterns, fine-scale activity patterns, microclimate selection and body temperature of sable antelope. My study is the first to demonstrate a mechanistic basis for the movement to resources in a free-living antelope species by showing a relationship between the movement to a water resource and maximum body temperature. My study also provides the first records of fine-scale activity, microclimate selection and body temperature of sable antelope, and the first record of perturbations in body temperature potentially related to gestation and lactation in a free-living antelope species. I have collected the most comprehensive data set to date, on the movement, fine-scale activity, microclimate selection and body temperature for any antelope species. This data set stems from, i) having the largest number of sable antelopes collared in the same area over two years and ii) using biologging technology which allows fine-scale activity, microclimate selection and body temperature to be measured remotely, continuously, and over long timeframes without human disturbance. My findings highlight the usefulness of biologging in complementing behavioural and ecological studies to provide a physiological (mechanistic) basis for movement and activity.

My results show that the resource-poor dry season is a critical period for sable antelopes inhabiting the semi-arid Bwabwata National Park of Namibia. In response to low vegetation greenness (proxy of reduced food availability) and low ambient temperature, conditions

characteristic of the early dry season, sable antelopes displayed a decrease in minimum 24-hour body temperature likely because of energy deprivation. When ambient temperatures increased during the late dry season and vegetation greenness remained low, minimum 24-hour body temperatures remained low, but maximum 24-hour body temperatures increased likely due to water deprivation. When the ambient temperature exceeds body temperature, the only way to dissipate heat is through evaporative cooling which costs body water (Tattersall et al., 2012). For some herds in my study, replenishing lost body water required long walks to water (~13-30 kms) every 4-5 days. Indeed, a high maximum body temperature (i.e. dehydration) increased the probability of a relocating behavioural state to water. These movements to water were likely associated with drinking (i.e. rehydration) because of a reduction in maximum body temperature the day after travelling to water. Seeking shade and reducing activity during the heat of the day may have helped save body water by reducing reliance on evaporative cooling, and potentially extending the time between walks to water. However, the long distance movements to water came at the expense of foraging-related movements, and sable antelopes could not compensate for the daytime activity lost to increased shade-seeking and reduced midday activity. These behaviours to rehydrate and reduce diurnal heat likely came at an energetic cost, as revealed by the low minimum body temperatures during the late dry season. The co-occurring high maximum and low minimum body temperatures during the late dry season suggest sable antelopes experienced dehydration alongside energy deprivation when vegetation greenness was at its lowest and ambient temperatures were high. Likely forced to trade off energy intake, osmoregulation and thermoregulation (Hetem et al., 2016), I suggest that the sable antelopes in my study may better tolerate a progressive loss in body condition compared to lethal dehydration-induced hyperthermia. Flexible behaviour is often viewed as an efficient means to buffer changes in environmental conditions but physiological measurements (in this case body temperatures)

revealed nutritional and water stress in sable antelopes despite behavioural adjustments – highlighting the importance and benefit of incorporating physiological measurements into movement and activity analyses (Chmura et al., 2018; Rutz and Hays, 2009).

6.2 Significance and future directions

The conceptual framework for movement ecology, proposed by Nathan et al (2008), outlines how movement is governed by the interplay among the mechanistic components of movement (i.e. internal state, motion and navigation capacity) and external biotic (e.g. foraging resources, competition, predation) and abiotic (e.g. temperature, location of water, shelter, rainfall) factors. Physiological responses underpin movement ecology. Advances in biologging technology allow for the incorporation of physiological variables into movement ecology studies (Williams et al., 2020). Biologging heart rate provides a proxy for energy expenditure (Green, 2011), while accelerometery can be used to quantify the activity-specific metabolic rate of free-living animals (Halsey et al., 2011). Estimates of daily energy expenditure can be achieved by combining accelerometery with measures of heart rate (Green et al., 2009). However, the physiological states underlying movement can be directly quantified through biologging body temperature. Biologging the body temperature of free-living herbivores can provide insights into the internal physiological state driving movement by providing an index of physiological well-being through the quantification of nutrition, hydration, reproductive and disease state (Fuller et al., 2016; Hetem et al., 2016).

