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How energy and thermal landscapes influence habitat use in chacma baboons (*Papio ursinus*)



For the degree: M.Sc. in Animal, Plant and Environmental Sciences

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Declaration

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



(Signature of candidate)

_____24th_____day of ____October_____2025_____at__Felixstowe_____

Abstract

Landscape heterogeneity drives chacma baboon movement, behaviour and habitat use. Here, baboons alter their responses to the changing environment to balance thermoregulation and resource acquisition. This study incorporated historical data from multiple habituated troops within the Swebeswebe Wildlife Estate, along with more current field data collected while following a troop of 69 individuals. Behavioural data were collected in 30-minute scan sampling intervals to assess activity budgets and shade use, while corresponding GPS data tracked movement. Climatic conditions were recorded through an onsite weather station along with miniglobe thermometers placed in representative microhabitats, including one carried while tracking the troop. Landscape features, and food and water availability were mapped to analyse how biotic and abiotic factors influenced troop movement, behaviour and habitat use. Baboons travelled further under high heat loads and low water availability. They, however, only expanded their home ranges, particularly along the main river system, during periods of water scarcity. In contrast to travel distance, the frequency of travel behaviour, as well as rest behaviour, increased with higher temperatures and water availability. As a result, a trade-off was observed in foraging behaviour, highlighting prioritisation between thermoregulation and energy acquisition with differing environmental drivers. Social behaviour decreased under higher water availability but, in contrast, increased with higher vegetation greenness. Vegetation greenness was a key driver to shade use, a behaviour critical for thermoregulation, particularly under higher heat loads. In line with thermoregulatory activity, baboons selected stable microclimates, preferring cooler, densely vegetated habitats, particularly during peak heat loads in the day and in the wet season. Baboon distribution shifted seasonally, with troops found closer to their main cave sleep site and rivers during the dry season and being found further away from fence lines. This indicated a more constrained spatial use pattern in times of resource scarcity. These findings highlight the flexible responses of baboons to thermal and resource landscapes. The understanding of these patterns is crucial for their conservation through the protection of heterogeneous landscapes, and a broader understanding of their ecological resilience in the face of worsening climate change.

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Introduction

The spatial needs of a species are shaped by multiple factors, including habitat structure, disease, competition (Nathan *et al.*, 2008), access to resources, predator avoidance (Willems and Hill, 2009; Coleman and Hill, 2014), as well as the thermal properties of the environment (Tracy and Christian, 1986; Stone *et al.*, 2013; Hetem *et al.*, 2014). In theory, when factors influencing habitat use remain constant, species should select microhabitats that maximize resource efficiency (Barton *et al.*, 1992). However, because landscapes are highly variable, interactions between ecological drivers can be complex, requiring species to balance competing priorities, such as securing food and shelter while minimizing predation risk (Cowlishaw, 1997b) and thermal stress. These dynamics require precise spatial and temporal decision-making by terrestrial mammals (Henzi, Byrne and Whiten, 1992) which can vary across seasons (Coleman and Hill, 2014) and be influenced by individual motivational states within a social group (Stueckle and Zinner, 2008). Significant drivers of landscape use include food and water availability, as well as thermal conditions, although the role of the thermal landscape remains underexplored in research, highlighting the need to examine it in conjunction with resource distribution.

The heterogeneous nature of landscapes requires continuous decision-making by animals regarding space use, movement, and behaviour (Gallagher *et al.*, 2017; Strandburg-Peshkin *et al.*, 2017), particularly when it comes to energy acquisition. When balancing the influence of multiple factors affecting landscape use, animals must make as finely tuned decisions as possible to meet their daily energetic requirements (Henzi, Byrne and Whiten, 1992) and lessen the costs of trade-offs that may arise. In many species, a critical trade-off is between energy acquisition and thermoregulation, as maintaining optimal body temperature often requires energy that could otherwise be used for foraging (Dunbar, 1992; Cunningham, Martin and Hockey, 2015). These trade-offs can become particularly pronounced under environmental stressors, such as extreme temperatures, which may force animals to restrict movement, alter their activity patterns to conserve energy or seek thermal refuge (Korstjens, Lehmann and Dunbar, 2010; Hetem *et al.*, 2014). Ultimately, the decisions animals make regarding these trade-offs have important implications for their overall fitness and survival.

The thermal landscape is highly heterogeneous, with factors such as slope, topography, aspect, and vegetation creating variation in temperature patterns (Sears, Raskin and Angilletta, 2011; Carroll *et al.*, 2016). To navigate this variation, terrestrial mammals avoid thermally stressful microhabitats as well as adjust their exposure to radiative, convective, and conductive heat transfers to reduce thermoregulatory costs (Stelzner and Hausfater, 1986; Mitchell *et al.*, 2018). Behavioural strategies such as microhabitat selection, shifts in activity, and altered movement patterns help buffer thermal extremes (Stelzner, 1988; Brain and Mitchell, 1999), however, prioritizing thermoregulation may limit the time available for other essential behaviours, such as foraging and social interaction. Assessing these trade-offs and the efficiency of thermoregulatory behaviours in buffering thermal extremes will become increasingly important as conditions in southern Africa become hotter and drier (Serdeczny *et al.*, 2017; Mitchell *et al.*, 2018). Such changes under climate change will likely make the thermal landscape more complex for animals to navigate and stronger pressures will apply in assessing trade-offs in movement, behaviour and habitat use.

Increasing temperature and aridity under climate change could also compromise physiological functions and elevate the risk of mass mortality, potentially leading to local extinctions for many large mammals (Mitchell *et al.*, 2018). For instance, South Africa may experience a decline of up to two-thirds of its mammalian species by 2050 if movement between thermally optimal habitats is restricted (Thomas *et al.*, 2004). Larger mammal species are especially at risk due to their limited ability to access thermal refuges within their environment, along with their greater space needs, slow reproductive rates, and confinement within fenced reserves (Stone *et al.*, 2013; Hetem *et al.*, 2014). These large mammals may, however, be able to mitigate the impacts of thermal extremes by employing behavioural adaptations that enable them to adjust to the changing landscape (Hetem *et al.*, 2014; Fuller *et al.*, 2016).

Primates are among the taxa better equipped to adapt to environmental changes, exhibiting heightened behavioural plasticity which aids them in overcoming environmental stressors (Kalbitzer and Chapman, 2018; McFarland, Barrett, Costello, *et al.*, 2020; McFarland, Barrett, Fuller, *et al.*, 2020). However,

despite their capacity for behavioural flexibility, primates are projected to face an 86% reduction in habitat and an increase of more than 3°C in maximum temperatures over the next 30 years (Graham, Matthews and Turner, 2016; Estrada *et al.*, 2017). These changes may push the limits of behavioural adaptation, leading to physiological stress and potential survival challenges. Generalist species, particularly within the concept of the thermal landscape, have a greater thermal tolerance making them better equipped to face climate challenges (Hetem *et al.*, 2014). Even with greater tolerance, generalist species such as chacma baboons (*Papio ursinus*) may lose up to 75% of their habitat within the next 5 decades (Hill and Winder, 2019) with temperatures in southern African systems rising at a rate twice that of the global average (Engelbrecht *et al.*, 2015). Primates in southern African systems may face a more than 33% increase in thermally enforced rest time with these rising temperatures, reducing their ability for energy uptake (Korstjens, Lehmann and Dunbar, 2010).

Chacma baboons thrive across a wide range of habitats, largely due to their generalist nature and dietary flexibility as omnivores (Barton *et al.*, 1992; Henzi, Byrne and Whiten, 1992; van Doorn, O'Riain and Swedell, 2009). Their success is further supported by complex social structures, cooperative behaviours, a combination of terrestrial and arboreal locomotion, dexterity, and an ability to adapt to human-modified landscapes (van Doorn, O'Riain and Swedell, 2009; Hoffman and O'Riain, 2012). Chacma baboons are expected to exhibit flexibility in their thermoregulatory behaviours, potentially modifying the range of environmental temperatures they encounter (Marais, 1969; Henzi and Barrett, 2016; Sha *et al.*, 2020; Grebe *et al.*, 2025). They may mitigate thermal stress through specific behavioural strategies, including postural adjustments (Stelzner, 1988), sand bathing, as observed in hamadryas baboons (*Papio hamadryas*) (Brain and Mitchell, 1999), and opportunistic shade-seeking (Hill, 2006). Additional cooling mechanisms involve increased exposure to wind for convective heat loss and occasional swimming. On hotter days, baboons frequently seek out shaded microhabitats to minimize radiant heat exposure, enhancing thermoregulatory efficiency (Sha *et al.*, 2020). Within these shaded areas, they tend to reduce movement, while increasing travel speeds when crossing open spaces between them (Stelzner, 1988; Hill, 2006).

For chacma baboons to maintain foraging efficiency while also balancing the cost of thermoregulation, and the need to rest under higher environmental temperatures, they may shift their activity period to earlier in the day during the summer months (Ayers *et al.*, 2020). On days with higher daily heat loads, baboons have also been found to leave their sleep site earlier, allowing them to maximize foraging intake while allowing for necessary resting periods (Noser and Byrne, 2015). When water resources are scarce, baboons further reduce activity during the warmest parts of the day, decreasing movement on days without access to water (Brain and Mitchell, 1999; Hill, 2006). As large mammals, baboons exhibit adaptive heterothermy, storing heat by allowing their core body temperature to rise during the day and dissipating it at night, which aids in conserving water (Fuller *et al.*, 2016). As ambient temperatures increase however, water access becomes essential, since evaporative cooling through panting or sweating becomes the primary means of heat dissipation. Baboons with access to water maintain similar core body temperatures across different environmental conditions, highlighting the critical role of water availability in thermoregulation (Mitchell, Fuller and Maloney, 2009).

In increasingly arid conditions, behavioural adaptations such as reduced activity and microhabitat selection become essential strategies for managing heat stress (Brain and Mitchell, 1999) with baboons and other primates showing preference for microhabitats near water sources. Baboon range use is strongly constrained by the availability of water sources, often structuring their habitat use and movement patterns around waterholes and other drinking sites (Barton *et al.*, 1992). The distance baboons travel and the duration they spend in different habitat types are directly linked to seasonal water distribution, particularly in times of food scarcity (Hamilton, 1985; Barton *et al.*, 1992). Under potential future drought conditions baboon habitat use may become increasingly constrained and the physiological demand of thermoregulation will be heightened. In vervet monkeys (*Chlorocebus pygerythrus*), drought conditions have been linked to elevated faecal glucocorticoid metabolite (fGCM) levels, a physiological indicator of stress (Young *et al.*, 2019). Prolonged periods of water shortages lead to reduced movement, increased resting time, and heightened mortality in vervets (Young *et al.*, 2019) and may affect baboons in a similar way, especially with these species occupying similar niches.

Along with thermoregulatory challenges, changes in water availability and rainfall patterns also impacts resource availability through the alteration of food productivity (Henzi, Byrne and Whiten, 1992; Fuller *et al.*, 2016). Baboons may be able to track seasonal changes in food availability or shift their diets from high energy forage to fall back foods , which are lower in nutrient quality but more abundant, to allow for maximum energy uptake during times of low vegetation productivity (van Doorn, O'Riain and Swedell, 2009). In times of food scarcity, baboons may need to consume lower quality forage as well as food items with a higher handling time (Hamilton, 1985) while spending a greater proportion of time in foraging patches, employing an energy maximising feeding strategy (Barton *et al.*, 1992; van Doorn, O'Riain and Swedell, 2009). Along with these movement patterns, baboons may also select specific microhabitats that offer better foraging resources and are characterized by a higher normalized difference vegetation index (NDVI) (Barton *et al.*, 1992; Zinner, Peláez and Torkler, 2001). Habitat selection is not purely based on food abundance or thermal properties, with predation risk being an important factor influencing landscape use. While areas with dense vegetation may offer abundant food, they can also obscure visibility, increasing the risk of ambush by predators such as leopards (*Panthera pardus*), which pose the greatest predation risk on baboon populations (Cowlishaw, 1994). Conversely, open areas may reduce predation risk by enhancing visibility but may not provide optimal foraging opportunities or thermal protection, leading to a trade-off between safety, resource availability and thermal comfort (Cowlishaw, 1997b; Willems and Hill, 2009; Coleman and Hill, 2014).

Movement and range use is further affected by changing forage availability with the need to search for food items in the dry season. Baboons increase their daily travel distances in times of food scarcity to meet their energetic requirements with increased search times for food (Barton *et al.*, 1992; Henzi, Byrne and Whiten, 1992; van Doorn, O'Riain and Swedell, 2009; Johnson *et al.*, 2015). During food scarcity daily distances also increase with larger troop numbers in order for all individuals in the social group to meet their daily energetic requirements (Barton *et al.*, 1992; Schreier, 2010; Pasternak *et al.*, 2013; Slater, Barrett and Brown, 2018). Additionally, low food abundance may result in changes in social dynamics of the troop with more antagonistic behaviours seen within as well as between troops (Strum, 1982; Hamilton, 1985; Alberts, 2019). These social dynamics may lead to changes in movement

patterns, habitat use and activity budgets (Hamilton, Buskirk and Buskirk, 1975; Stueckle and Zinner, 2008).

Microhabitat and landscape selection are influenced by the trade-offs between competing ecological pressures. For instance, caves can serve as thermal refuges, shielding baboons from radiant heat on warm days (Hill, 2006) and minimizing heat loss in cooler conditions (Barrett *et al.*, 2004), while also offering protection from predators. Staying near sleeping sites during the hottest parts of the day also reduces travel distances (Hill, 2006) and enhances safety from predators while resting (Cowlishaw, 1997a). However, proximity to sleep sites may not always provide optimal foraging opportunities or favourable thermal conditions throughout the day. This study aims to quantify both the thermal landscape and resource availability to determine whether microhabitats are primarily selected for based on thermal pressures or food and water accessibility, and how these priorities shift seasonally.

Research Statement

Chacma baboons, known for their generalist behaviour, have been extensively studied, yet key factors influencing their landscape use (Stone *et al.*, 2013) and the role of temperature as an ecological constraint (Stelzner and Hausfater, 1986; Hill *et al.*, 2004) remain underexplored. There are few studies highlighting the thermal landscape as a driver of baboon ecology, despite it being found to be crucial in shaping ecological conditions that affect baboon behaviour, such as foraging (Hill and Dunbar, 2002). This study sought to address the influence of resource availability and thermal heterogeneity on the spatial behaviour of free-ranging baboons.

The study particularly focused on enhancing our understanding of thermal ecology in free-ranging baboons by investigating the impact of abiotic factors, including black globe temperature, on their landscape use, activity budgets, thermoregulatory strategies such as shade use, and movement. With climate change expected to increase thermal stress and contribute to habitat loss (Hill and Winder, 2019;

Sha *et al.*, 2020), understanding these dynamics is crucial. Rising annual temperatures may force primates to spend more time resting to avoid heat stress, reducing time available for nutrient acquisition and other essential behaviours (Korstjens, Lehmann, and Dunbar, 2010). Furthermore, selecting optimal thermal microclimates may result in trade-offs, such as reduced access to resources or increased predator exposure (Dunbar, 1992; Korstjens, Lehmann, and Dunbar, 2010).

Hypotheses and Aims

The aim of this study was to examine the potential drivers of wild chacma baboon landscape use, including food and water resource availability as well as the thermal landscape. I specifically aimed to examine how these landscape characteristics affect baboon movement (i.e., travel distance, travel rate, home range size and direction of travel), behaviour (i.e., resting, moving, feeding, socialising and shade use), and location of the troop; this being where in the landscape the troop spent more of their time.

The hypotheses that follow are based on the expectation that temperature, food availability (quantified through vegetation greenness, (NDVI; normalized difference vegetation index), and water availability (NDWI; normalized difference water index) interact to influence how baboons use their environment. In the Waterberg, the warm, wet season is characterised by high temperatures, as well as greater food and water availability, during which the thermal environment is expected to be the strongest driver of baboon movement, behaviour, and habitat use. Conversely, during the drier months, when NDVI and NDWI values are lower, baboons are expected to increase their travel rates and adjust their habitat selection to locate scarce food and water resources, while thermal constraints are likely to play a weaker role in shaping these patterns.

Research Objective 1

To evaluate how abiotic (temperature, water availability) and biotic (vegetation greenness) factors influence different aspects of baboon movement ecology. Within this research objective, I hypothesised that:

- baboons will reduce their travel distances as heat loads increase as well as during times of high vegetation greenness (NDVI) and water availability (NDWI).
- baboons will travel faster on days with higher heat loads, as well as when vegetation greenness (NDVI) and water availability (NDWI) is low.
- baboons will exhibit more directed travel patterns on days with higher heat loads, as well as when vegetation greenness (NDVI) and when water availability (NDWI) is low
- baboons will have smaller two-week home ranges with higher heat loads as well as when vegetation greenness (NDVI) and water availability (NDWI) is high.

Research Objective 2

- To evaluate how abiotic (temperature, water availability) and biotic (vegetation greenness) factors influence baboon behaviour. Within this objective, I hypothesised that: baboons will spend more time seeking shade with higher heat loads, as well as when vegetation greenness (NDVI) and water availability (NDWI) is low.
- baboons will spend more time resting and socialising as heat loads increase as well as when food and water availability (NDVI and NDWI) are high.
- travelling and feeding behaviours will increase with lower heat loads but will decrease when vegetation greenness and water availability (NDVI and NDWI) are high.

Research Objective 3

To evaluate how abiotic (temperature, water availability), biotic (vegetation greenness), and landscape factors influence baboon habitat selection.: Within this objective, I hypothesised that:

- baboons will select cooler microclimates as heat loads increase.

- baboons will prefer densely vegetated, low-elevation microhabitat types which may offer cooler microclimates.
- during the dry season when water availability is low, baboons will be found closer to river sites.

Methods

Study Species and Site

The *Papio* genus is distributed throughout sub-Saharan Africa (fig. 1) with *Papio ursinus* found in southern Africa, within a diverse range of habitats such as forests, savannas and desert regions (Barrett and Henzi, 2008; Town, 2018). Along with a broad distribution, chacma baboons have a diverse diet as generalist omnivores including various plant species, invertebrates and small vertebrates (Barrett and Henzi, 2008; Segal, 2008). Chacma baboons are sexually dimorphic with females weighing between 15 and 20 kg and males weighing twice that at 30 and 40 kg. Social groups range from 22 to 80 individuals with both male and female dominance hierarchies (Barrett and Henzi, 2008). These socially determined hierarchies influence individual access to resources, with higher-ranking individuals typically having priority access to food and greater reproductive success (Alberts, 2019).