When ambient temperature exceeds body temperature during periods of limited water availability, endotherms prioritize conserving body water over evaporative water loss to regulate body temperature, causing a rise in maximum body temperatures (Cain et al., 2006; McKinley et al., 2008; Tattersall et al., 2012). These high body temperatures may drive

movements to distant water sources to replenish body water lost through evaporative cooling (Figure 6.1c). By confirming that the elevated maximum 24-hour body temperatures of the sable antelope in my study were likely linked to their hydration state, I was able to demonstrate that dehydration-induced hyperthermia may drive movements to water during a period of high heat load and reduced water availability and that these movements to water were likely associated with drinking because of a reduction in maximum 24-hour body temperatures the day after travelling to water. While I was unable to confirm actual drinking events, tri-axial accelerometers can detect drinking behaviour based on head-neck position, activity and movement frequency, thereby quantifying the frequency and duration of visits to water and drinking events (Williams et al., 2020b). These additional measurements may elucidate the physiological basis of drinking behaviour during hot and dry conditions by enabling the opportunity to investigate variations in maximum body temperature in relation to the frequency and duration of visits to water and drinking events. My findings show that relocating movements to water can come at a cost to time spent foraging, which may have energetic consequences as revealed by low minimum body temperatures during the late dry season. Indeed, integrating body temperature, accelerometery data and heart rate measurements may provide additional insight into the energetic consequences and trade-offs associated with travelling long distances to access water during energy-limited periods.

During hot and dry conditions, seeking shelter from high radiant heat loads during the heat of the day (e.g. shade-seeking or using cool microclimates) may reduce reliance on evaporative cooling (Hetem et al., 2014), extending the time between visits to water (see Figure 6.1c). My results show that sable antelope used increasingly cooler microclimates and spent more time in the shade in response to hot and dry conditions. Mapping selected microclimates relative to landscape features, like permanent water sources, may give insight into the relative importance of the location and quality of microclimates utilised during hot and dry

conditions. Indeed, integrating body temperature into microclimate selection studies may provide insight into the efficacy of increased shade-seeking during hot, water-limited periods and complement habitat selection studies (Chmura et al., 2018).

Low minimum 24-hour body temperatures during periods of reduced food availability are likely the consequence of energy deprivation or starvation in response to reduced quality and/or quantity of food intake (Fuller et al., 2016). Low minimum body temperatures may therefore drive movements in search of more food and/or higher quality food (Figure 6.1b). To improve our understanding of the physiological mechanisms underlying movement behaviours, it would be useful to integrate body temperature measurements into foraging ecology studies. For example, audio loggers on GPS collars can be used to record components of foraging such as individual steps and bites (Northrup et al., 2019), allowing for location-specific foraging, foraging intensity, and foraging efficiency to be related to minimum body temperatures (a measure of nutritional state). Indeed, with sufficient ground truthing of behaviours through direct observations, supervised machine learning can discern specific behaviours such as searching for forage, feeding/grazing, and ruminating from accelerometer data (Berry et al., 2024). Incorporating body temperature measurements into daily energy expenditure assessments may help quantify the energetic costs associated with acquiring resources (Green et al., 2009), particularly during resource-limited periods when individuals contend with reduced forage and water availability. With body temperature providing an index of nutritional state, remote monitoring of changes in body mass using mineral-baited scales and camera traps (Fuentes-Allende et al., 2023) can further improve our understanding of the mechanistic basis of movement in response to fluctuations in resource availability.