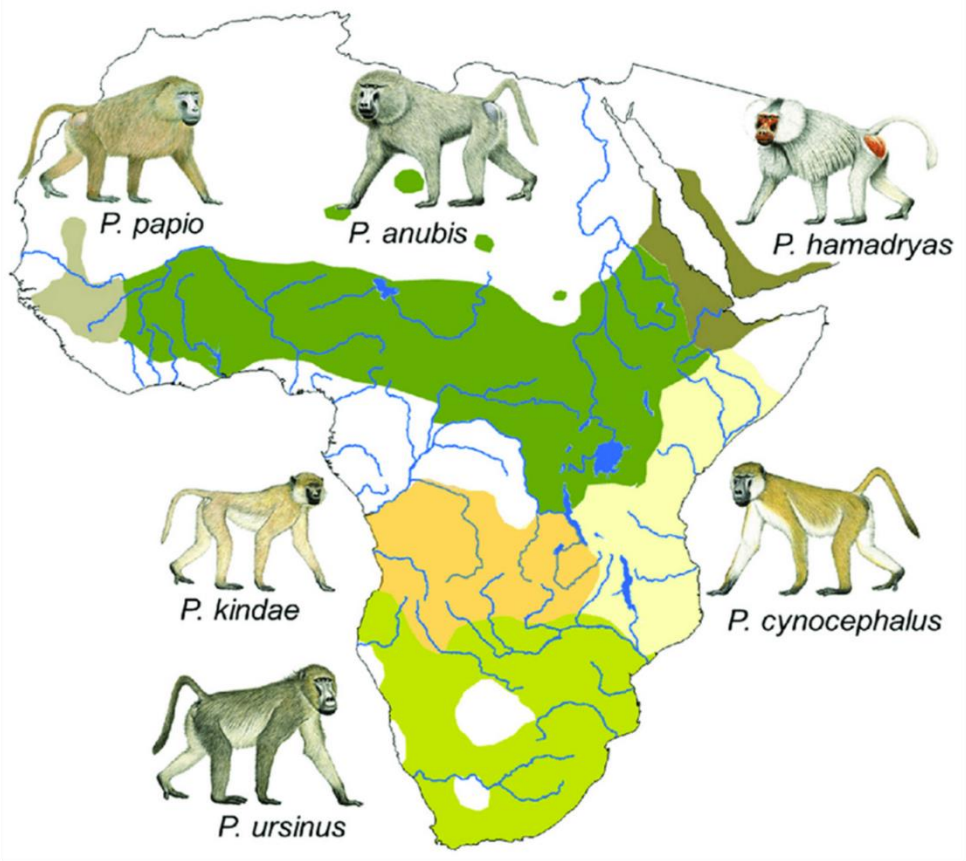


Fig. 1: Distribution map of six Papio species with P. ursinus shown in the southern African region (Fischer *et al.*, 2019)

The study troops were fully habituated to the presence of researchers in 2019, with each individual identifiable by natural markings and body variations. The troop included in my field data collection consisted of 69 individuals including 6 adult males, 20 adult females, 5 sub adult males, 6 sub adult females, 7 juvenile males, 9 juvenile females and 16 infants. The troop occupied a cliff cave sleep site with a river system directly below. Vegetation surrounding the river system includes species such as *Olea europaea subsp. cuspidate, Ficus cyathistipula* and *Commiphora pyracanthoides* with vegetation becoming sparser and grass dominated on the surrounding mountain ridges and plateaus.

Data were collected from multiple troops of free ranging chacma baboons (*Papio ursinus*) in the Swebeswebe Wildlife Estate (-23.743, 28.091) within the Waterberg region, in northern Limpopo province, South Africa (fig. 2). The study site covered approximately 50 km^2 and currently supports an estimate of four baboon troops, along with predator species such as leopard (*Panthera pardus*) and occasionally wild dogs (*Lycaon pictus*). The site also included vervet monkeys (*Chlorocebus pygerythrus*), which have a similar diet to the chacma baboon, potentially resulting in interspecific interactions and competition for resources (Lavigne and Matthews, 2009; Findlay and Hill, 2020).

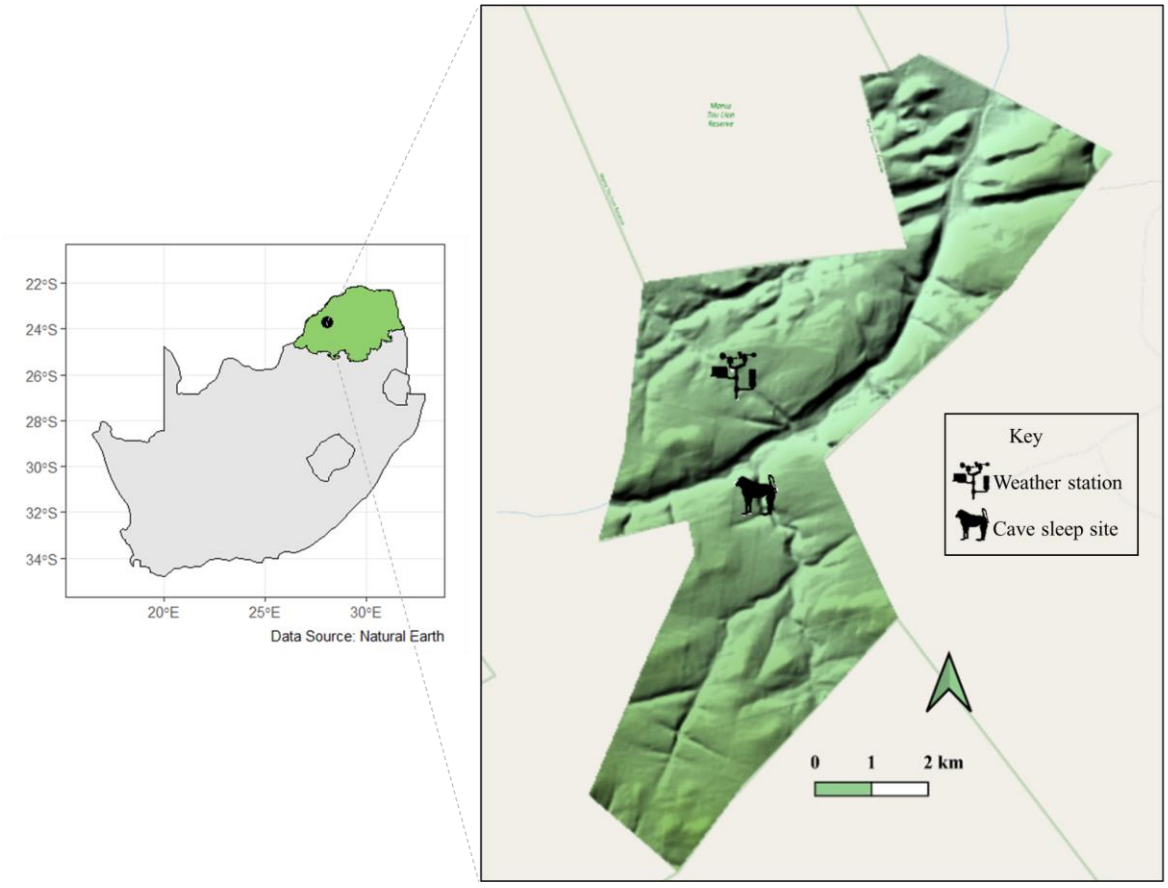


Fig. 2: Map of South Africa (left) produced in R 4.3.1 (R Core Team, 2022) with Swebeswebe Wildlife Estate (-23.743, 28.091) marked in black within Limpopo Province filled in green. Insert map of the study site, Swebeswebe Wildlife Estate, produced in QGIS (Version Bratislava, 2024) highlighting the location the Davis weather station (top) (-23.789, 28.060), and the troop cliff sleep site (bottom) (-23.809, 28.065). The main river system is found below the troop sleep site within the valley contours, as well as along the deep valley system separating the cave and weather station horizontally.

The wildlife estate is characterized by a complex network of rivers and tributaries, supporting diverse microhabitat types. The Waterberg region, classified as Bushveld (Codron *et al.*, 2005; Pitman *et al.*, 2013), encompasses distinct sub-habitats, including high-plateau savanna, riverine areas, and vegetated cliff sites, all actively utilized by the baboon population. These microhabitats vary in altitude, with the savanna plateau representing the highest elevations and the riverine areas the lowest, creating an elevation gradient of approximately 100 meters. Dominant vegetation includes species such as

Combretum spp., *Pterocarpus rotundifolius*, *Grewia flava*, *Commiphora marlothii*, and *Senegalia spp*. (Codron *et al.,* 2005).

The area experienced annual air temperature fluctuations ranging from 0°C to 42°C, with an average annual temperature of 25°C. Precipitation averages approximately 600 mm per year, with the warm wet season occurring between October and March and the cool, dry season occurring from April to September (Codron *et al.*, 2005; Pitman *et al.*, 2013). During the dry season average temperatures range from 14.5°C to 20°C, with the least precipitation recorded in June through to September, while the warmer wet season shows average temperatures of 16°C to 33°C (climate data sourced from Polokwane weather station and an online Waterberg weather archive, Meteoblue (n.d.)).

Behavioural Observations

For this study, I followed a single troop of baboons on foot for as long as possible during their activity period. Data collection typically started at dawn at the troop's sleeping cliff site (fig. 2) and concluded either at 17:15 on full collection days or earlier if the troop was lost for more than two hours. The troop had been habituated to the presence of observers, allowing data collection to be conducted at approximately five meters from individuals without disturbing natural behaviours. I collected data over a period that spanned roughly one year from March 2023 to January 2024, and for my analysis, I incorporated historical data from an additional three troops. It is important to note that two of the troops included in the previously collected data merged into a single troop at the end of 2021. The four troops included in the study were known as the Babes (n=25), Broken Tail, Kink Tail and the merged troop of Broken Tail and Kink Tail (n=69).

This historical data were collected between 2020 and 2023 by a team of field assistants from the Swebeswebe Primate Research Project. To maintain consistency in observational methods, documents outlining behavioural definitions and observation protocols were provided to incoming researchers and field assistants. Furthermore, experienced researchers provided training in the field to new team

members. Data collection by new personnel commenced only after their ability to accurately record observations was evaluated. Across the full dataset, data collection occurred an average of four days per week, with a median of 8 (IQR = 6.7) hours per day. There was a total of 1108 data collection days, with 582 days in contact with the various troops, resulting in 3483 contact hours and 99,025 behavioural scans. Contact days were distributed across all four troops, years, and seasons, though summer was underrepresented relative to other seasons. A detailed breakdown of contact days by troop, year, and season is provided in Table 1. During my fieldwork, I completed 155 days of data collection, with 442 contact hours and 9553 behavioural scans.

Table 1: Summary table of contact days by troop, year and season

	2020				2021			
	summer	autumn	winter	spring	summer	autumn	winter	spring
Babes	8	46	48	64	16	17	1	-
Broken Tail	-	-	-	-	-	11	-	-
Kink Tail	-	-	-	-	-	23	18	-
Broken Tail & Kink Tail	-	-	-	-	-	-	-	10

	2022				2023			
	summer	autumn	winter	spring	summer	autumn	winter	spring
Babes	-	-	-	-	-	-	-	-
Broken Tail	-	-	-	-	-	-	-	-
Kink Tail	-	-	-	-	-	-	-	-
Broken Tail & Kink Tail	20	36	46	56	23	38	40	57

	2024			
	summer	autumn	winter	spring
Babes	-	-	-	-
Broken Tail	-	-	-	-
Kink Tail	-	-	-	-
Broken Tail & Kink Tail	5	-	-	-

This research was conducted in accordance with ethical clearance from the University of Witwatersrand Animal Research Ethics Committee (AREC) (clearance number: 2022/03/04/B). Research was also conducted with permission from the Swebeswebe Wildlife Estate with section 20 permits obtained from the Department of Agriculture, Land Reform and Rural Development (04/05/2023).

Activity Budget and Thermoregulatory Behaviour

Behaviour was assessed by collecting behavioural data from as many individuals in the focal troop that could be located in the scanning period, using scan sampling methods at 30-minute intervals (Altmann, 1974). During each scan, troop members were classified into one of several mutually exclusive behavioural categories, namely social behaviour, resting, moving, or foraging. Within social behaviour, the behaviours of grooming or being groomed by others, aggression which is further defined as displacement, chasing, biting, facial and vocal threats were included. Social behaviour also included infant handling, mating and play behaviour which consists of multiple behaviours such as mock fighting and chasing without aggression. Resting behaviour included non-social, inactive behaviour such as sitting, sleeping and self-grooming while travel behaviour consisted of travelling in and with the group including walking, running and climbing. Lastly, foraging was grouped by ingestion of food or the preparation thereof, including the categories of feeding, suckling, digging and rock flipping. In addition, the specific thermoregulatory behaviour of shade seeking was recorded during these intervals. Data

collection was conducted on handheld Kindle Fire 7 devices (Amazon, 2019 release) equipped with Zoho Form software.

During each scan, GPS coordinates and elevation readings were recorded using a handheld Garmin eTrex 10 (Model 00970-00, Garmin) at the troop level to track movement patterns and calculate the rate of travel.

Table 2: Summary table of behavioural categories with corresponding behavioural descriptions and examples

Behaviour	**Description**	
Socialising	Grooming	Being groomed by others or grooming others
	Aggression	Displacement, chasing, biting, facial and vocal threats
	Infant handling	
	Mating	Including copulation, mounting, female presenting and resisting, male soliciting, mate guarding and following
	Play	Mock fighting and chasing without aggression
Resting	Non-social, inactive behaviour	Sitting
		Sleeping or laying down
		Self-grooming
Moving	Travelling in and with the troop	Walking
		Running
		Climbing
Foraging	The ingestion or preparation of food items	Feeding
		Suckling
		Digging
		Rock flipping

Weather Data

The onsite weather station (Davis Instruments, Vantage Pro2, Hayward, California, 94545, USA) recorded weather readings for the macrohabitat including black globe temperature, humidity, wind speed and rainfall. The Davis weather station was positioned approximately at the centre of the study site (fig. 2) and collected data at 30-minute intervals throughout the study period, coinciding with behavioural observations. Miniglobes (30 mm diameter copper globes painted matt black) were used to

assess environmental heat loads within representative microhabitats (Hetem *et al.*, 2007; Mitchell *et al.*, 2024). A minimum of three miniglobe thermometers were placed within each representative microhabitat to measure heat loads of open, shaded, and mixed coverage areas within each habitat type. Temperatures were taken at 30-minute intervals at a resolution of 0.0625 °C by data loggers (iButton, Maxim iButton DS1922E, Fairbridge Technologies, Gauteng, 2090, South Africa) placed within the miniglobes. Lastly, a handheld miniglobe thermometer was carried when tracking the troops to measure environmental heat loads at the troop level.

Microclimate Classification

During my year of observations, I positioned several miniglobe thermometers across the landscape to quantify microclimates. To quantify microclimates across the microhabitat types for earlier datasets, I interpolated the miniglobe logger data collected during my year of fieldwork to the broader field site dataset. The site was divided into labelled 100 m² grid cells based on both elevation and vegetation density. Elevation was categorized into three groups: low elevation (913 m – 1039 m), mid elevation (1040 m – 1152 m), and high elevation (1153 m – 1286 m), based on the range of elevation readings across the study area. Vegetation density was assessed using Google Earth imagery and a previously developed vegetation classification map of the site (Appendix S1).

A miniglobe was placed in full sun, partial shade and full shade within each vegetation and elevation type and extrapolated to similar grid cells across the field site. I calculated the difference in temperature between the miniglobe thermometers located within each microclimate and the black globe temperature data obtained from the weather station. These deltas were then used to interpolate the estimated microclimate temperatures for previous years based on historical macroclimate globe temperature data taken from the onsite weather station (n = 1566 days). The R^2 values for the interpolated miniglobe temperatures ranged from 0.75 to 0.98 with an average value of 0.9, indicating a strong correlation with the observed macrohabitat temperatures.

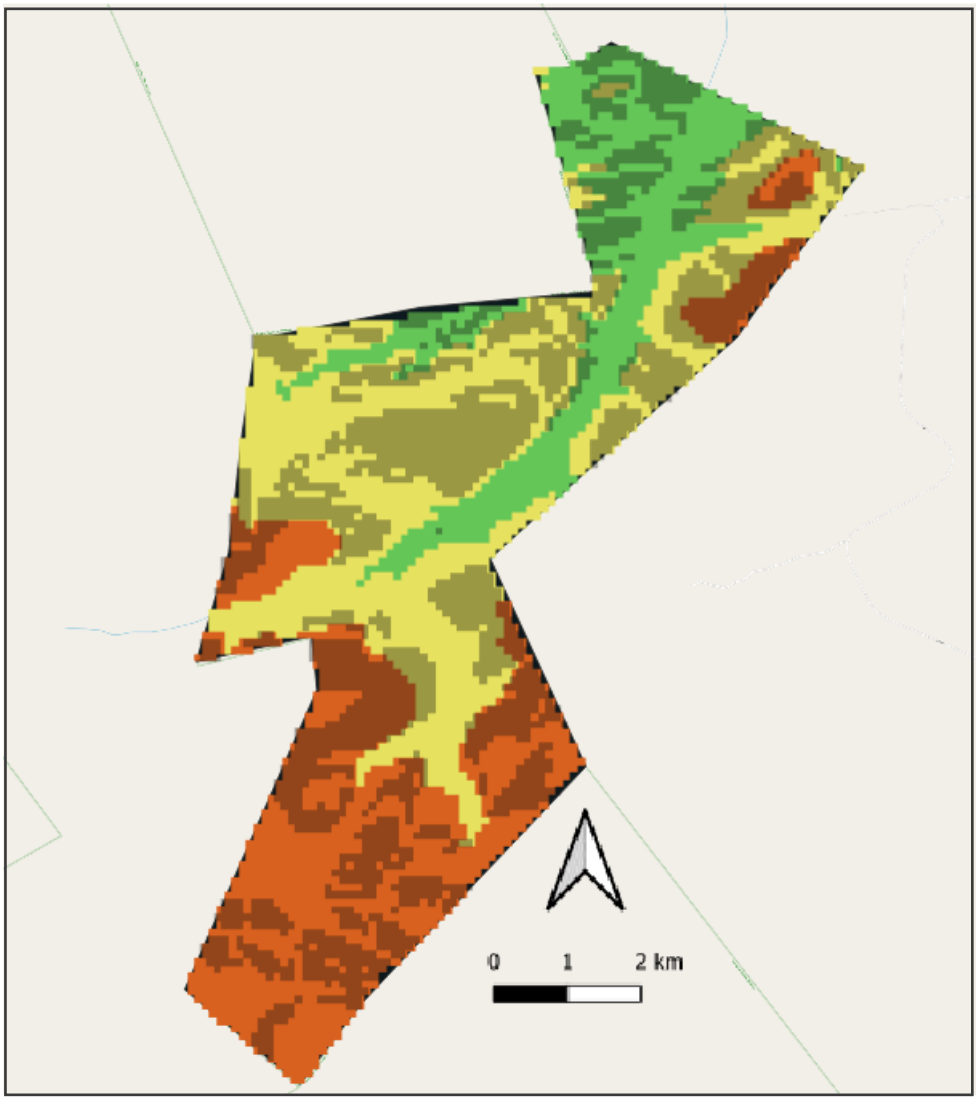


Fig. 3: Map showing the classified microhabitat types based on elevation (lowest being green 913 m – 1039 m, mid-level being yellow 1040 m – 1152 m, and highest orange 1153 m – 1286 m) as well as sparse vegetation shown by the shaded areas.