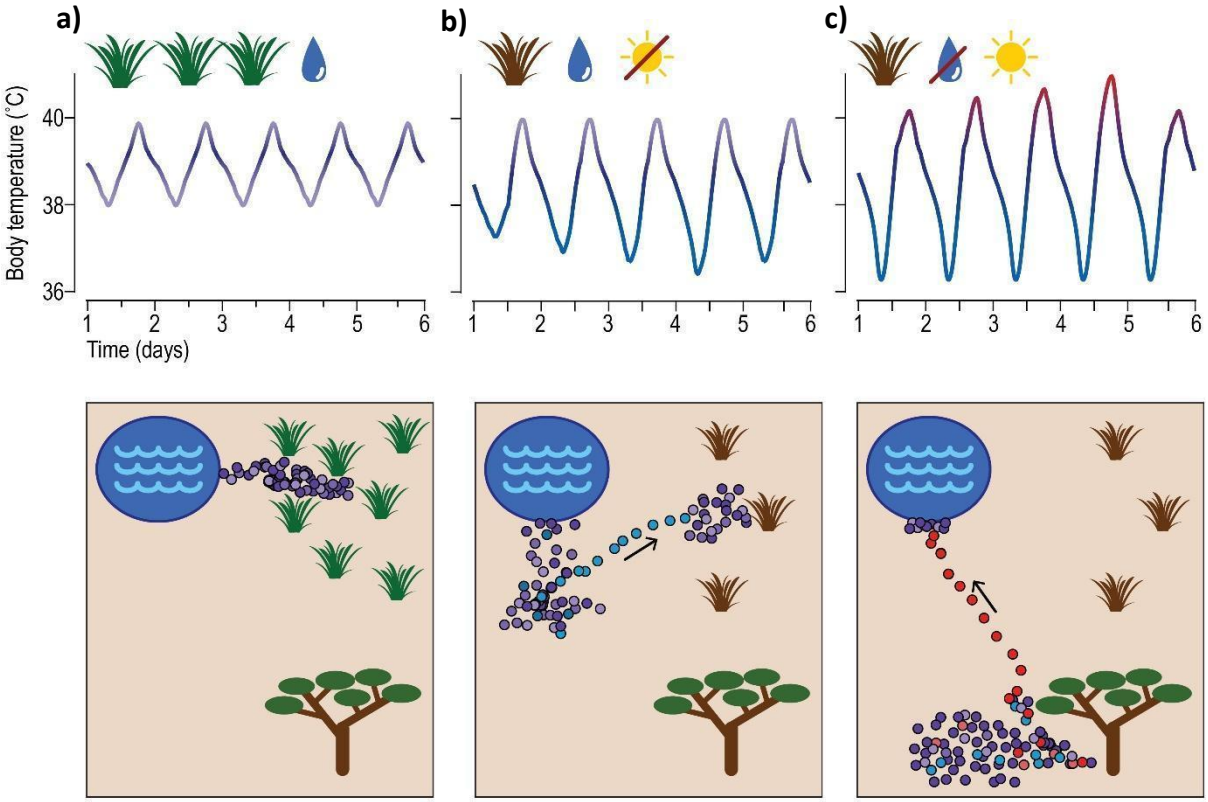

Figure 6.1. Biologging the body temperature of free-living mammalian herbivores may provide insight into the mechanistic drivers of movement paths. The movement path of an individual is shown by the coloured points, with the changes in the colour of the points corresponding to changes in body temperature. a) When an individual has access to sufficient food and water it will maintain a narrow rhythm of body temperature and move little in search of resources. b) When forage is limited, but the individual can maintain body water balance either through access to water or low reliance on evaporative cooling, minimum body temperatures progressively decline as energy stores are depleted and may ultimately drive the individual to search for higher quantity/quality forage. c) In hot and dry conditions, maximum body temperatures increase as dehydration switches off evaporative cooling to conserve body water and may drive movement to known water sources. *Adapted from Hetem et al. Integrating physiology into movement ecology. Journal of Experimental Biology, in press.*

Fluctuations in body temperature also provide insight into reproductive state which may influence movement as individuals seek to meet the energy and water demands of gestation and lactation. Incorporating measures of body temperature into resource selection studies may provide insight into the effectiveness of selective movements to meet the energy and water demands associated with different stages of reproduction, for example, selecting greener patches during gestation (Heffelfinger et al., 2020) or selecting habitats closer to permanent water sources during lactation (Long et al., 2009). Long-term studies collecting continuous data are useful for capturing annual and seasonal variations in behaviour and physiological state and detecting life events such as pregnancy. Long-term biologging of body temperature may therefore act as an early warning system to detect when resource limitations pose a risk to reproductive success and fitness by compromising gestation and lactation (McFarland et al., 2024) and may even be used to detect abortions (Trethowan et al., 2016).

Considering the increasing demand for interdisciplinary studies in the face of future climate changes, such as the integration of movement ecology and conservation physiology, there is a growing need for the development of quantitative statistical methods (i.e. integrative models) to cohesively analyse movement, behavioural, physiological and/or environmental data (Williams et al., 2020). For example, integrating physiological measurements (like body temperature) into decision-based movement models (Hooten et al., 2019), energy-based movement models (Klappstein et al., 2022), movement-based habitat selection models (e.g. resource and step selection functions (Avgar et al., 2016) and spatial distribution models to improve our understanding of the fundamental mechanisms (i.e. physiological processes) of movement behaviour.

My findings also contribute to ecological theory from an African perspective (Owen-Smith et al., 2020). Although the field of movement ecology is rapidly growing, for large herbivores the literature is dominated by studies conducted on cold-adapted herbivores inhabiting northern temperate and arctic environments (Franke et al., 2004; Morales et al., 2004; Prima et al., 2022) which fail to capture important features of highly dynamic African dryland ecosystems, particularly high spatiotemporal heterogeneity in vegetation and climate. Using quantitative analytical/statistical methods to interpret movement and activity patterns (as I have done in my analyses) has been underutilised for African herbivores (Owen-Smith et al., 2020, 2012b; Owen-Smith and Goodall, 2014). Future studies on the movement ecology of African herbivores should utilise more sophisticated technology (i.e. high-resolution GPS units and accelerometers), informative movement metrics and quantitative analytical methods to improve our understanding of the intricate movement patterns of these large herbivores. Studies on African herbivores inhabiting highly dynamic and heterogenous environments (e.g. savannas), also need to start incorporating quantifiable measures of key environmental factors (e.g. ambient temperature, vegetation quality/quantity, water availability) into behavioural and physiological assessments, rather than inferring spatiotemporal changes in resource availability and climate through presumed seasonal changes. Studying and monitoring changes in movement, behaviour and physiological state in relation to key environmental factors allows for assessment of well-being before populations start to decline, enabling targeted and more informed management decisions (Madliger et al., 2022).

In the face of hotter and drier conditions, research efforts should prioritise non-migratory, water-dependent, grazing and mixed-feeding species inhabiting arid and semi-arid environments where herbivore populations are greatly constrained by resource availability, making them highly susceptible to increases in the frequency and intensity of droughts (Duncan et al., 2012). Integrating measures of movement, behaviour and physiological state

is essential for assessing the sensitivity of large herbivore species to fluctuations in resource availability. Since species-specific traits can modify responses and resilience to future climate change, inter- and intra-specific variations in the behavioural and physiological sensitivity to spatiotemporal fluctuations in food and water must be incorporated into predictive models to improve their predictive utility for conservation and management (Evans et al., 2015; McCain and King, 2014). Future studies should therefore focus on collecting long-term, fine-scale movement, behavioural and physiological data from free-living herbivores across their distribution range, particularly if their distribution spans gradients of temperature, rainfall or aridity to improve our understanding of the phenotypic plasticity of species (Chmura et al., 2018).

6.3 Conservation implications

My results highlight the importance of resource availability, resource distribution and habitat structure (e.g. availability of shade) to the well-being of an African herbivore that exhibits specialist grazing and water-dependency, much like roan antelope *Hippotragus equinus*, tsessebe *Damaliscus lunatus*, waterbuck *Kobus ellipsiprymnus*, mountain reedbuck *Redunca fulvorufula*, blesbok *Damaliscus pygargus phillipsi* and wildebeest *Connochaetes taurinus*. During increasingly hot and dry conditions, these specialist antelope will likely need to trade off food intake, travel to water, thermal refuge, and predation risk as spatiotemporal variations in the availability of food and water increase. Conservation and management should therefore focus on protecting key resources and access to these resources. Indeed, maintaining and preserving key foraging areas during the dry season such as floodplains, wetlands, vleis or dambos (Fynn et al., 2015; Parrini, 2006) and controlled burning protocols to encourage green grass flush during the dry season (Parrini and Owen-Smith, 2010) will

become increasingly important. Circumventing limited surface water availability is not as straightforward as adding artificial water points. The addition of artificial waterpoints is known to influence herbivore distribution patterns (Smit et al., 2007) and disrupt ecological dynamics through resource depletion and increased predation as seen by the crash in populations of rarer antelopes (e.g. sable antelope and roan antelope) in Kruger National Park (Harrington et al., 1999; Owen-Smith and Mills, 2006). Indeed, the addition of artificial waterpoints can lead to landscape homogenisation which may reduce ungulate resistance to climate change (Giralt-Rueda and Santamaría, 2023) and decrease large herbivore diversity (Veldhuis et al., 2019). Emphasis should rather be placed on preserving the landscape features, habitats and corridors used to move between foraging areas and existing permanent water sources when ephemeral surface water dries up. Habitat diversity and connectivity facilitate annual and seasonal variation in access to resources and shelter from thermal extremes which is vital to meeting resource requirements and managing thermal load while avoiding competition and reducing predation risk.