Food Abundance and Availability

Normalized Difference Vegetation Index (NDVI) provided an indication of seasonal changes in vegetation cover and productivity (Wiegand *et al.*, 2008; Wang *et al.*, 2021), as it provides a measure of the density of greenness and vegetational health in an area. NDVI datasets were obtained from the Sentinel-2 dataset (European Space Agency, 2022) at a 10 m spatial resolution and a 16-day temporal

resolution. The 16-day NDVI values represent past vegetation conditions, and the dataset was aligned with GPS data by matching each GPS point to the closest NDVI date within the collection period.

NDVI data were collected using Google Earth Engine (Gorelick *et al.,* 2017) and exported into QGIS (Version Prizren) (QGIS Development Team, 2023) for further analysis. NDVI values were extracted for 100 m² quadrats covering the study site. Each troop GPS coordinate was linked to the NDVI value of the quadrat within which it fell, allowing for the spatial alignment of NDVI data with the troop's movement patterns. These NDVI values were used in habitat selection analyses (discussed below) and exported into R 4.1.3 (R Core Team, 2022) to analyse the effects of vegetation greenness on daily movement and behavioural metrics, as well as habitat use. Temporal alignment and spatial extraction steps were implemented to ensure accurate association between NDVI and GPS data.

Water Availability

Normalized Difference Water Index (NDWI) datasets are commonly used to map and detect seasonal changes in surface water (Özelkan, 2020), providing insights into water availability within the study site. Normalized Difference Water Index datasets were obtained from the Sentinel-2 dataset (European Space Agency, 2022) at a 20 m spatial resolution and a 16-day temporal resolution. The 16-day NDWI values represent past surface water conditions which were linked to GPS data of the troops. Each GPS point was temporally aligned to the NDWI data by matching the GPS points that fell within the 16-day time frame of NDWI data collection, throughout the study period. NDWI data was accessed and processed using Google Earth Engine (Gorelick *et al.*, 2017), covering the entirety of the study period, and subsequently exported into QGIS (Version Bratislava) (QGIS Development Team, 2024) to calculate NDWI values within each grid of the study site. NDWI values were extracted for 100 m² quadrats within the study area. Troop GPS coordinates were then linked to the corresponding NDWI value of the quadrat within which each coordinate fell. The extracted NDWI values were used in habitat

selection analyses and were also exported into R 4.1.3 (R Core Team, 2022). In R, NDWI values were analysed to assess their effects on daily movement patterns, behavioural categories and habitat use.

Landscape features

The locations of critical resources such as water sources, caves and sleeping sites (Barton *et al.*, 1992; Willems and Hill, 2009), were recorded opportunistically whilst following the troop. Coordinates were placed on a topographical map of the baboon home range using QGIS and were layered with 100 m^2 gridded cells to create quadrats for spatial analysis (Barton *et al.*, 1992; Henzi, Byrne and Whiten, 1992) (fig. 4).

Features of the anthropogenic landscape were mapped including fences, buildings, sporadically filled cattle feeders, augmented watering holes and other manmade landmarks (fig. 4). Anthropogenic sources such as buildings have been included in the study due to the human shield effect (Nowak *et al.*, 2014). Baboons may slow their movement in these areas as well as increase feeding or resting behaviour due to a lowered perceived predation risk. Baboons may also have preference to areas of augmented watering holes and feeder sites, particularly in the dry season when food and water availability is scarce. These locations were recorded using GPS coordinates and Google Earth images and have been superimposed on a topographical map of the baboon home range. Gridded cells, 100 m^2 in size, were then placed over these landmarks along with daily GPS coordinates of the troop movement.

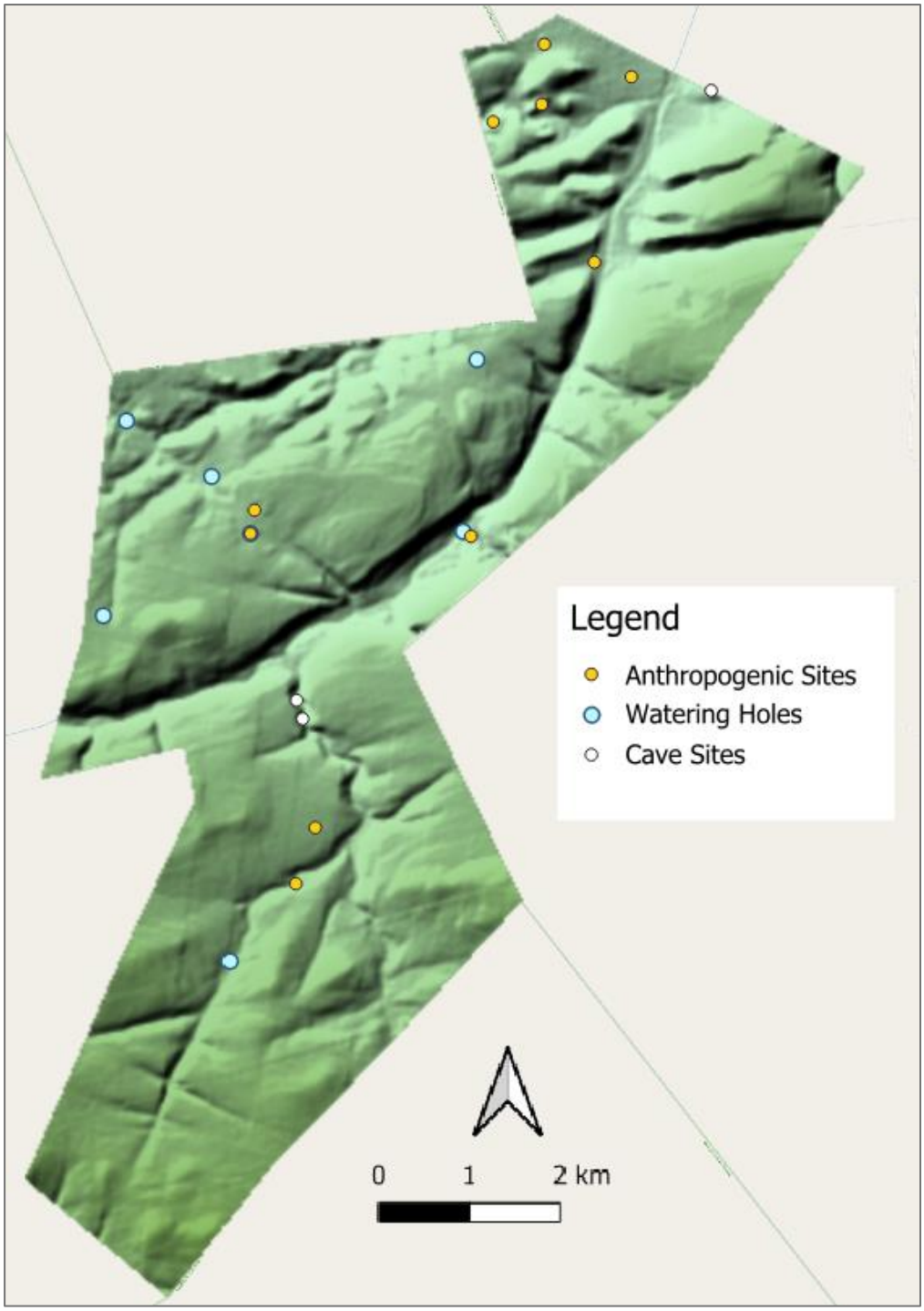


Fig. 4: Map showing GPS points of caves sites in white, anthropogenic sites in orange (buildings, augmented feeders and other built landmarks), watering holes in blue and fences found along the borders of the study site. Other water sources shown in figure 7.

Data analysis

Movement

To assess troop movement, I calculated the sum distance travelled between consecutive GPS points taken at 30-minute intervals across the day for each full day spent following the troop. I assessed daily travel rate by dividing the daily troop travel distance by the time spent following the troop for each full day. I calculated troop turning angles from GPS locations using the adehabitatLT package in R 4.1.3 (Calenge, Dray and Royer, 2024) where turning angle refers to the change in direction between consecutive movement steps, measured in degrees. I obtained turning angles for each movement step and calculated their absolute values to focus on movement deviations rather than directionality. Absolute angle values were then averaged across the day. Home range size was calculated using kernel density estimates in QGIS (Version Bratislava, 2024) in two-week intervals of daily GPS coordinates taken from the troops.

To evaluate the potential influence of abiotic variables, NDVI, and NDWI on daily troop travel distance, travel rate, and turning angle, as well as two-weekly home ranges, I conducted linear mixed models (LMMs) and confirmed appropriateness of the models by testing for heteroscedasticity. The movement LMMs and corresponding graphs were generated using R 4.1.3 (R Core Team, 2022). Only days with a complete set of GPS data were included to provide a more accurate representation of daily movement patterns (n = 285). For these complete days, daily travel distance was summed, travel rate was calculated as distance divided by time, and turning angles were averaged across all recorded movement steps for that day. Home range estimates were generated from GPS data collected over two-week intervals but were based on these complete daily datasets. In the LMMs, predictor variables included NDVI, NDWI and macroclimate temperature taken from the black globe thermometer of the onsite weather station. In the LMMs troop ID was specified as a random effect to account for variations between study troops. Photoperiod was included in each model as a fixed covariate to account for seasonal changes in daylight hours which may influence time available for travel as well as the number of recorded observations.

To check for collinearity amongst predictors I calculated the variance inflation factor (VIF). A threshold of VIF values less than five was used to confirm that multicollinearity was not a concern, as this threshold is appropriate for ecological analyses (Cobos *et al.*, 2019). In all movement models, predictors had VIF values below five, indicating acceptable levels of multicollinearity. To determine the most suitable model for each movement model, all potential models were compared based on the Akaike Information Criterion (AIC), using the MuMIn (Kamil Bartoń, 2010) and gtools (Warnes *et al.*, 2005) R packages. During model selection, the top five models, defined by the lowest AIC values, as well as the null model were included (Appendix) to compare weighting and AICc values (Wagenmakers and Farrell, 2004) as well as conditional R^2 values. If a model differed by less than two delta AIC from the top model, the most parsimonious model, defined by the fewest predictors, was selected as the top model (Aho, Derryberry and Peterson, 2014).

To further visualize the effects of vegetation greenness and water availability on two-weekly home range size, heat maps of baboon distribution were created in QGIS and overlaid onto maps showing NDVI and water sources for the dry and wet season. For vegetation greenness NDVI values were taken from one 16-day measurement period in the dry season (taken as the first measurement period of June) as well as for the wet season (taken as the first measurement period of January) for one year of the study. These were overlaid with the corresponding two-week home range values, visualised using kernel density estimates. With water availability, the entirety of the study period was used, with home ranges delineated into the dry and wet season. The home ranges were visualised using the stylized heatmap function in the density analysis plugin in QGIS (Hamilton, 2024). GPS locations of watering holes and a polygon layer of the river system (taken from Appendix S1) within the study site were overlaid to visually assess distribution regarding water sources.

Behaviour

I ran a series of generalized linear mixed models (GLMMs) to investigate the effects of mean daily black globe temperature, NDVI, and NDWI on baboon activity budgets (i.e., the count of foraging,

resting, moving, and socializing) as well as shade use behaviour. These models used a negative binomial distribution (McFarland, Barrett, Costello, *et al.*, 2020) and included troop ID as a random factor to account for variation amongst troops. The total number of behavioural scans per day was included as an offset. Collinearity was assessed using the variance inflation factor (VIF), where all models showed VIF values below 2.5, indicating minimal collinearity. As per the movement models, top models were defined by the lowest AIC values with the most parsimonious model selected.

Spatial Analysis

To visually compare the range of temperatures available to the baboons within each microhabitat, I plotted a mean temperature graph across a 24-hour period for each elevation category in both dense and sparse areas.

To quantify microclimate selection by the baboons in the wet and dry season, I correlated the handheld miniglobe readings used to measure the microclimate at the troop level with readings taken from an identical miniglobe thermometer placed in full sun in the top elevation in sparse microhabitat. A line of identity was then fitted, and regression lines fitted to assess selection of different microclimates during the wet and dry seasons. Slopes of the regression lines were compared to the line of identity (slope = 1) to determine the extent of selection for more stable microclimates, where slopes less than one indicate selection for more stable conditions (Hetem *et al.*, 2007). These patterns were visually assessed and statistically compared using a linear model with season as a covariate to determine whether baboons selected different microhabitat temperatures between the wet and dry seasons.

I then quantified microclimate selection by calculating the difference between troop-level miniglobe temperature, and the temperature recorded by the miniglobe in full sun at the highest elevation sparse microhabitat. Temperature differences were taken over the baboon activity period (06:00 – 17:00)

during both wet and dry seasons, with data collection in the 30-minute intervals collapsed into hourly temperatures by averaging the values.

I ran a linear mixed model (LMM) to assess the relationship between microclimate selection and NDVI, NDWI and black globe temperature, with season and time of day ran as fixed covariates. The random effect of troop ID used to account for variation amongst troops. Model selection was performed using Akaike Information Criterion (AIC) values, with model comparisons based on AIC weights and conditional R^2 values. Competing models within two delta AICs of the best-supported model were considered, and model selection was based on the most parsimonious model.

To assess preference for different microhabitats, I calculated Ivlev's electivity index [EI=$(ri-ni)/(ri+ni)$]. This calculation indicates which microhabitats are preferred by comparing the proportion of time baboons spend in each microhabitat to its relative availability within the study site (Ivlev, 1961; Martinoli *et al.*, 2006; Henzi *et al.*, 2011). Within the electivity index, *i* represents the microhabitat, *ri* the proportion of study subject observations in that area and *ni* the proportion of microhabitat *i* available within the study bounds. Values range from -1 to 1, where positive values indicate preference, negative values indicate avoidance, and values near zero suggest use proportional to availability. I used the index on troop GPS data to assess the proportion of time each troop spent in the respective microhabitats. A linear mixed model (LMM) was used to assess how factors such as season, time of day, and microhabitat type influenced the Ivlev's Electivity Index. The LMM included troop ID as a random effect to account for variability among troops.

To assess seasonal patterns of occupancy, predicted troop count per grid was modelled in R 4.1.3 (R Core Team, 2022). Data linked to the grid cells on the study map were aggregated by day to be run as generalised linear mixed model (GLMM) predictors, with the frequency of troop occurrence per grid cell used as the response variable. The GLMMs were run separately for the dry and wet seasons, to assess the landscape features preferred by the troops at different times of the year. NDVI, NDWI, modal microhabitat type as well as distances from river sites, watering holes, the main cave sleep site, fences,

and other anthropogenic sites (such as buildings) were included as predictors. Troop ID and grid cell ID were treated as random effects to account for repeated measurements per troop and grid cell. Model selection was conducted for both the wet and dry season models by comparing the top five models and null models based on their AIC values, weighting and R^2 value. As above, models that differed by less than two delta AIC from the top model were chosen if they were the most parsimonious. I ran a global Moran I statistic test on the GLMMs to assess spatial autocorrelation (Moran, 1950; Willems and Hill, 2009) using the spdep package in R 4.1.3 (Bivand, 2002). The Moran I values were close to zero as well as a negative value (-0.02) for the dry season model and (-0.03) for the wet season model indicating the model residuals were spatially independent and nearby values were dissimilar from each other. The original models were kept without needing to incorporate spatial dependencies.

Visualizations of the predicted data were generated as 3D heatmaps in QGIS to illustrate spatial and seasonal variations in troop distribution. Inverse Distance Weighted (IDW) interpolation, weighted by the predicted count data, was used to create these heatmaps. The heatmaps were overlaid on the landscape of the study site to identify key features influencing troop movement, and were then visualized in the QGIS2threejs plugin (Akagi, 2025) to produce three-dimensional plots.

To further assess the relationship between troop movement and landscape features, I ran linear mixed models (LMMs) for distances from the river network with the predictors of NDVI, black globe macrohabitat temperature and troop level microclimate temperatures, with season and photoperiod as fixed effects. Troop ID was included as a random effect to account for variability among the four study troops. NDWI was not included as it covaries with surface water found at river sites. Model variance inflation factor showed values under five for all predictors. Model selection was based on comparing Akaike Information Criterion (AIC) values weight and R^2 values, with the most parsimonious model selected if it fell within two delta AIC of the top model.

Results

Macrohabitat Summary

Black globe temperature, humidity, wind speed and rainfall was summarized in terms of daily averages, maximums and minimums for the dry and wet season (Table 3). The wet season was ~5 °C warmer than the dry season on average. The wet season also had higher humidity readings with an average of 73% compared to 66% in the dry season, while wind speed had similar values for both seasons. The wet season had far greater total rainfall over the entire four-year study period with readings of 1233.91mm compared to the dry season with a total of 304.78mm. Within the wet season the months of January, February and March had the highest rainfall values.

Table 3: Summary table of weather variables in the dry season (left) and wet season (right) taken from the onsite weather station in Swebeswebe wildlife estate. Weather variables include daily averages of black globe temperature, humidity, wind speed and rainfall over four years of data collection (n = 1481). Standard deviation represents variability between days.

	Wet season			Dry Season		
Weather Variables	Mean ± SD	Maximum	Minimum	Mean ± SD	Maximum	Minimum
Temperature (°C)	27.83 ± 2.79	34.82	15.19	22.01 ± 3.14	29.93	14.14
Humidity (%)	73 ± 18	97	8	66 ± 17	97	9
Windspeed (m/s)	1.2 ± 1.6	11.3	0.0	1.2 ± 1.6	11.3	0.0
Total Rainfall (mm)	1233.91			304.78		

Movement

Baboons travelled greater distances when heat loads were high, and vegetation greenness (NDVI) and water availability (NDWI) was low. The best model for daily distance travelled included all predictors: NDVI, NDWI, and black globe temperature (Table 2). This model had the lowest AIC value with no other models being within two delta AIC. The model used also had the highest weight (0.995), providing strong support for its selection (Appendix S2). The conditional and marginal R^2 values indicate that

while fixed effects explain 16.9% of the variance in travel distance, the inclusion of random effects improved the model fit, capturing 22.4% of the total variance. NDVI was the strongest predictor of daily distances travelled by the troop along with confidence intervals which were both below zero. While NDWI had the same directional effect as NDVI in this model, it was the weakest predictor of travel distance with a CI range that overlaps with zero, and so suggesting it is not as influential a factor in driving daily travel.

Table 4: Factors influencing daily distance travelled by four *P. ursinus* troops in Swebeswebe wildlife estate with the predictors of NDVI, NDWI and macrohabitat temperature as well as photoperiod as a fixed covariate and troop ID as a random effect. A sample size of 285 full days over four years. Intraclass correlation coefficient (ICC) is included.

	Effects on daily distance travelled (m)	
Predictors	*Estimates*	*CI*
(Intercept)	2007.53	-4515.24 – 8530.29
NDVI	-815.61	-1256.55 – -374.67
NDWI	-222.66	-644.05 – 198.72
Macroclimate Temperature	706.18	152.42 – 1259.95
Photoperiod	425.69	-117.00 – 968.38
Random Effects		
σ^2	9018325.30	
$\tau_{00\ TravelTroop}$	635484.66	
ICC	0.07	
$N_{\ TravelTroop}$	4	
Observations	285	
Marginal R^2 / Conditional R^2	0.169 / 0.224	

Although the baboons travelled greater distances when vegetation greenness was low, they did not travel these distances faster. Within the models for daily travel rate, the null model was the strongest, with an AIC of -609.51 and a weight of 0.82 (Appendix S3), indicating that none of the predictors (NDVI, NDWI, and black globe temperature) included in the tested models provided additional

explanatory power beyond random variation. No models were found to be within two delta AIC of the top, null model.

Baboons also did not alter their direction of travel with changing heat loads, vegetation greenness and water availability with the null model being the top model after selection processes (Appendix S4). The null model had an AIC of 457.81 and a weighting of 0.83 with no other models falling within two delta AIC of this model.

Greater daily travel distances aligned with two-weekly home range sizes. Home range size was negatively associated with water availability (NDWI), (fig. 5), with the best model including only NDWI as a predictor. There was one other model within two delta AIC of the top model which included vegetation greenness (NDVI), with home ranges larger when it was greener (fig. 6). However, water availability was the stronger driver of home range size and selected as the most parsimonious model. The top model had the lowest AIC and the highest weight of 0.37, indicating moderate support (Appendix S5). The fixed effects of the model explained 9.7% of the variance in home range size, but the inclusion of random effects greatly improved the model fit, explaining 47.5% of the total variance.

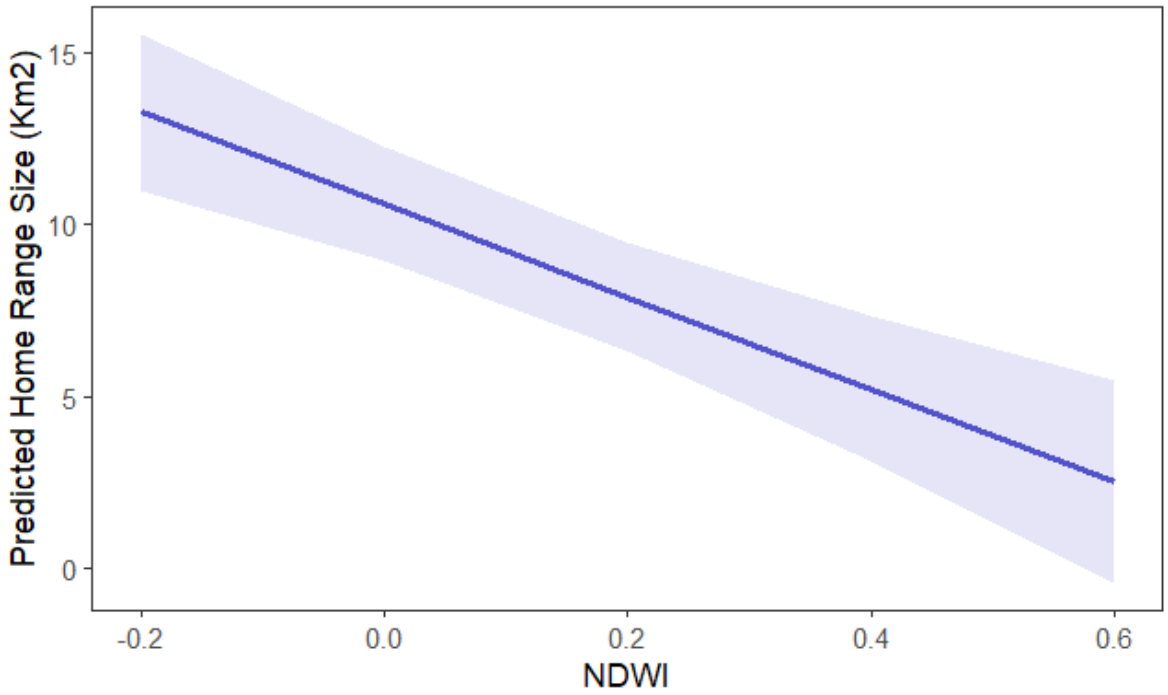


Fig. 5: Predicted two-weekly home range size (km^2) of four *P. ursinus* troops against normalized difference water index (NDWI) values. Movement measurements are taken as the average daily distance travelled by the troop in two-week intervals over four years in Swebeswebe wildlife estate. Linear mixed models were fitted with the troop ID as a random effect and photoperiod as a fixed covariate where models followed gaussian distribution. N = 284.

Two-week home ranges in the dry and wet season overlaid on top of NDVI maps showed that in the wet season, when vegetation greenness was greater, baboons had less constrained distribution as compared to the dry season (fig. 6). In the dry season baboon distribution is concentrated along the main valley system of Swebeswebe while in the wet season their distribution spreads further north and south of these valleys.

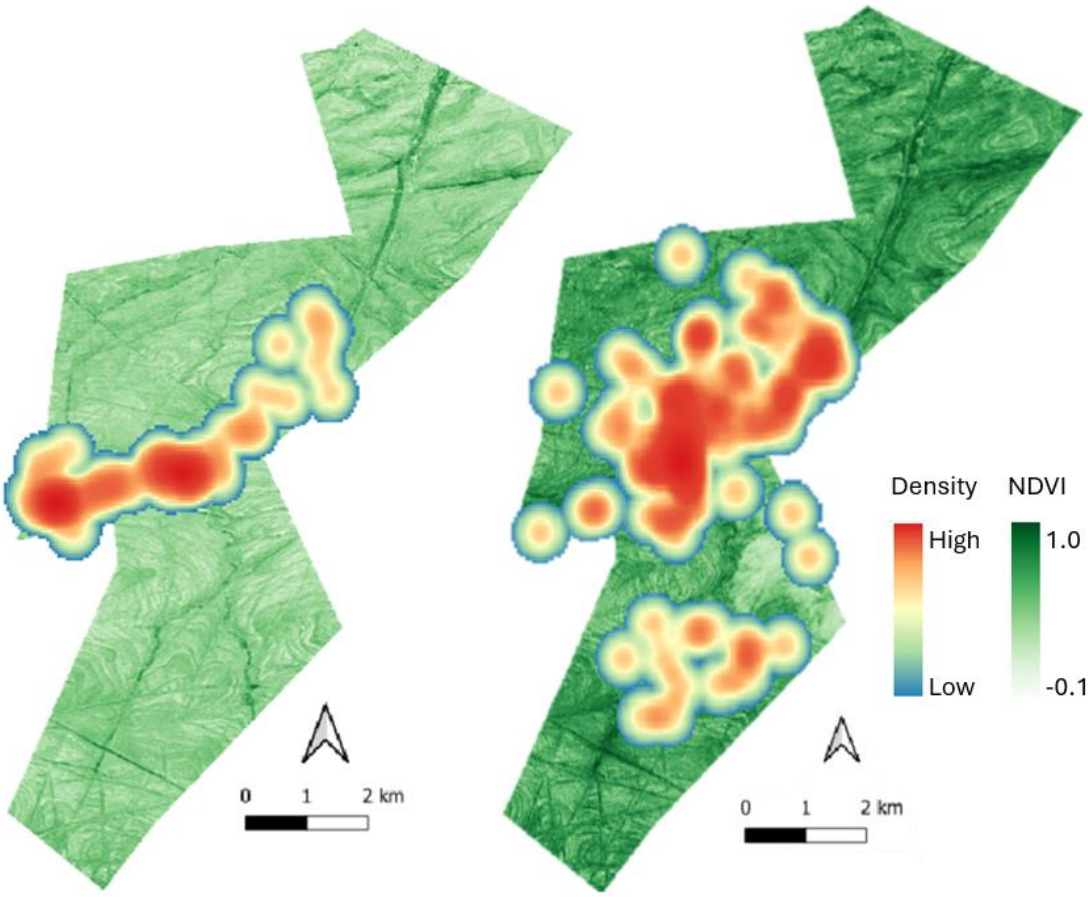


Fig. 6: Map of Swebeswebe field site showing NDVI measurements for one 16-day period in the dry season (June) (left) and a 16-day period in the wet season (January) (right) in 2023. The NDVI maps were overlaid with kernel density estimates of two-weekly home range use aligning with the NDVI period for one troop of *P. ursinus.*

Heat maps of the two-weekly home ranges in the dry and wet season overlaid with water sources were created to help visualise the spatial distribution of baboons in response to water availability (fig. 7). The dry season shows a more pronounced distribution along the main river system, branching in both easterly and westerly directions, along with a greater central distribution around the cave area as compared to the wet season.

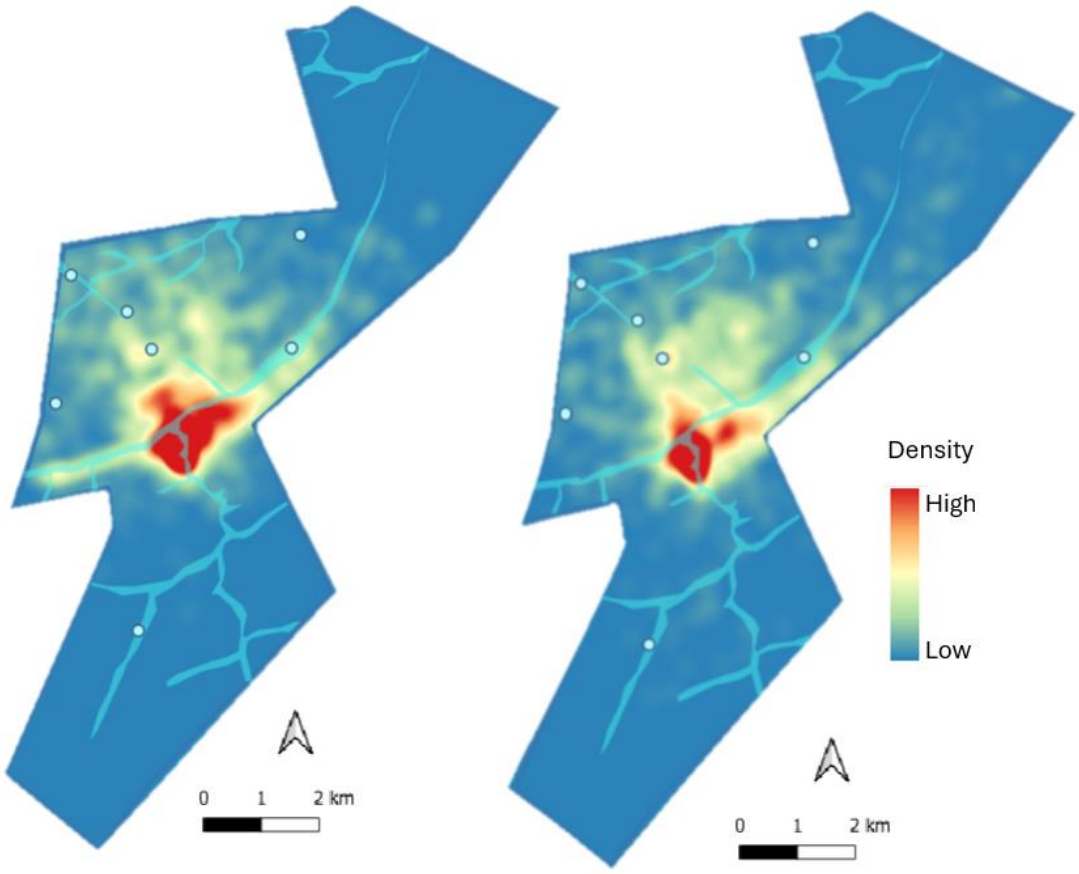


Fig. 7: Map of Swebeswebe field site showing a heat map of the two-week baboon home range for the dry season (left) and wet season (right) taken over four years of data collection, sampling four baboon troops. The maps are overlaid with watering hole points and a polygon of the main river network (Appendix S1).

Behaviour

Consistent with baboons travelling greater distances with increasing heat loads, the time engaged in travel behaviour increased with black globe temperatures shown by an incident rate ratio (IRR) above one (1.04) (Table 3.1). The incident rate ratio of 1.04 indicated that for every 1°C increase in black globe temperature, the predicted counts of travel behaviour increased by 4%. Baboons also spent a greater amount of time engaged in travelling with greater water availability (IRR = 1.08), contrasting with previous travel distance results. The second model was chosen during model selection as it was the most parsimonious, leading to the exclusion of NDVI as a predictor. This chosen model had a weight

of 0.27 as opposed to 0.59 in the top model (Appendix S6). The chosen model's conditional R^2 value was low (0.02), suggesting that these variables explain only a small proportion of the variation in travel behaviour, although the inclusion of random effects slightly improved the model's fit.

Similarly to travel behaviour, baboons increased their time spent resting when NDWI and macrohabitat black globe temperature increased (IRR of 1.11 and 1.22 respectively) (table 3.1). This model had the lowest AIC with one other model within two delta AIC, although the top model was kept as it was the most parsimonious, excluding NDVI as a predictor. The top model further had the highest weight (0.69), indicating strong support (Appendix S7). The model's conditional R^2 was low (0.03), indicating that the predictors accounted for only a small proportion of the variation in resting behaviour. Additionally, the marginal and conditional R^2 values were identical, suggesting that the inclusion of random effects did not contribute to explaining additional variance in the model.

Unlike travel and rest behaviour, baboons foraged less with increasing NDWI, and black globe temperatures shown by IRR values below one (0.89 for both predictors) (table 3.1). The incident rate ratios for foraging behaviour indicated that every unit of increase in temperature and NDWI corresponded with a 11% reduction in predicted foraging counts. The selected model had the lowest AIC, with one other model within two delta AIC. However, the top model was preferred as it was the most parsimonious, again excluding NDVI as a predictor. Additionally, the top model had the highest weight (0.63), suggesting strong support (Appendix S8) but, as with the other behavioural models, it showed a low conditional R^2 value of 0.03. While random effects explained additional variance in the model this was slight (marginal $R^2 = 0.026$ and conditional $R^2 = 0.034$).

Baboons increased social behaviour with increasing NDVI values (IRR = 1.16), unlike other behaviours that do not show NDVI to be a significant influencer. Interestingly, baboons also increased their time engaged in social behaviours as NDWI values decreased (IRR = 0.92) with the indices for water and vegetation not showing any correlation during model selection (VIF: NDVI = 1.16, NDWI = 1.06). The best model (table 3.1) had the lowest AIC with one other model falling within two delta AIC of

this, however it included the predictor of black globe temperature and so it was not chosen following parsimony. The chosen model had the highest weight of 0.53 (Appendix S9) and another low conditional R^2 value of 0.05. Even though the conditional R^2 was low, the addition of random effects improved the models fit, explaining 5.4% of the model's variance as opposed to 0.8% explained by fixed effects alone.

Table 5.1: Factors influencing activity budget categories with the predictors of NDVI, NDWI and macrohabitat black globe temperature from three troops of *P. ursinus* taken over four years of data collection in Swebeswebe wildlife estate. Photoperiod was run as a fixed effect and troop ID (BehTroop) as a random effect. Incidence ratio rate and confidence intervals included, with 464 observations for each model.

	Travel Behaviour		**Rest Behaviour**		**Foraging Behaviour**		**Social Behaviour**	
Predictors	*Incidence Rate Ratios*	*CI*	*Incidence Rate Ratios*	*CI*	*Incidence Rate Ratios*	*CI*	*Incidence Rate Ratios*	*CI*
Intercept	1.09	0.80 – 1.49	0.03	0.02 – 0.05	0.19	0.12 – 0.28	0.09	0.04 – 0.20
NDWI	1.08	1.05 – 1.11	1.11	1.05 – 1.17	0.89	0.85 – 0.92	0.92	0.86 – 0.99
Macrohabitat Temperature	1.04	1.01 – 1.07	1.22	1.16 – 1.30	0.89	0.85 – 0.93		
Photoperiod	0.93	0.91 – 0.96	1.11	1.06 – 1.16	1.04	1.01 – 1.08	1.00	0.94 – 1.06
NDVI							1.16	1.07 – 1.25
Random Effects								
σ^2	1.13		2.36		1.47		2.44	
τ_{00}	0.01_{BehTroop}		0.00_{BehTroop}		0.01_{BehTroop}		0.12_{BehTroop}	
ICC	0.01		0.00		0.01		0.05	
N	3_{BehTroop}		3_{BehTroop}		3_{BehTroop}		3_{BehTroop}	
Observations	464		464		464		464	
Marginal R^2 / Conditional R^2	0.013 / 0.021		0.029 / 0.029		0.026 / 0.034		0.008 / 0.054	

Baboons sought out shade more frequently with increasing heat loads and vegetation greenness (IRR of 1.27 and 1.14 respectively) (table 3.2.). There was one model within two delta AIC of the top model, and this model was chosen as it excluded the predictor of NDWI (Appendix S10). The chosen model had a weighting of 0.26 compared to the top model's weight of 0.66 with the chosen model also showing a low conditional R^2 value of 0.08, similar to the above behavioural models. However, random effects again improved the models fit, explaining 8.4% of the model's variance compared to 3.9% explained by the fixed effects.