Conclusively, my research findings advocate for the long-term study and monitoring of water-dependent, selective grazing herbivores using biologging technology to simultaneously measure fine-scale movement, behavioural and physiological responses to spatiotemporal fluctuations in resource availability and climate to, i) assess physiological well-being before population declines manifest, ii) identify environmental and ecological stressors before and potentially amid population declines, and iii) assess the capacity of phenotypic plasticity to buffer variability in resource availability in the face of a hotter and drier future.

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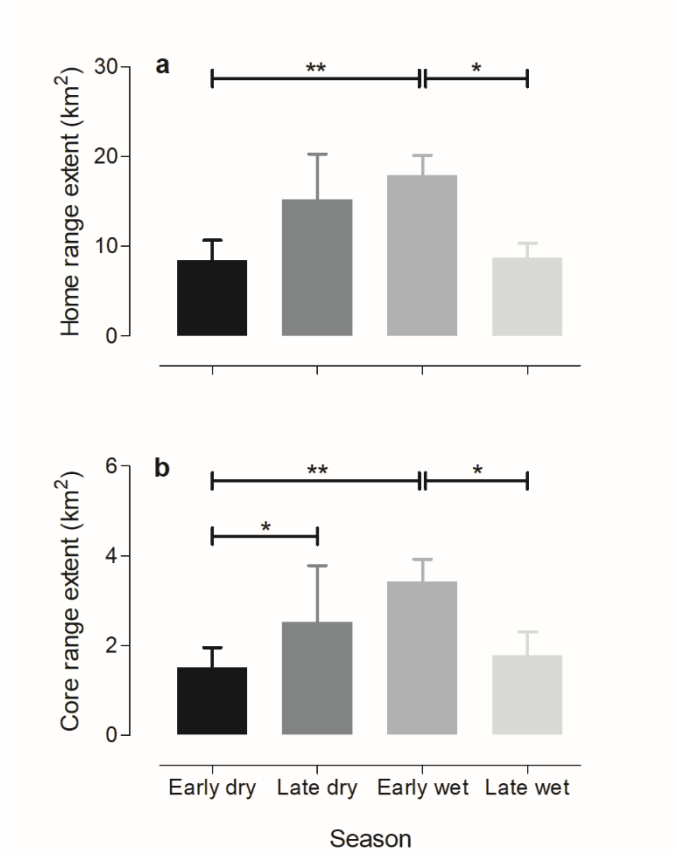
Appendices

Appendix 1. Prevailing environmental conditions (mean ± SD) during the early dry (May – July), late dry (August – October), early wet (November – January) and late wet (February – April) season from May 2017 – April 2018 during which sable antelopes were free-ranging within Bwabwata National Park, Namibia.

	Early dry	Late dry	Early wet	Late wet
Total rainfall (mm)	0	0	65	154
Area average EVI*	0.27 ± 0.04	0.19 ± 0.01	0.19 ± 0.01	0.39 ± 0.02
Brown vegetation exposure (%)	34.0 ± 6.1	96.7 ± 2.2	16.9 ± 2.7	0
Dry-bulb air temperature (^{o}C)				
24-hour mean	18.1 ± 0.6	25.0 ± 4.2	27.7 ± 1.2	24.0 ± 0.2
24-hour minimum	7.7 ± 1.2	14.1 ± 5.4	18.7 ± 1.2	17.2 ± 3.1
24-hour maximum	30.5 ± 0.8	36.2 ± 3.5	38.9 ± 1.8	35.3 ± 5.3
Environmental heat load (^{o}C)				
24-hour mean	21.5 ± 0.8	28.6 ± 4.2	31.1 ± 0.6	26.9 ± 1.1
24-hour minimum	6.9 ± 1.2	13.5 ± 5.3	18.3 ± 1.2	17.2 ± 2.7
24-hour maximum	45.1 ± 1.6	50.0 ± 4.0	52.7 ± 1.5	45.6 ± 1.4

Area average EVI was obtained using the Application for Extracting and Exploring Analysis Ready Samples (AppEEARS) interface (https://lpdaacsvc.cr.usgs.gov/appeears/) which provided area averaged EVI (MODIS 13Q1.006, 250 m with 16-day composites) for the total spatial area covered by all GPS locations of free-ranging sable antelopes. Black globe temperature is indicative of environmental heat load.