Table 5.2: Factors influencing daily shade use of three *P. ursinus* troops in Swebeswebe wildlife estate with the predictors of NDVI and macrohabitat black globe temperature as well as photoperiod as a fixed covariate and troop ID as a random effect. A sample size of 464 days has been used over four years. Intraclass correlation coefficient (ICC) is included.

	Effects on shade use	
Predictors	*Incidence Rate Ratios*	*CI*
(Intercept)	0.13	0.05 – 0.35
NDVI	1.14	1.04 – 1.25
Macroclimate Temperature	1.27	1.16 – 1.38
Photoperiod	1.05	0.97 – 1.14
Random Effects		
σ^2	1.70	
$\tau_{00\ BehTroop}$	0.08	
ICC	0.05	
$N_{\ BehTroop}$	3	
Observations	464	
Marginal R^2 / Conditional R^2	0.039 / 0.084	

Habitat Selection

To understand how baboons used different microhabitats, variations in temperature across open and densely vegetated areas were assessed across three elevation categories (fig. 8). Within the open (sparsely) vegetated areas, the mid-elevation microhabitat peaked earliest, on average, reaching its maximum temperature of 33.0±5.8 ℃ at 13:30, closely followed by the low-elevation microhabitat, which peaked at 31.4±7.1 ℃ at 14:00, and the high-elevation microhabitat, which peaked at 33.7±5.5 ℃ at 14:30. The open areas within the riverine microhabitat peaked at 15:00, with a maximum temperature of 30.6±9.6 ℃. Notably, the small differences in peak temperatures across these sites fall within the variability (SD) of each microhabitat, suggesting that the timing of peak temperatures may be more significant than the absolute temperature differences.

In contrast, within dense vegetation areas, lower elevation microhabitats exhibited slightly higher temperatures than high-elevation areas. The low-elevation dense microhabitat reached its maximum temperature of 30.8±6.2 ℃ at 13:30, compared to 30.0±7.0 ℃ at the high-elevation site at the same time. However, the large standard deviations suggest that these differences of less than 1 ℃ were not significant. The mid-elevation, dense microhabitat peaked slightly later at 14:00, with a maximum temperature of 30.6±9.6 ℃.

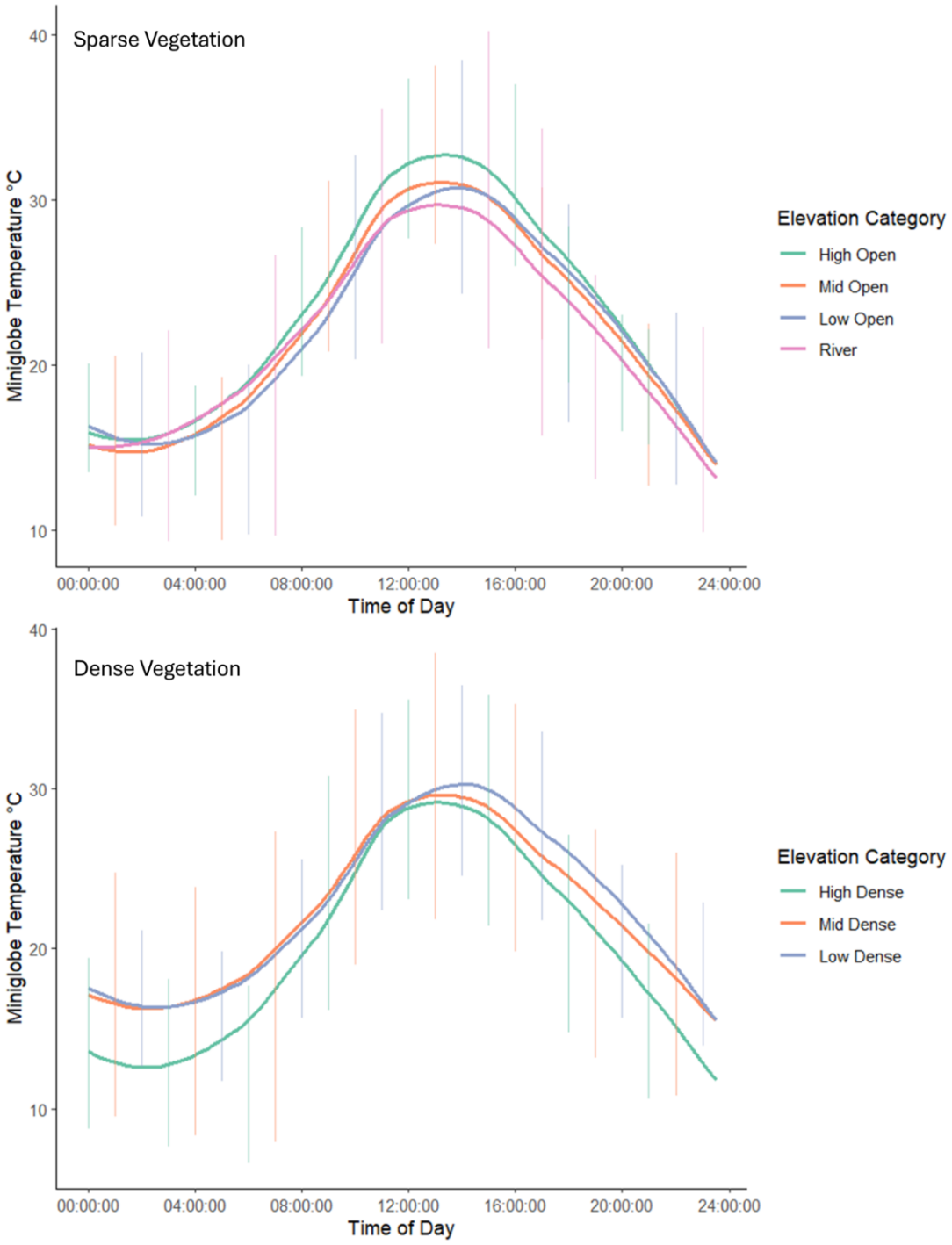


Fig. 8: Line graphs showing the average temperatures taken from miniglobe thermometers throughout a 24-hour day with standard deviation for different elevation categories. Line graphs separated into the sparsely vegetated category (above) and the densely vegetated category (below) with categories defined using fig. 3 and appendix S1. Data was taken from miniglobe thermometers placed in representative microhabitats over the course of a year in Swebeswebe wildlife estate.

While the above patterns outlined the microclimates available to baboons, I further assessed how baboons adjusted their microclimate temperature selection, specifically across seasons. I correlated the troop-level miniglobe temperature with that of an identical miniglobe positioned in the sun at the top elevation open vegetation site for both the dry and wet seasons (fig. 9). In the dry season, the regression slope under one and high R^2 value ($R^2 = 0.80$, slope = 0.74, $P = 6.97e^{-156}$) indicates that baboons actively selected for more stable microclimates. When comparing the slope to the line of identity, the dry season showed to have a slope significantly less than one ($t = -14.48$, $p < 1e^{-5}$). The wet season showed a similar pattern with a slightly lower r^2 value and a slightly higher slope value ($r^2 = 0.77$, slope = 0.78, $P = 2.51e^{-57}$) as well as a slope again significantly less than one ($t = -6.73$, $p < 1e^{-5}$). The steeper slope in the wet season suggests that baboons exhibited less selection for stable microclimates and had greater exposure to variable temperatures compared to the dry season. A comparison of the dry and wet season slopes revealed a significant difference ($p = 0.02$). Additionally, in the wet season, baboons selected temperatures that were, on average, 0.68°C higher than in the dry season.

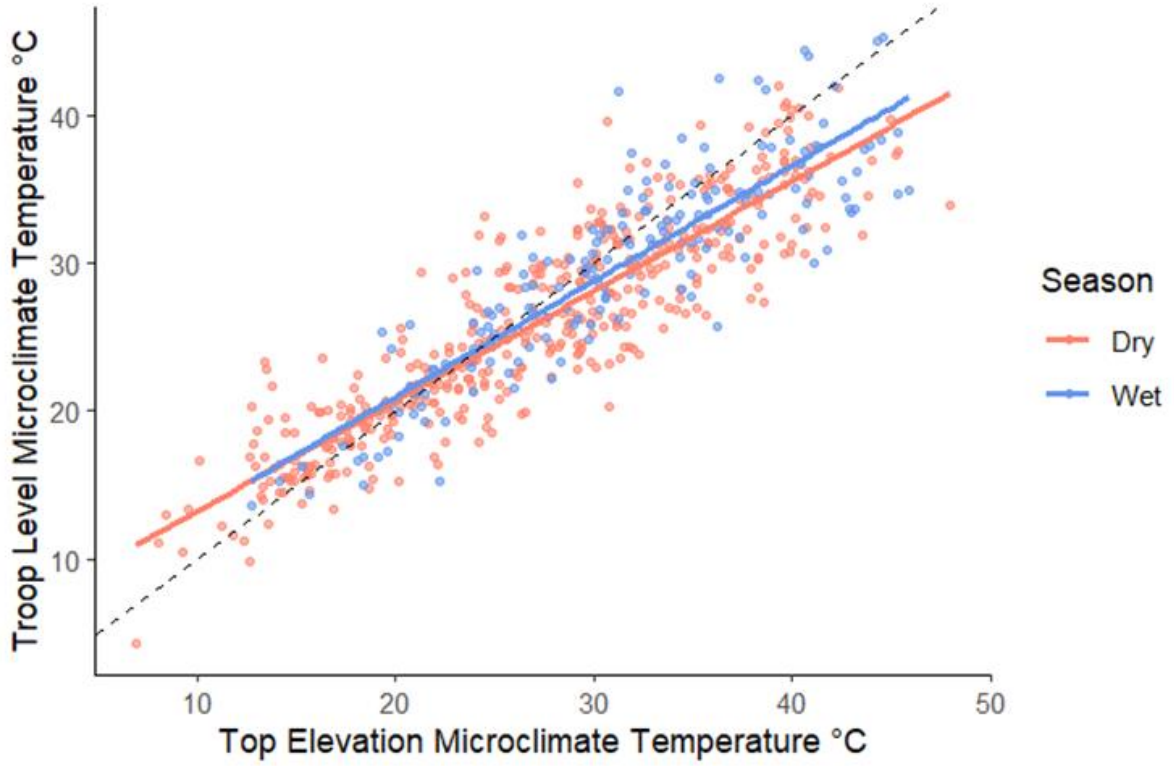


Fig. 9: Scatter diagram showing the relationship between miniglobe temperatures at the troop level against that of an identical miniglobe temperature logger placed in full sun at a top-level elevation sparse microhabitat site for the dry and wet season. A line of identity has been fitted (black) as y = x as well as regression lines of each season (dry: y = 5.76 + 0.74x, wet: y = 5.29 + 0.78x). Data was taken from miniglobe thermometers placed in representative microhabitats over the course of a year in Swebeswebe. wildlife estate following one troop of *P. ursinus.*

I further examined temperature differences between the troop-level miniglobe and a reference miniglobe thermometer placed in full sun at a sparsely vegetated high-elevation site during the baboon activity period (06:00 – 17:00). The negative values indicate that the troop's microclimate temperatures were lower than those at the high elevation site, suggesting a preference for cooler areas (fig. 10). This preference for cooler microclimates is evident from midday in both seasons but becomes more pronounced during the wet season, when mean daily temperatures are higher. In the wet season, baboons selected microclimates that were up to 4°C cooler than the top elevation site whereas this selection is closer to 2°C cooler in the dry season. Additionally, baboons show a tendency to select warmer

microclimates toward the end of their activity period in the wet season as opposed to the dry season where they continue to select for cooler temperatures nearing the end of day. A linear mixed model

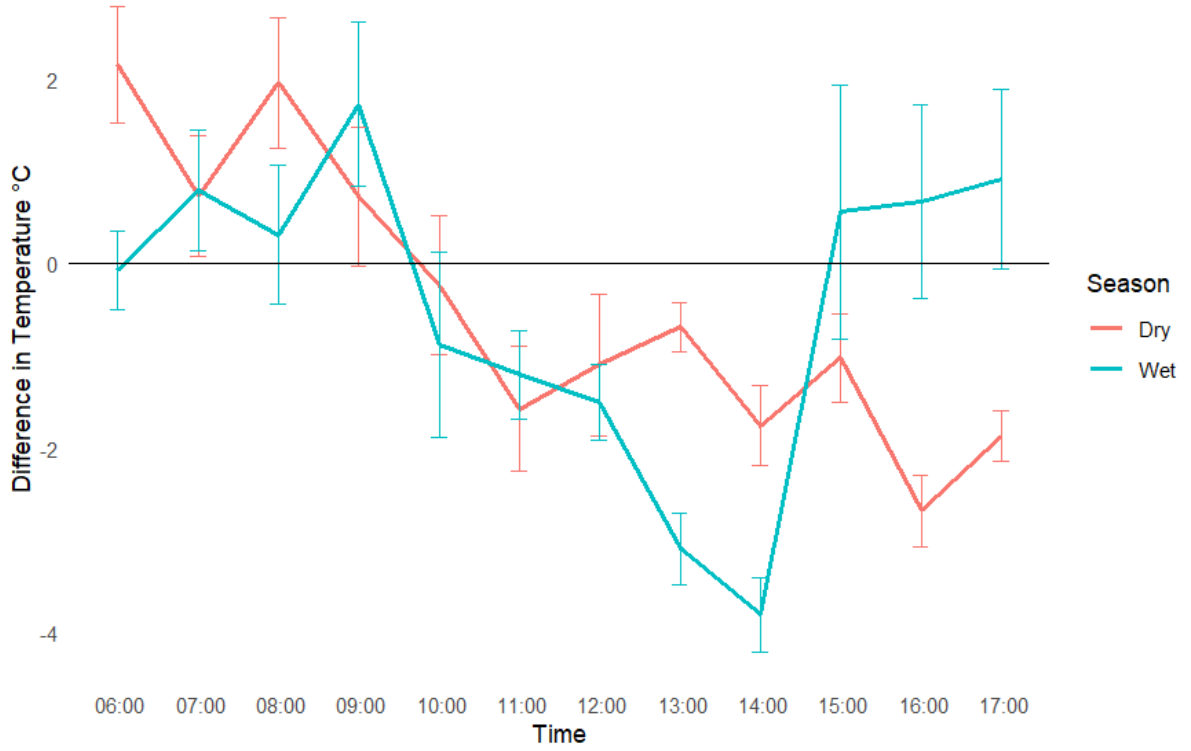


Fig. 10: Mean ± SD of the difference between troop-level microhabitat temperature (°C) and top-elevation sparse microhabitat temperature (°C) over the baboon activity period (06:00–17:00) during the dry and wet seasons. Negative values indicate cooler temperatures in the troop's microhabitat compared to the top-elevation site, suggesting selection for cooler microclimates. Temperature data were recorded using a single miniglobe thermometer placed in full sun at a sparsely vegetated, top-elevation site over the course of a year in Swebeswebe Wildlife Estate, following one troop of *Papio ursinus*.

highlighted drivers of microclimate selection influencing the difference between troop-level microclimate temperature and top elevation full sun temperature. Microclimate selection was best explained by vegetation greenness, season, and time of day, with baboons choosing cooler sites during the wet season and in midday/afternoon, but warmer sites in the morning. The top model yielded a weight of 0.35 (Appendix S11). However, there were three other models, all within two delta AIC of the top model but ultimately the fourth model was chosen as it was the most parsimonious, excluding

NDWI and macrohabitat heat load. The chosen model included NDVI as well as season and time category (morning: 06:00 – 09:00, midday: 10:00 – 13:00 and afternoon: 14:00 – 17:00). The chosen model had a weighting of 0.14 (Table 4.1). Fixed effects alone explained only 1.8% of the model variation while the addition of random effects significantly improved the model's fit, explaining 66.9% of the variation. Baboons showed a stronger selection for cooler temperatures in the wet season compared to the dry season as well as during the midday and afternoon time periods compared to the morning period. Within the morning time category, baboons selected for warmer microclimates with a predicted difference in temperature close to 1.5 °C warmer than the top elevation microhabitat temperature. Additionally, baboons sought cooler microhabitats during periods of greater vegetation greenness.

Table 6.1: Factors influencing the difference in temperature between troop level microclimate and sparsely vegetated, top elevation microclimate for one troop of *P. ursinus* troops in Swebeswebe wildlife estate with the predictors of NDVI, time category and season as predictors and Julian day as a random effect. A sample size of 638 observations has been used over one year of field data collection.

	Difference in Temperature °C	
Predictors	*Estimates*	*CI*
(Intercept)	-0.59	-2.06 – 0.88
NDVI	-0.65	-1.14 – -0.17
Time Category [Morning]	1.50	0.70 – 2.30
Time Category [Afternoon]	0.79	-0.15 – 1.73
Season [Wet]	-0.67	-3.17 – 1.83
Random Effects		
σ^2	17.14	
$\tau_{00\ JulianDay}$	33.68	
ICC	0.66	
$N_{\ JulianDay}$	111	
Observations	638	
Marginal R^2 / Conditional R^2	0.018 / 0.669	

Intraclass correlation coefficient (ICC) is included.

To assess habitat preferences, I used Ivlev's electivity index, which quantifies an animal's preference or avoidance of specific habitat types. Ivlev's index ranges from -1 to +1, where values close to +1 signify strong selection and values close to -1 indicate strong avoidance. I retained the full model to examine how electivity varied with season, time category, and microhabitat type (including elevation and vegetation type), ensuring that all relevant ecological factors were considered. This approach allowed for a comprehensive assessment of habitat selection across different conditions, rather than focusing solely on the strongest predictors. The model had a high conditional R^2 value of 0.87, indicating strong explanatory power (Appendix S12).

Baboons demonstrated a strong preference for low elevation, densely vegetated microhabitats, especially during the midday period in the wet season, with an Ivlev's index of 0.603 (Fig. 11). In contrast, baboons strongly avoided high elevation microhabitats, particularly in the afternoon, across both the dry and wet seasons. This strong avoidance was found in both open and densely vegetated areas; however the strongest avoidance occurred in high elevation, densely vegetated areas during the afternoon in the wet season, with an Ivlev's index value of -0.966. Throughout both seasons, positive selection values were observed exclusively in dense microhabitats, particularly at low and mid elevations.

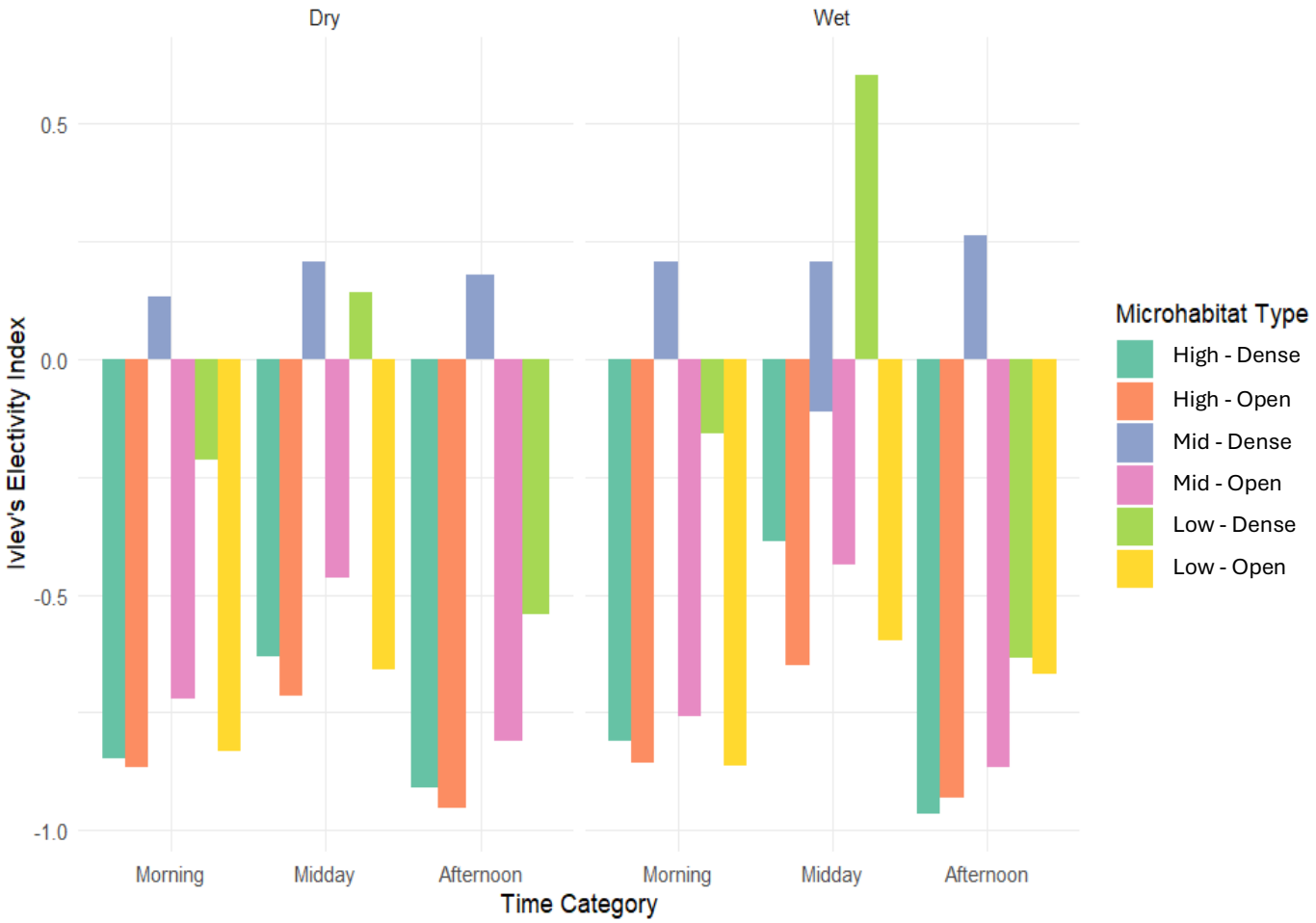


Fig. 11: Ivlev's electivity index by season and time category showing troop preference for different microhabitat types over four years of data collection. Ivlev's electivity index quantifies habitat preference, with positive values indicating selection and negative values indicating avoidance. Data were collected from four troops of *P. ursinus* in Swebeswebe Wildlife Estate, based on 5142 GPS observations. The linear mixed model had 97 observations, categorized by troop ID, season, time category and microhabitat type (Appendix S12).

Models predicting troop occupancy for both the dry and wet seasons were constructed using landscape features including NDVI, NDWI, distances to rivers, waterholes, the main cave site, anthropogenic structures, fences, and the modal microhabitat type occupied by baboons daily. The top-performing model for the dry season (Appendix S13) included the predictors of distances to rivers, waterholes, the main cave site and fence lines, as well as the modal microhabitat type. This model was both the most

parsimonious and robust, as it excluded predictors such as NDVI, NDWI, and distances to anthropogenic buildings, and outperformed four other models that were within two delta AIC of the top model. The marginal R^2 value shows that fixed effects explained 28.2% of the model variance while the inclusion of random variable produced a better model fit, explaining 67.8% of the variance (Table 4.2). In the dry season, predicted troop occupancy increased with proximity to rivers and the cave sleep site, and decreased with proximity to watering holes and fences. Baboons also preferred mid elevation sparse and dense microhabitats as well as high elevation dense areas compared to low elevation dense sites. There was no significant difference between low and high elevation sparsely vegetated areas as compared to the low elevation dense microhabitat type.

Table 6.2: Factors influencing dry season occupancy for four troops of *P. ursinus* troops in Swebeswebe wildlife estate with the predictors of microhabitat type, distances from rivers, watering holes, caves and fences as predictors, with troop ID and grid cell ID as a random effects. A sample size of 2727 observations has been used over four years of data collection. Intraclass correlation coefficient (ICC) included.

	Occupancy Model: Dry Season	
Predictors	*Incidence Rate Ratios*	*CI*
Intercept	3.95	3.49 – 4.48
Microhabitat: Low Open	1.05	0.88 – 1.27
Microhabitat: Mid Dense	1.07	1.03 – 1.10
Microhabitat: Mid Open	1.08	1.03 – 1.12
Microhabitat: High Dense	1.30	1.20 – 1.42
Microhabitat: High Open	1.04	0.95 – 1.14
Distance from Rivers	1.00	1.00 – 1.00
Distance from Waterholes	1.00	1.00 – 1.00
Distance from Caves	1.00	1.00 – 1.00
Distance from Fences	1.00	1.00 – 1.00
Random Effects		
σ^2	0.29	
$\tau_{00\ Troop.ID}$	0.00	
$\tau_{00\ gridcellID}$	0.36	
ICC	0.55	
$N_{\ Troop.ID}$	4	
$N_{\ gridcellID}$	1086	
Observations	2727	
Marginal R^2 / Conditional R^2	0.282 / 0.678	

The best model for the wet season included all predictors (Appendix S14). During model selection there were no other models that fell within two delta AIC of the top model, with this chosen model having a weight of 0.52. The model fit improved from 13.8% of variance explained to 59.3% with the inclusion of random effects (Table 4.3). Baboons showed higher occupancy in areas close to rivers, the cave sleep site as well as anthropogenic sites such as buildings. In the wet season there was reduced occupancy in

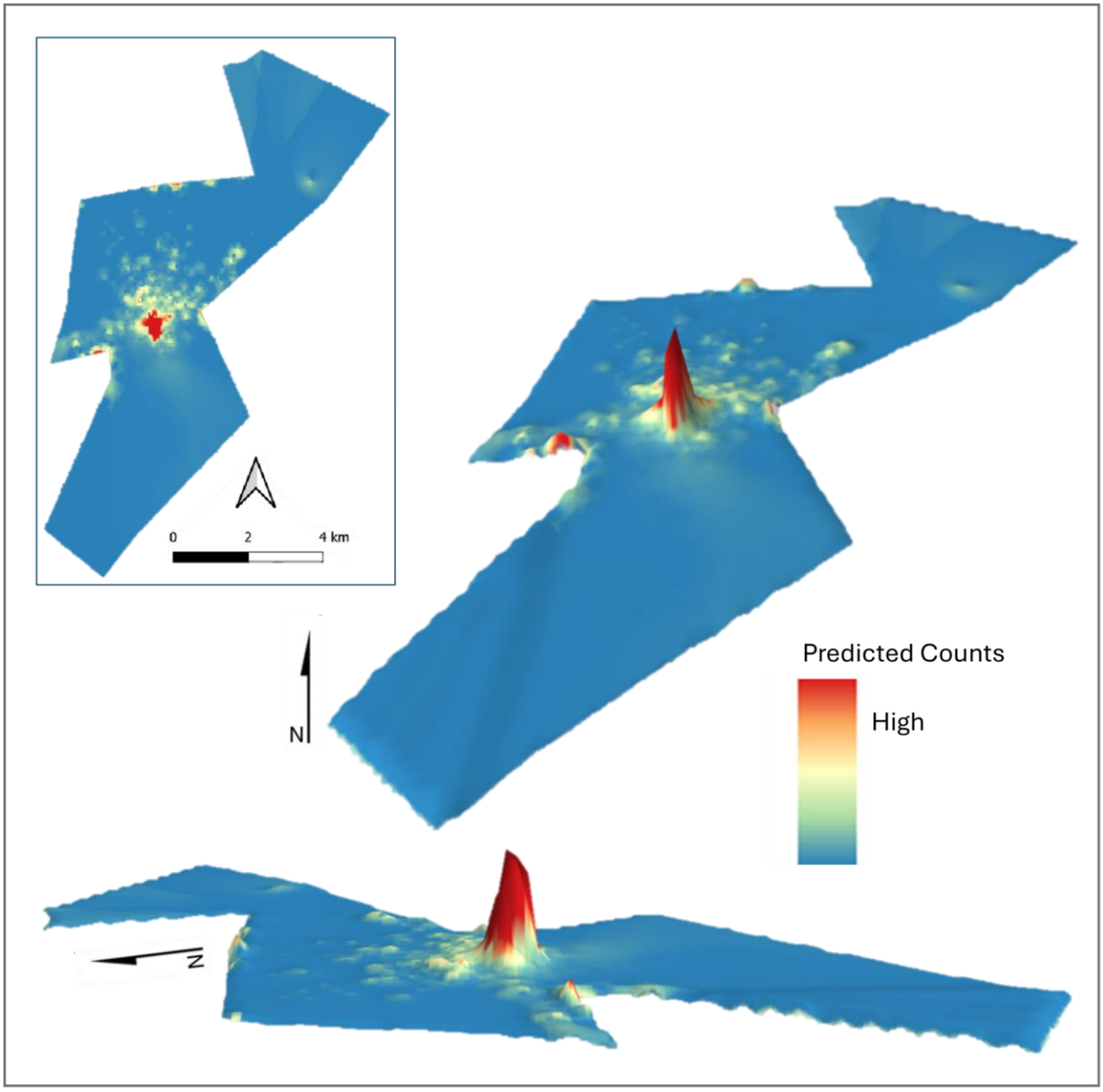
proximity to fences and watering holes. Baboons also had higher predicted counts in areas with both lower NDVI and NDWI values, although they showed preference for densely vegetated microhabitats at all elevation categories as well as a preference for high elevation sparsely vegetated areas.

Table 6.3: Factors influencing wet season occupancy for four troops of *P. ursinus* troops in Swebeswebe wildlife estate with the predictors of NDVI, NDWI, microhabitat type, distances from rivers, watering holes, caves, anthropogenic sites and fences as predictors, with troop ID and grid cell ID as a random effects. A sample size of 2177 observations has been used over four years of data collection. Intraclass correlation coefficient (ICC) included.

	Occupancy Model: Wet Season	
Predictors	*Incidence Rate Ratios*	*CI*
Intercept	3.77	3.28 – 4.32
NDVI	0.86	0.78 – 0.95
NDWI	0.84	0.72 – 0.98
Microhabitat: Low Open	0.83	0.68 – 1.00
Microhabitat: Mid Dense	1.04	0.99 – 1.09
Microhabitat: Mid Open	0.94	0.89 – 0.99
Microhabitat: High Dense	1.25	1.11 – 1.40
Microhabitat: High Open	1.15	1.01 – 1.32
Distance from Rivers	1.00	1.00 – 1.00
Distance from Waterholes	1.00	1.00 – 1.00
Distance from Caves	1.00	1.00 – 1.00
Distance from Anthropogenic Sites	1.00	1.00 – 1.00
Distance from Fences	1.00	1.00 – 1.00
Random Effects		
σ^2	0.33	
$\tau_{00\ Troop.ID}$	0.00	
$\tau_{00\ gridcellID}$	0.37	
ICC	0.53	
$N_{\ Troop.ID}$	4	
$N_{\ gridcellID}$	1022	
Observations	2177	
Marginal R^2 / Conditional R^2	0.138 / 0.593	

While the directional relationships between predicted troop counts and predictor variables are similar in both the wet and dry season models, the strength of these relationships varies by season. Proximity to the cave, river, watering holes and fences were slightly stronger predictors in the dry season compared to the wet season. Additionally, baboons show a stronger preference for dense vegetation during the wet season compared to the dry season.

Visual representations of predicted troop count data, displayed as 3D occupancy models, revealed distinct seasonal patterns in troop movement and distribution (fig. 12). In the dry season, there is a higher peak near the main cave sleep site compared to the wet season. Additionally, the dry season plot shows more pronounced elevated occupancy aligning with the main valley system in the Swebeswebe Wildlife Estate (as seen in fig. 6 and 7). In contrast, the wet season plot has less pronounced branches along the main river system as well as having greater peaks along the northern, horizontal fence line. Interestingly the wet season also shows a peak in occurrence at one of the watering holes (as can be found in fig. 4 and 7).


0
2
4 km
N
Predicted Counts
High
N

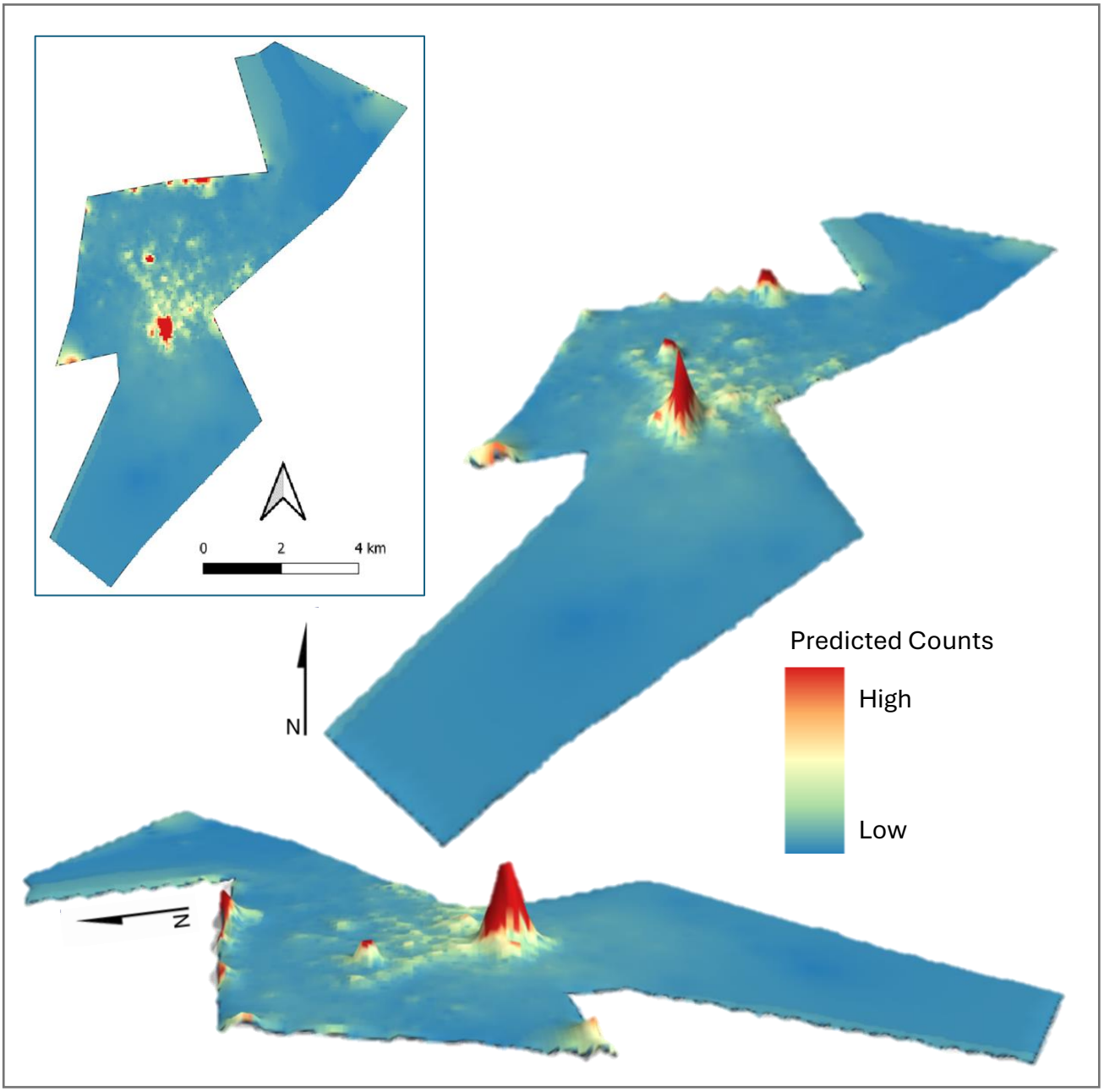


Fig. 12: Three and two-dimensional graphical representations of troop occupancy on the Swebeswebe map with the dry season shown above and the wet season below. Data used were taken from the entirety of the four-year study period from four troops of *P. ursinus* with a total of 2727 observations for the dry season and 2187 observations for the wet season.

To assess if baboons were found closer to river networks, particularly in the dry season which shows higher occurrence along the main river valley system of Swebeswebe (Fig. 13), I used a linear mixed model. The model included NDVI, macrohabitat black globe temperature, and troop-level microclimate

temperature as predictors, with season as a fixed covariate. No other models fell within two delta AIC of this model, and the top model had the highest weighting (0.94) (Appendix S15). Baboons reduced their distance from the river with increasing vegetation greenness while they increased their distance with higher microhabitat and macrohabitat heat loads (Table 4.4). Baboons were also found further away from the river in the wet season when water availability is higher as compared to the dry season. The marginal R^2 value showed that fixed effects alone only accounted for 2.4% of the model's variance and while random effects improved the model fit, it only explained 6% of the variance.

Table 6.4: Predictor variables influencing distances from river sites of four *P. ursinus* troops in Swebeswebe wildlife estate with the predictors of NDVI, macrohabitat temperature and microhabitat temperature as well as season and photoperiod as a fixed covariate and troop ID as a random effect. A sample size of 2851 observations have been used over four years. Intraclass correlation coefficient (ICC) is included.