Appendix 2. Mean (± SD) seasonal home (95% isopleth) and core (50% isopleth) range sizes of free-ranging female sable antelopes in the early dry (May – July), late dry (August – October), early wet (November – January) and late wet (February – April) seasons of 2017/2018. Linear Mixed-effects Models were significant for the influence of season on both the home range ($F[7, 39.98] = 10.861$, $p<0.001$) and core range ($F[7, 38.97] = 10.691$, $p<0.001$) size. Asterisks indicate statistically significant differences according to pairwise multiple comparisons using a Tukey adjustment (* = $p<0.05$, ** = $p<0.01$, *** = $p<0.001$). Seasonal ranges were estimated using the *a*-LoCoH method.

Appendix 3: Candidate mixed effects models for the relationship between 24-hour mean hourly displacement distance and proportion of 24-hour cycle spent in a particular behavioural state response variables and fixed explanatory variables. Every candidate model included the individual identity of sable antelopes as a random effect. Candidate models are listed in ascending rank according to their corrected Akaike information criterion (AICc). Delta AICc (Δ_i) is the difference between the AICc for a given model and the best fitting model, k is the number of estimated parameters in the model and the Akaike weight (ω_i) is the model selection probability.

	Fixed effects	k	AICc	Δi	ωi
24-Hour mean hourly displacement distance					
	proportion of brown vegetation exposure + 24-hour mean black globe temperature	5	-6951.06	0.00	1.00
	proportion of brown vegetation exposure + 24-hour maximum black globe temperature	5	-6922.52	28.54	0.00
	proportion of brown vegetation exposure	4	-6857.88	93.18	0.00
	24-hour mean black globe temperature	4	-6702.20	248.86	0.00
	24-hour maximum black globe temperature	4	-6665.47	285.58	0.00
Proportion of 24-hour cycle in relocating state					
	proportion of brown vegetation exposure + 24-hour mean black globe temperature	5	13705.43	0.00	1.00
	proportion of brown vegetation exposure + 24-hour maximum black globe temperature	5	13724.73	19.3	0.00
	proportion of brown vegetation exposure	4	13773.92	68.49	0.00
	24-hour mean black globe temperature	4	13860.10	154.67	0.00
	24-hour maximum black globe temperature	4	13888.89	183.45	0.00
Proportion of 24-hour cycle in foraging state					
	proportion of brown vegetation exposure + 24-hour mean black globe temperature	5	25590.71	0.00	1.00
	proportion of brown vegetation exposure + 24-hour maximum black globe temperature	5	25669.85	79.14	0.00
	proportion of brown vegetation exposure	4	25828.28	237.57	0.00
	24-hour mean black globe temperature	4	26062.86	472.15	0.00