	Effects on distance to riverine sites (m)	
Predictors	*Estimates*	*CI*
(Intercept)	619.60	439.21 – 799.99
NDVI	-45.72	-58.01 – -33.43
Macroclimate Temperature	14.41	-0.36 – 29.18
Microclimate Temperature	12.30	-1.78 – 26.38
Photoperiod	-30.02	-45.01 – -15.02
Season [Wet]	33.42	3.95 – 62.89
Random Effects		
σ^2	85216.71	
$\tau_{00\ Troop.ID}$	3265.25	
ICC	0.04	
$N_{\ Troop.ID}$	4	
Observations	2851	
Marginal R^2 / Conditional R^2	0.024 / 0.060	

Discussion

Baboons altered their movement, thermoregulatory behaviour, activity budget, and microhabitat selection in response to diurnal and seasonal changes in environmental conditions. As predicted, baboons travelled further when resource availability low and increased their home range size when water was limited. Contrary to my hypotheses, baboons travelled further when heat loads were high but did not change their travel rate or directionality in response to heat load or resource availability. Increased time spent travelling on hot days was also detected in behavioural observations, with a corresponding decrease in time spent foraging in the heat. The increased time spent resting on hot days, likely corresponded to time spent in the shade. As predicted, baboons selected cooler, densely vegetated, areas during higher heat loads and were generally found closer to river sites during the dry season. These responses to the changing environment highlight the behavioural flexibility shown by primates to buffer thermal extremes (Kalbitzer and Chapman, 2018; McFarland, Barrett, Costello, et al., 2020) as well as to maximize their energy intake (van Doorn, O'Riain and Swedell, 2009; Hoffman and O'Riain, 2012). The relationship between staying within optimal thermal zones and maximising energy acquisition varied across seasons, with thermoregulation taking precedence in the warmer, wetter season when ambient temperatures are higher. In contrast, during the dry season, when food and water resources are scarcer, baboons likely shifted their focus toward foraging and energy acquisition, which may result in longer travel distances or increased time spent in high-quality food patches, even at the cost of thermoregulation.

Movement

The movement patterns of baboons in this study possibly reflect their adaptive response to fluctuating resource availability and thermal conditions. Baboons travelled further with higher ambient temperatures as well as when resources such as vegetation and water were scarce. Despite energetic costs associated with movement under increased temperature, baboons in this study travelled further with higher heat loads. This pattern is of interest with movement under higher temperatures requiring

greater evaporative cooling and additional metabolic effort for thermoregulation (Mitchell, Fuller and Maloney, 2009; Thompson and Hermann, 2024). While distances travelled increased with higher temperatures, it is likely that baboons adjusted their activity budgets and selected cooler microhabitats to manage potential heat stress. These patterns highlight the importance of variable microhabitats in allowing baboons to balance thermoregulation with resource acquisition. However, increasing aridity under future climate change may increase energetic trade-offs, potentially constraining movement and access to critical resources.

The abundance and distribution of water influences baboon daily ranges, particularly during food-scarce periods when access to water reduces thermoregulatory stress (Stone et al., 2013). Daily travel distances in this study were greater when water availability was lower, however, likely reflecting the need to search for widely dispersed water sources or forage. Notably, despite lower NDWI values, permanent water remained accessible near the main cave sleep site, suggesting that baboons were not entirely water-limited but still adjusted their ranging behaviour in response to seasonal variation. Among the predictors, NDVI had the strongest effect on daily distance travelled, highlighting the critical role of vegetation productivity, and ultimately food availability, in shaping movement decisions. During these times of lower vegetation greenness, energy acquisition was likely prioritised, driving baboons to travel further in search of food to meet their energetic needs. As noted above, increasing aridity can lead to periods of lower water availability, creating energetic trade-offs for baboons. During these times, individuals must balance the need to forage over larger areas with the necessity of minimising heat stress during the hottest parts of the day. This trade-off may, in turn, result in a nutrient deficit if energy acquisition is constrained by both water scarcity and thermal stress.

While baboons travelled further when heat loads were high and when food and water resources were scarce, their travel rate remained unchanged. This apparent discrepancy may partly reflect longer daylight hours during warmer periods, as extended daylight could allow baboons to travel greater total distances without necessarily increasing their rate of movement. The lack of influence on travel rate in this study could reflect the behavioural adaptations of baboons to balance energy expenditure and

thermoregulation (Porter and Gates, 1969) over the course of the day. Baboons may prioritise maintaining consistent daily energy expenditure by changing speeds across different microhabitats along with opportunistic shade-seeking behaviour (Stelzner, 1988; Hill, 2006). By slowing their movement in shaded areas and increasing speed in open microhabitats, baboons can potentially mitigate heat stress without significantly altering their overall daily travel rate.

Similarly to daily travel rate, baboons did not exhibit changes in their daily movement direction even with the potential of goal-oriented movement during the dry season. Within goal-orientated behaviour, baboons may employ more linear movement during lower food or water availability to reduce the energetic costs associated with movement. The null model for movement direction may have been the strongest due to the nature of the analysis taken as daily averages as opposed to a finer resolution. This analysis scale may be the cause as baboons in this study began their foraging activity from the main cave sleeping site and returned to this point at the end of their activity period for most days within the study. This consistent pattern of starting and ending their foraging activity at the same location may have reduced the strength of ecological variables on movement direction, as direction could have been constrained by their daily routine rather than being directly influenced by temperature, NDVI, or NDWI.

Home range size was, however, associated with variation in water availability. Similarly to increased daily travel distances, two-week home range size also increased when water was scarce. While daily travel distances and home range size are related, they reflect different spatial scales. Home range size represents the total area used by the baboons over a two-week period, rather than just the distance travelled per day. The home ranges of baboons are particularly limited by the seasonal availability of standing water pools and other drinking sites, with animals expanding their ranges to access widely distributed water sources (Hamilton, 1985). During drier periods, baboons expand their home ranges and may also adopt more goal-directed movement strategies, minimizing the costs associated with searching for resources (Spencer, 2012). This was seen with home range heatmaps in the dry season expanding along the main river system in a more linear pattern than in the wet season. Such variation in home range size highlights the potential behavioural flexibility of chacma baboons in adjusting their

spatial use to changing environmental conditions. This plasticity allows for the balance of energetic costs associated with movement with the need to access food and water resources. Although these patterns in home range size may be an indication of behavioural flexibility, it also highlights a potential vulnerability under future climate change, with increased resource patchiness potentially forcing larger home ranges with greater energetic demands.

Behaviour

While daily distances travelled and home range size was reduced with greater water availability, baboons were found to allocate more of their activity budget to travel behaviour when water was available. These differing results regarding travel distances and travel behaviour may suggest that under conditions of high water availability, baboons may have engaged in more frequent bouts of movement interspersed with resting behaviour, rather than covering greater distances overall. Baboons could spend more time travelling during wetter times of the year to reach spatially distributed water patches, but such patches may not be far apart in distance. In addition, baboons engaged more in travel behaviour when heat loads were high, aligning with greater daily distances travelled in the heat. Increased travel counts under higher temperatures could reflect the need to navigate between resource patches while seeking cooler microhabitats for thermoregulation.

While the proportion of time spent traveling rises with temperature and water availability, there was similarly an increase in rest behaviour. This relationship between travel and rest can be seen with baboon movement described as a pattern of abrupt pauses for rest (Henzi, Byrne and Whiten, 1992) whereby travel and rest behaviour alternate in brief moments throughout their activity period. The increased time spent resting in areas with greater water availability may be due to the closer distribution of resources, reducing the need for prolonged searching and allowing for more frequent rest periods. Additionally, during periods of higher ambient temperatures, baboons may adjust their behaviour by engaging in enforced resting to manage potential heat stress (Korstjens, Lehmann, & Dunbar, 2010). Along with enforced rest, baboons may also adopt opportunistic shade-seeking strategies, where

movement slows within shaded microhabitats, allowing for brief periods of sedentary behaviour (Stelzner, 1988). Enforced resting times, however, have further implications for the energy requirements of baboons, reducing the time available in their activity budget for behaviours such as foraging.

This trade-off becomes particularly evident as travel and rest increased with higher temperatures and water availability while foraging behaviour decreased, highlighting the importance of balancing thermoregulation and energy acquisition. Although baboons demonstrate significant behavioural and dietary flexibility, temperature plays a key role in regulating foraging time, with higher temperatures reducing the amount of time spent feeding (Hill and Dunbar, 2002). In this context, higher temperatures affect foraging behaviour by increasing the energetic demands for thermoregulation as well as by reducing the quality of available forage (Dunbar, 1992). Foraging time also decreased with increasing NDWI values as a trade-off with increased travelling and rest. While NDVI did not predict the frequency of foraging, there is a strong ecological link between water availability and vegetation greenness (Gu et al., 2007; Chen, Guan, and Batelaan, 2022). This pattern may then further reflect how baboons adjusted their foraging behaviour in response to abundant resources where there is a reduction in the need for prolonged foraging to meet nutritional and energetic needs.

As vegetation greenness increased, baboons spent more time engaged in social activities; suggesting that abundant resources allowed baboons to allocate more energy to socially significant behaviours. Within environments that have a high quality and quantity of forage available, particularly in the wet season, there is a reduction in intra-troop competition and in turn an increase in positive social interactions such as grooming and play behaviour (Sharman, 1982). During periods of greater vegetation greenness, activity budgets are also less constrained by the need to meet daily energetic requirements and so trade-offs with social behaviour are less prominent. Interestingly, social behaviour decreased with increasing NDWI values even though vegetation greenness and water availability are highly linked as mentioned (Gu et al., 2007; Chen, Guan and Batelaan, 2022). Higher NDWI values indicate the presence of standing water, however, which has different ecological pressures as opposed

to areas with high vegetation greenness. These areas could potentially see an increase in vigilance behaviour (Hammond et al., 2022) due to increased predation risk, particularly from ambush predators, as well as increased competition around water sites (Hayward and Hayward, 2012). Along with vigilance behaviour there could also be an increase in thermoregulatory behaviours such as resting as mentioned above, or drinking — all of which may limit opportunities for social interactions. Although competition decreases when resources are abundant, baboons may still follow a priority-of-access model (Strum, 1982), where acquiring access to water resources involves a hierarchical order, potentially resulting in social interactions being less apparent to human observers.

While increased vegetation greenness supports social behaviours by reducing energetic constraints, it also plays a crucial role in thermoregulation by providing shade. Shade use plays a crucial role in maintaining thermal comfort, with baboons seeking shade more frequently in areas with greater vegetation greenness and under higher heat loads. Increased vegetation cover provides cooler microclimates, reducing exposure to direct solar radiation, and mitigating the physiological stress of heat. As environmental temperatures rise, the need for thermoregulation intensifies, leading to shifts in activity budgets, including an increased reliance on resting, particularly in shaded areas (Bronikowski and Altmann, 1996; Hill, 2006). Higher NDVI values also indicate denser vegetation, offering more opportunities for baboons to find effective shade within the landscape. This increased access to shade may be especially important during peak heat load periods, allowing baboons to avoid excessive water loss through evaporative cooling. However, a greater proportion of time spent in shaded areas, particularly when resting, could lead to trade-offs, reducing the time available for foraging as mentioned. This trade-off, in turn, may lower daily energy intake rates and potentially impact overall fitness (Fuller et al., 2016).

To contextualize these findings of the influence of landscape drivers on movement and behavioural patterns, Table 5 provides a summary of how the biotic and abiotic variables of NDVI, NDWI, and macrohabitat black globe temperature shaped baboon activity. This table highlights the directional effects of these predictors on both behaviour metrics (travel, rest, forage, social, and shade use) and

movement metrics (daily travel distances, daily travel rates, daily movement direction, and two-week home range size), illustrating the trade-offs baboons made in response to changing environmental conditions.

Table 7: Summary of the directional effects of NDVI, NDWI, and macrohabitat temperature on troop behaviour metrics (travel, rest, forage, social and shade use) as well as troop movement metrics (daily travel distances, daily travel rates, daily movement direction and two-weekly home range size).

Variable	NDVI	NDWI	Temperature
Behaviour			
Travel	NA	+	+
Rest	NA	+	+
Forage	NA	-	-
Social	+	-	NA
Shade Use	+	NA	+
Movement			
Travel Distance	-	-	+
Travel Rate	NA	NA	NA
Travel Direction	NA	NA	NA
Home Range Size	NA	-	NA

Habitat selection

As temperature and resource availability shaped how baboons move and behave within the heterogeneous landscape, these factors also influenced where troops were found according to their spatial use and microhabitat selection. Within microhabitat selection, it was observed that sparse vegetation, low elevation sites had the lowest temperatures, making these areas more thermally preferable for baboons, as indicated by the positive Ivlev's electivity index for these sites. The opposite can be seen with baboons strongly avoiding the warmer high elevation sites, particularly those that are

sparsely vegetated. Although low elevation microhabitats in dense vegetation were warmer than higher elevation sites, there remained a strong preference for these lower areas and an avoidance of higher microhabitats. While higher temperatures in low elevation dense microhabitats contrast with expected patterns, the differences between high and low sites were minimal. Furthermore, higher temperatures in low elevation sites may be influenced by abiotic factors such as airflow changes or increased local humidity (Jia *et al.*, 2024). Additionally, the timing of temperature peaks varies by elevation in both vegetation types, highlighting the importance of microhabitat variability throughout the day, which is influenced by both vegetation density and elevation.

Within these microhabitat temperature differences it was seen that baboons selected for areas that provided more stable thermal conditions with observations showing slight seasonal variation in this selection. During the dry season, the regression slope (0.74) suggests that troop-level microclimate temperatures were relatively stable compared to the warmer high elevation open microhabitat. This pattern indicates that while baboons were exposed to a range of temperatures, they tended to occupy microhabitats that buffered against extreme temperature fluctuations. In the wet season, the regression slope increased slightly (0.78), suggesting that baboons selected microhabitats with less variability than in the dry season. Selection for less variable environments may indicate a weaker preference for thermally stable environments during wetter, warmer conditions, however, the differences between seasons are slight. Overall, these findings support the idea that baboons engage in behavioural thermoregulation by selecting microhabitats that provide more stable temperatures compared to the open, high-elevation habitat, which was the warmest amongst all microhabitat types.

Along with the seasonal scale, diurnal patterns showed that while baboons avoided warmer temperatures more in the wet season, they also showed an avoidance of warmer microhabitats during the midday and afternoon periods when ambient temperatures were highest. In the morning, particularly in the winter period, the study troops often occupied open, sunny areas on the plateau above their sleeping site, a behaviour consistent with other primates that seek warmer microhabitats to regain heat after cool nights (Gestich, Caselli and Setz, 2014). Along with the delineation of season and time of

day, baboons also altered their thermal selection with changing resource abundance such as vegetation greenness. When NDVI values were lowest, baboons selected for warmer microclimates. Lower NDVI values could coincide with the cool dry season when resource availability is typically lower, and as a result, baboons may prioritize energy acquisition over thermoregulation. Selection for warmer microclimates during the cooler dry season may help baboons maintain optimal body temperatures during cooler conditions, especially in the early morning when temperatures are at their lowest. In contrast, areas with low NDVI often correspond to more open or exposed habitats, which may force baboons to use warmer, sunlit areas due to the lack of thermal buffering provided by vegetation (Townsend and Fuhlendorf, 2010; Palmer *et al.*, 2021); though the first explanation is supported from field observations.

Baboons strongly selected for low elevation, densely vegetated microhabitats, particularly during the midday and in the warmer wet season. This preference, highlighted by an Ivlev's electivity index of 0.603, suggests that such microhabitats may provide favourable thermal and ecological conditions, likely offering shade during periods of peak heat loads. Along with providing shade, these areas are spatially linked to river systems within the study site, ensuring access to water resources during warmer periods. Due to their vegetation structure and proximity to rivers, low elevation, densely vegetated areas may also have enhanced foraging opportunities. Baboons strongly avoided high elevation microhabitats across both seasons and vegetation types, with the most pronounced avoidance seen in high elevation densely vegetated areas during the wet season (index value of -0.966). This likely reflected the harsher thermal conditions in these areas, where dense vegetation may increase humidity as mentioned previously. In contrast, baboons exclusively selected densely vegetated microhabitats at low and mid elevations, emphasizing the importance of vegetation cover in shaping habitat use (DeWoskin, 1980; Stelzner, 1988).

Visual representations of troop occupancy highlighted distinct seasonal differences in baboon movement and distribution (fig. 12). For both seasons, the most dominant peak was associated with their main cave sleeping site as this is the point from which movement stemmed from in the mornings,

although this peak was higher in the dry season. It was observed that troops left the main cave sleep site later in the morning period in the cooler dry season as compared to the wet season, likely explaining the higher peak around the cave in the dry season. Along with this movement routine, it has been found that while sleeping sites are few in number in baboon home ranges, they create dramatic features in the spatial landscape (Strandburg-Peshkin *et al.*, 2017). The dry season heatmap also revealed more pronounced lateral branches of troop occupancy, following the main valley and river system in the study site, indicating that these valleys served as critical pathways during resource limited periods. This aligns with the fact that baboons were found closer to river sites during the dry season, likely influenced by the need to stay close to reliable water sources (Hamilton, 1985; Stone *et al.*, 2013). In contrast, baboons tended to stay further from watering holes during the dry season. Although the opposite pattern is expected, these watering holes were not consistently filled, and therefore did not serve as reliable water sources for the troops. Additionally, traveling to these sites could have been energetically costly if watering holes were empty. While NDWI did not have a direct influence on the dry season model, proximity to rivers emerged as a significant predictor of baboon presence, further emphasizing the importance of permanent water sources in shaping movement patterns during resource scarce periods.

In the wet season, greater water and vegetation availability across the landscape provides increased foraging opportunities, allowing baboons to range further from reliable food and water resources. This ability to travel further was highlighted by occupancy peaks along the horizontal northern fence line of the study site, with the troops crossing more into neighbouring reserves. These peaks most likely indicate repeated use with certain sections of the fence being more accessible as crossing points. As neighbouring reserves were not included in daily follows, it was not possible to confirm their activities beyond this boundary, however, these patterns likely reflect the seasonal expansion of ranging areas when resources are more widely distributed. The ability to travel further was also highlighted by the fact that baboons were found further from rivers during the wet season. While troop occupancy decreased near fence lines in both seasons, this factor was a weaker predictor in the wet season compared to the dry season. Baboons also occupied areas with lower NDWI values during the wet season, suggesting that with water sources more widely distributed across the landscape, there is less

reliance on the primary river system and other large standing water sources. Baboon occupancy also increased in areas of low vegetation greenness during the wet season. While NDVI values are generally higher in the wet season, the preference for areas with lower values could be linked to easier movement through potentially less dense vegetation along with increased visibility of other troop members for movement coordination (Strandburg-Peshkin *et al.*, 2017). Along with increased visibility of group members in sparser vegetation, there is also increased visibility of predators, with these areas likely then having a reduced perceived predation risk (Cowlishaw, 1994, 1997; Coleman and Hill, 2014).