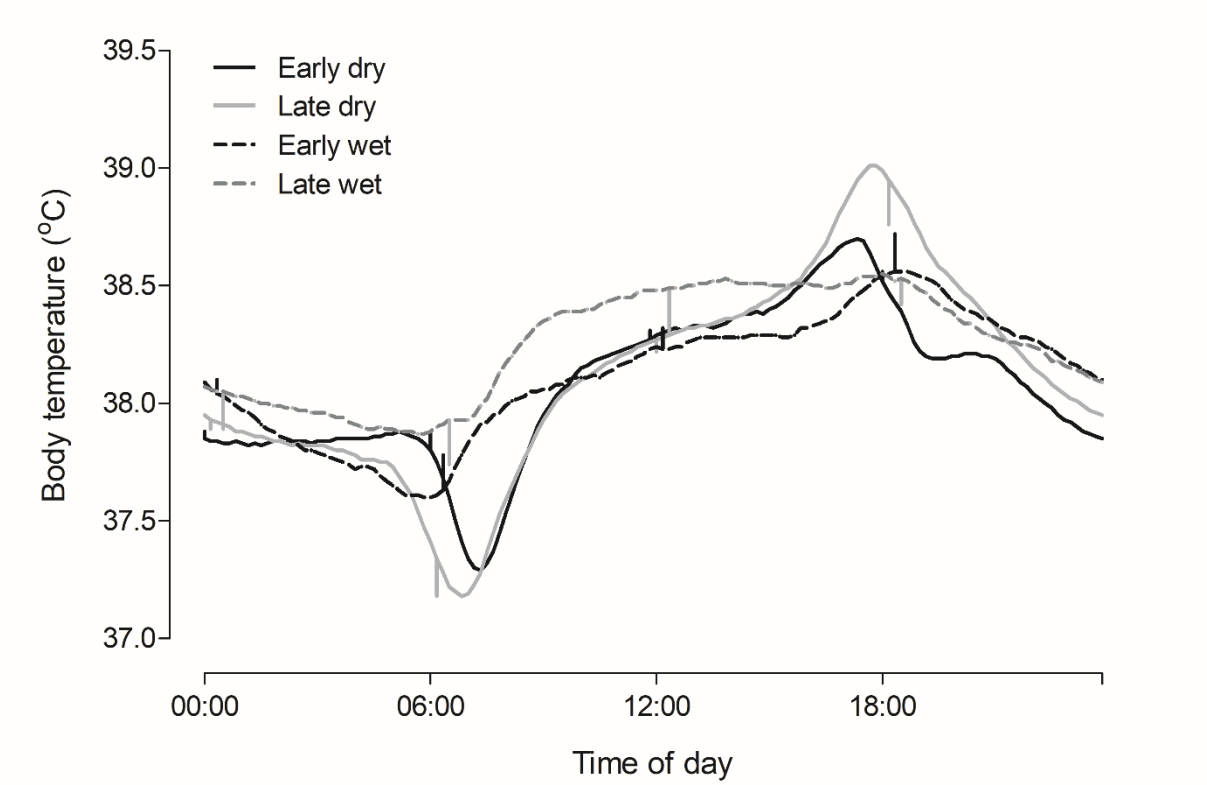
	24-hour maximum black globe temperature	4	26144.32	553.61	0.00
Proportion of 24-hour cycle in local movement					
	proportion of brown vegetation exposure + 24-hour mean black globe temperature	5	24069.24	0.00	1.00
	proportion of brown vegetation exposure + 24-hour maximum black globe temperature	5	24094.21	24.96	0.00
	proportion of brown vegetation exposure	4	24182.56	113.31	0.00
	24-hour mean black globe temperature	4	24336.45	267.21	0.00
	24-hour maximum black globe temperature	4	24373.98	304.74	0.00
Proportion of 24-hour cycle in resting state					
	proportion of brown vegetation exposure + 24-hour mean black globe temperature	5	26127.61	0.00	0.71
	proportion of brown vegetation exposure + 24-hour maximum black globe temperature	5	26129.40	1.79	0.29
	proportion of brown vegetation exposure	4	26180.37	52.76	0.00
	24-hour maximum black globe temperature	4	26623.68	496.07	0.00
	24-hour average black globe temperature	4	26623.86	496.24	0.00

Appendix 4. Candidate mixed effects models for the relationship between activity and microclimate response variables and fixed explanatory variables. Every candidate model included the individual identity of sable antelopes as a random effect. Candidate models are listed in ascending rank according to their corrected Akaike information criterion (AICc). Delta AICc (Δ_i) is the difference between the AICc for a given model and the best fitting model, k is the number of estimated parameters in the model and the Akaike weight (ω_i) is the model selection probability.

	Fixed effects	**k**	**AICc**	**Δ_i**	**ω_i**
total 24-hour activity ~					
	proportion of brown vegetation exposure + 24-hour mean black globe temperature	5	7272.61	0.00	0.94
	proportion of brown vegetation exposure + 24-hour maximum black globe temperature	5	7278.04	5.43	0.06
	proportion of brown vegetation exposure	4	7301.40	28.79	0.00
	proportion of brown vegetation exposure	4	7637.04	364.44	0.00
	24-hour maximum black globe temperature	4	7655.73	383.12	0.00
24-hour proportion of diurnal activity ~					
	proportion of brown vegetation exposure + 24-hour mean black globe temperature + diurnal photoperiod	6	-2961.92	0.00	0.99
	proportion of brown vegetation exposure + 24-hour mean black globe temperature	5	-2951.66	10.26	0.01
	proportion of brown vegetation exposure + 24-hour maximum black globe temperature	5	-2942.52	19.40	0.00
	proportion of brown vegetation exposure + 24-hour maximum black globe temperature + diurnal photoperiod	6	-2940.69	21.22	0.00
	proportion of brown vegetation exposure	4	-2906.09	55.83	0.00
	24-hour mean black globe temperature	4	-2664.56	297.36	0.00
	24-hour maximum black globe temperature	4	-2639.10	322.82	0.00
24-hour proportion of nocturnal activity ~					

	proportion of brown vegetation exposure + 24-hour mean black globe temperature + nocturnal period	6	-2945.36	0.00	0.99
	proportion of brown vegetation exposure + 24-hour mean black globe temperature	5	-2936.90	8.46	0.01
	proportion of brown vegetation exposure + 24-hour maximum black globe temperature	5	-2928.85	16.51	0.00
	proportion of brown vegetation exposure + 24-hour maximum black globe temperature + nocturnal period	6	-2926.91	18.45	0.00
	proportion of brown vegetation exposure	4	-2891.64	53.72	0.00
	24-hour mean black globe temperature	4	-2654.99	290.37	0.00
	24-hour maximum black globe temperature	4	-2631.29	314.07	0.00
proportion of midday spent in shade ~					
	proportion of brown vegetation exposure + 24-hour maximum black globe temperature	4	8259.08	0.00	1.00
	proportion of brown vegetation exposure	3	8296.73	37.65	0.00
	proportion of brown vegetation exposure + 24-hour mean black globe temperature	4	8298.71	39.63	0.00
	24-hour maximum black globe temperature	3	9103.94	844.86	0.00
	24-hour mean black globe temperature	3	9192.23	933.15	0.00
quality of midday microclimate selected ~					
	proportion of brown vegetation exposure + 24-hour maximum black globe temperature	5	13346.10	0.00	1.00
	proportion of brown vegetation exposure	4	13431.22	85.12	0.00
	proportion of brown vegetation exposure + 24-hour mean black globe temperature	5	13432.79	86.69	0.00
	24-hour maximum black globe temperature	4	13484.43	138.33	0.00
	24-hour mean black globe temperature	4	13530.00	183.90	0.00
total midday activity ~					

	proportion of brown vegetation exposure + 24-hour mean black globe temperature + proportion of midday spent in shade	6	6423.83	0.00	1.00
	proportion of brown vegetation exposure + 24-hour maximum black globe temperature + proportion of midday spent in shade	6	6518.09	94.26	0.00
	proportion of midday spent in shade	4	7277.11	853.28	0.00
	proportion of brown vegetation exposure + 24-hour mean black globe temperature	5	10144.69	3720.85	0.00
	proportion of brown vegetation exposure + 24-hour maximum black globe temperature	5	10298.49	3874.65	0.00
	proportion of brown vegetation exposure	4	10563.18	4139.35	0.00
	24-hour mean black globe temperature	4	11307.75	4883.92	0.00
	24-hour maximum black globe temperature	4	11505.81	5081.98	0.00



Appendix 5. The mean (± SD) 24-hour body temperature rhythm of eight free-living female sable antelopes over four seasonal periods occurring between May 2017 and April 2018 in Bwabwata National Park, Namibia.

Appendix 6. Candidate linear mixed effects models for the relationship between body temperature response variables and explanatory environmental variables. Every candidate model included the individual identity of sable antelopes as a random effect. Candidate models are listed in ascending rank according to their corrected Akaike information criterion (AICc). Delta AICc (Δ_i) is the difference between the AICc for a given model and the best fitting model, k is the number of estimated parameters in the model and the Akaike weight (ω_i) is the model selection probability.

	Fixed effects	**k**	**AICc**	**Δ_i**	**ω_i**
minimum 24-hour body temperature ~					
	proportion of brown vegetation exposure + 24-hour mean black globe temperature	5	4277.06	0.00	1.00
	proportion of brown vegetation exposure + 24-hour max black globe temperature	5	4441.61	164.55	0.00
	proportion of brown vegetation exposure	4	4613.96	336.91	0.00
	24-hour mean black globe temperature	4	7263.63	2986.58	0.00
	24-hour maximum black globe temperature	4	7379.63	3102.57	0.00
maximum 24-hour body temperature ~					
	proportion of brown vegetation exposure + 24-hour maximum black globe temperature	5	3756.45	0.00	1.00
	proportion of brown vegetation exposure + 24-hour mean black globe temperature	5	3778.82	22.36	0.00
	proportion of brown vegetation exposure	4	3801.27	44.82	0.00
	24-hour maximum black globe temperature	4	5415.53	1659.08	0.00
	24-hour mean black globe temperature	4	5442.89	1686.44	0.00