The preference for areas with lower NDVI values may be linked to the strong selection of high-elevation, sparsely vegetated microhabitats, as indicated by the wet season occupancy model. However, overall, baboons showed a stronger preference for densely vegetated microhabitats in the wet season compared to the dry season. This preference aligns with higher Ivlev's electivity values for dense microhabitats during the wet season, as well as the fact that these areas typically had lower average temperatures than sparser microhabitats, as shown in Fig. 8. These patterns of microhabitat selection in the wet season suggest that habitat preferences may be linked to both the thermoregulatory needs of baboons through the selection of cooler microclimates as well as the need for high visibility in sparse areas.

Limitations

While the study revealed valuable trends in baboon habitat selection, behaviour, and movement, there were certain limitations. The sample size was constrained by the duration of the baboon activity period and the number of full observation days achieved while following the troops. During the wet season, longer daylight hours allowed for extended periods of behavioural and movement observations, however, the wet season posed logistical challenges. Within the summer months, the landscape became more difficult to traverse due to dense vegetation and frequent water crossings, leading to higher chances of losing sight of the troops. These challenges likely reduced the consistency of data collection and may have introduced seasonal biases into the results shown by 607 data days and 318 full days in

the dry season compared to 501 data days and 246 full days in the wet season. Additionally, data collection exhibited a morning bias which could introduce inaccuracies when evaluating behavioural responses and movement. Animals naturally exhibit circadian rhythms in their movement patterns and behaviours (Lorenz, 1981; Favreau *et al.*, 2009) and as a result, predominantly collecting data in the morning may lead to a bias in the types of behaviours recorded. To minimise these potential effects, photoperiod was included as a fixed effect in the models to account for seasonal variation in day length and activity duration, and analyses were based on full observation days to ensure consistency in the time period represented. Future studies could further reduce temporal bias by incorporating a more even distribution of morning, afternoon and evening follows across seasons.

Within microhabitat temperature analyses, it is important to note that miniglobe thermometers collected data over the span of a year whereas the study data was collected over four years. While extrapolation of miniglobe temperatures to the greater dataset was strong (r^2: 0.75 - 0.98), data analysis would benefit from microhabitat temperature collection spanning over the full study period. Behavioural models in this study also produced low r^2 values, suggesting that a substantial proportion of variation remains unexplained, which can limit the predictive capacity of the models. However, low r^2 values are common in behavioural and ecological research, where complex systems and numerous unmeasured variables constrain the variance explained by fixed effects. Low r^2 values in ecology can highlight patterns such as functional diversity within a system or the adaptive strategies of organisms (Lin and Wiegand, 2023). More broadly, in empirical research, a low r^2 can still be acceptable when predictors are statistically significant, as the main aim is often to understand relationships rather than maximise predictive accuracy (Ozili, 2023).

Factors not included may influence baboon habitat selection, behaviour, and movement such as troop social dynamics as well as inter-troop interactions. In social primates, such as baboons, movement patterns are influenced by the action of other individuals (Bonnell et al., 2017), especially with higher ranking individuals having a stronger weighting in decision making processes (Stueckle and Zinner, 2008). Along with ingroup social interactions, intertroop encounters also impact behaviour, movement,

and space use, most noticeably through troop displacement (Hamilton, Buskirk and Buskirk, 1975; Markham, Alberts and Altmann, 2012). While intertroop encounters were recorded at the study site, these were not specifically included in my analyses, and with 808 observations over the course of the study period, this may be influential to troop movement analysis. Additionally, troop size may influence movement patterns, with larger troops exhibiting greater ranging behaviour than smaller troops. This is likely due to increased group foraging effort required to meet the energetic demands of each individual, as larger groups experience greater intragroup competition and resources within patches are depleted quicker. These patterns have been observed in chacma baboon (Slater, Barrett and Brown, 2018) as well as in primates more broadly (Johnson *et al.*, 2015) including vervets (*Chlorocebus pygerythrus*) (Pasternak *et al.*, 2013), olive baboon (*Papio anubis*) (Barton *et al.*, 1992) and hamadryas baboon (*Papio hamadryas*) (Schreier, 2010). Although troop home range overlap can affect movement and behavioural patterns, and contribute to intertroop dynamics, this was not analysed in the present study, due to limited data regarding this as troops were largely studied at different time periods.

Alongside social interactions, predation risk may also influence troop decision making by which baboons may avoid areas with a high perceived predation risk. However, these areas of low perceived predation risk may not offer optimal foraging opportunities or have optimal thermal properties (Willems and Hill, 2009; Coleman and Hill, 2014) and result in an expensive trade-off for baboons (Cowlishaw, 1997a). While baboons may have avoided certain areas as well as altered their behaviour and movement due to predation pressures, I was unable to quantify the risk of predation across the landscape. Moreover, the primary source of predation risk at the study site and in the greater Waterberg area comes from leopards (*Panthera pardus*) (Jooste *et al.*, 2013), however, since leopards are predominantly nocturnal predators, the impact of this predation pressure during the day may not be significant.

Implications and Findings

Despite these limitations, this study shows the influence of the thermal and energetic landscapes on baboon movement, behaviour and habitat selection, as well as highlighted the complex trade-offs

between thermoregulation and energy acquisition. Within movement patterns, increased daily distances travelled with lower food abundance is consistent with studies of *Papio ursinus* and other *Papio* species across southern, western, eastern, and central Africa (Henzi, Byrne, and Whiten, 1992; Johnson *et al.*, 2015). Within these studies, food scarcity was measured through vegetation transects (Henzi, Byrne, and Whiten, 1992) and NDVI values, aligning with my study (Johnson *et al.*, 2015), as baboons seek high-quality forage to maximize energy intake (van Doorn, O'Riain, and Swedell, 2009). Similarly, yellow baboons (*Papio cynocephalus*) have been found to travel further during the dry season compared to the wet season with seasons categorised by both rainfall and vegetation quality (Pochron, 2000) linking to the metrics of NDVI and NDWI in my study. Research on hamadryas baboons (*Papio hamadryas*) in Ethiopia found that the abundance of dominant fruit species did not affect daily travel distances (Schreier, 2010), contrasting to my findings that with lower food availability baboons travelled further. However, the study by Schreier (2010) found that the distribution of fruiting trees influenced baboon range use. Within the southern African context, it was found that chacma baboons in the Suikerbosrand had longer mean daily travel distances in the warm wet season (Slater, Barrett and Brown, 2018). While these align with my movement results regarding temperature it potentially contrasts with the findings on resource abundance. These opposing findings may be a result of differences in troop behavioural strategies whereby baboons may either travel further distances in search of high-quality forage or conserve energy invested in travel by foraging on nearby, lower quality foods.

It has also been found that on the continental scale, baboons (*Papio ursinus* amongst other *Papio* species) increased their travel distances with increasing temperatures (Johnson *et al.*, 2015) aligning with the results of this study, both in travel distances and time engaged in travel behaviour. However, the study by Johnson *et al.* (2015) also highlighted that on the local scale, baboons travelled less with increasing temperatures. This discrepancy could be due to differences in environmental conditions and resource availability between study sites. The local-scale data in Johnson *et al.* (2015) was collected solely on *Papio cynocephalus* in Tanzania, where abiotic factors, such as humidity, differ making overheating more likely and necessitating reduced travel on hot days. A similar pattern between

movement and temperature as seen in this study has also been observed in other primates such as Yunnan snub-nosed monkeys (*Rhinopithecus bieti*) which travel further with higher ambient temperatures (Baoping et al., 2009).

When food and water sources are abundant, troop daily travel distances are primarily influenced by the thermal environment, with increased travel on warmer days (Henzi, Byrne, and Whiten, 1992). This movement may serve two key functions: seeking thermally suitable areas for cooling and accessing high-quality forage that is spatially dispersed across the landscape. Specifically, the spatial distribution of resources plays a key role, with patchy resource availability likely driving baboons to travel greater distances in search of concentrated food and water sources (Slater, Barrett and Brown, 2018). Following the optimal foraging theory, animals should spend time and energetic resources on moving to new foraging patches when the resources in the current patch are depleted (Charnov, 1976). Animals inhabiting high-quality habitats are therefore expected to have smaller home ranges compared to those residing in low-quality habitats (Wagler *et al.*, 2024), aligning with the findings of this study that baboons had smaller home ranges with greater water availability. The importance of water availability in travel patterns is largely due to the thermoregulatory needs of baboons, particularly when ambient temperatures increase (Barton *et al.*, 1992). When food, and likely water sources, are abundant, daily travel distances of baboons was determined by the thermal environment, with baboons travelling further on warmer days (Henzi, Byrne and Whiten, 1992). These greater travel distances are possibly a response to reach more thermally suitable areas or high-quality forage dispersed within the landscape.

Although travel rate and direction were not predicted by temperature, NDVI, or NDWI in this study, previous research has shown that chacma baboons tend to follow straighter travel paths in sparsely vegetated areas (Noser and Byrne, 2015). This behaviour may serve as a strategy for more efficient resource searching, minimizing thermal stress, or reducing exposure to areas with a higher perceived risk of predation. The travel rate findings in this study differ from those of Stelzner (1988), who observed a decrease in baboon travel rate as temperatures increased, particularly when baboons travelled through shaded areas. These contrasting results may arise from the difference in methodology

as while Stelzner (1988) focused on displacement rates within specific vegetative zones, this study averaged daily travel rates across all habitat types. As a result, the finer-scale changes in travel rate driven by shade-seeking behaviour may not have been captured at this broader scale. However, beyond movement patterns, behavioural adaptations to temperature also play a crucial role in how baboons respond to heat stress.

Within behaviour, the findings that baboons spend more time resting with higher ambient temperatures align with previous studies, particularly Hill (2006) that found higher temperatures directly influenced the amount of time baboons spent resting, as part of their adaptation to manage heat stress and conserve energy (Hill, 2006). This along with studies on thermally enforced rest times amongst various primates, including chacma baboons (Korstjens, Lehmann and Dunbar, 2010), whereby baboons prioritised energy-saving behaviours under high temperatures (Dunbar, 1992). In contrast, a study by van Doorn, O'Riain, and Swedell (2009) found that rest behaviour in chacma baboons increased during the dry season when daily temperatures and water availability were lower. This discrepancy may be linked to the reduced availability of water during the dry season, prompting baboons to seek shade and conserve their internal water. In such conditions, increased resting behaviour may serve as a strategy to minimize water loss and regulate body temperature, allowing baboons to avoid excessive heat exposure while conserving energy. These patterns are also seen in primates such as common brown lemurs (*Eulemur fulvus fulvus)* in northern Madagascar where the dry season is marked by high temperatures and low water availability (Sato, 2012). Here, lemurs employ diurnal rest to minimise water loss through heightened respiratory evaporative water loss.

As shown in this study, increased time spent resting, and furthermore travelling, with temperature and water availability saw a reduction in foraging behaviour. Particularly with temperature as a driver, it was found in *Papio anubis*, *Papio hamadryas* and *Papio papio* that the proportion of time spent foraging decreased with higher mean annual temperatures (Hill and Dunbar, 2002). As temperatures rise, food quality decreases which may result in more time spent engaged in searching for higher quality food (Barton *et al.*, 1992). However, what is perhaps more crucial is the trade-off in activity budget with

higher temperatures resulting in the need for thermoregulatory behaviours as opposed to foraging. Reduced feeding behaviour in chacma baboons has also been linked to low food availability (van Doorn, O'Riain, & Swedell, 2009). While NDVI did not affect foraging behaviour in the current study, there is limited research on the influence of NDWI on primate foraging. Since vegetation greenness is often correlated with water availability, patterns of NDVI and foraging behaviour can be related to NDWI. This contrasts with the findings of van Doorn *et al.* (2009), possibly because their study focused on food scarcity in the Cape Peninsula, a winter rainfall region where the dry season occurs during cooler months, rather than the interplay between thermoregulation and resource availability observed in this study.

However, social behaviour was influenced by NDVI, with baboons socialising more with higher NDVI and lower NDWI values. Previous research has shown that baboons engaged in more social interactions during the summer months (van Doorn, O'Riain, & Swedell, 2009). While this seasonal pattern in the Cape Peninsula may correspond to summer temperatures rather than vegetation productivity, the higher NDVI values observed in the Waterberg likely reflect the combined effects of summer rainfall and increased food availability. Within water availability, studies on vervet monkeys (*Chlorocebus pygerythrus*) have shown that drought conditions lead to reduced social behaviour, likely as a response to resource scarcity and increased competition (Young *et al.*, 2019). This finding contrasts with the results of the present study, where social behaviour increased under lower NDWI conditions. However, this discrepancy may be attributed to the severity of water shortages in the Young *et al.* (2019) study, where drought conditions may have heightened stress and reduced opportunities for social interactions, whereas in this study, water availability may not have reached similarly critical levels.

Primates, among other animals, select for cooler microhabitats as environmental temperatures increase in order to reduce heat exchange with their surroundings (Hetem *et al.*, 2007; McFarland, Barrett, Costello, *et al.*, 2020; Sha *et al.*, 2020). This thermal selection aligns with the findings of this study with baboons selecting for more stable microclimates compared to the high elevation sparsely vegetated microhabitat type, this being the hottest of the classified microhabitat types. Here, stable microclimates

are defined as areas with relatively low fluctuations in temperature. By selecting for these microclimates, baboons can reduce the energetic costs associated with thermoregulation under both hot and cold conditions. Baboons also had a stronger selection for thermally comfortable areas during the midday and afternoon periods, when heat loads were highest, as well as strongly preferring densely vegetated microhabitats during this time. Along with densely vegetated areas, baboons also preferred low elevation sites during the midday as well as during the wet season. These results align with previous research on primate thermoregulation, such as in black-fronted titi monkeys (*Callicebus nigrifrons*), which adjusted their habitat use to achieve thermal comfort. During the hottest times of the day, black fronted titi monkeys selected for cooler, shaded areas which were found lower in the forest strata (Gestich, Caselli and Setz, 2014).

Baboons also selected for warmer temperatures in the morning period, particularly in the dry season, likely to warm themselves after cooler nights in the cave sleep site. This sunbathing behaviour during cool morning periods is consistent with observations in other southern African primates, such as vervet monkeys (*Chlorocebus pygerythrus*), which exhibit extended periods of inactivity following cooler overnight temperatures (Danzy *et al.*, 2012). Ring-tailed lemurs (*Lemur catta*) also follow this pattern of morning thermoregulation, in which individuals sunbathe during low morning temperatures and typically end this behaviour around 10:00 (Kelley et al., 2016). This behaviour in chacma baboons may explain the higher peaks around the cave site in the dry season occupancy model compared to the wet season. Baboons likely spent more time at the top of the cave for thermoregulation before beginning their foraging routes, a pattern supported by field observations showing later departures after the start of their activity period during the dry season. Patterns of later departure in the cooler dry season compared to the wet season align with other studies on chacma baboons in Limpopo, whereby troops departed from their sleep site earlier on days with higher maximum heat loads (Noser and Byrne, 2007). Earlier departures during warmer periods of the year suggest that baboons aim to reach resources before rising temperatures make thermoregulation more costly, and subsequently are faced with a trade-off in energy acquisition.

This seasonal shift in activity timing also reflects broader changes in habitat use, as baboons adjust their spatial distribution in response to resource availability. In the wet season, when water sources are more widely distributed across the landscape, baboons were found further from rivers, suggesting a reduced dependence on primary water sources and subsequently greater flexibility in foraging routes. This reduced dependency on water sites is shown in other studies on chacma baboons in South Africa where water availability increased the ability for further ranging behaviour (Hoffman and O'Riain, 2012; Stone *et al.*, 2013). It has been found that water availability strongly limits travel patterns in baboons, whereby patches with high food abundance are left unvisited if they are outside the range of a reliable water source (Altmann, 1974; Hamilton III, Buskirk and Buskirk, 1976; Hoffman and O'Riain, 2012; Stone *et al.*, 2013). Similarly, in red-fronted lemurs (*Eulemur fulvus rufus*), access to permanent water sources during the dry season strongly influences ranging behaviour, with troops located further from reliable water sources expanding their home ranges to maintain access (Scholz and Kappeler, 2004). This suggests that for baboons dependent on consistent water availability, increasing aridity may necessitate greater ranging distances, potentially affecting the balance between thermoregulation and energy intake.

While baboons exhibit heightened behavioural and dietary flexibility in response to seasonal changes (Barton *et al.*, 1992; Henzi, Byrne and Whiten, 1992; Hill and Dunbar, 2002; Barrett and Henzi, 2008; Hoffman and O'Riain, 2012), their ability to maintain this balance may be challenged by rising temperatures and increasing aridity. As thermal stress intensifies, the need for rest, particularly in shaded areas, may restrict the time available for foraging (van Doorn, O'Riain and Swedell, 2009; Korstjens, Lehmann and Dunbar, 2010), leading to potential nutritional deficits. Studies on other primates, such as vervet monkeys, show similar behavioural adjustments to thermal stress, with individuals increasing inactivity and shade-seeking at high environmental temperatures, which in turn aids in body temperature regulation (McFarland *et al.*, 2020). Given that baboons also exhibit shade-seeking behaviour, particularly in hot and dry conditions (Stelzner, 1988), such thermoregulatory strategies are crucial for mitigating heat stress but come with trade-offs in activity budgets. Currently, the *Papio* genus shows to have a general enforced rest time of 19% of their total daily activities but this

is predicted to rise to between 20 and over 33% across the majority of southern Africa with both a 2 °C and 4 °C increase (Korstjens, Lehmann and Dunbar, 2010). Similarly, reduced water availability may further constrain movement and habitat use, particularly in regions where surface water sources are limited (Barton *et al.*, 1992; Stone *et al.*, 2013). Baboons are a water-dependent species and so with drier conditions, there is again an increased need to reduce activity dramatically to meet evaporative cooling needs (Brain and Mitchell, 1999; Hill, 2006) leading to further implications for energy intake rates.

Climate change poses a significant threat to large terrestrial mammals, which face challenges related to their size, habitat requirements, and limited dispersal opportunities (Hetem *et al.*, 2014; Fuller *et al.*, 2016; Mitchell *et al.*, 2018). Unlike smaller species, which can exploit microclimates more effectively, large mammals rely heavily on phenotypic plasticity to buffer against environmental changes (Hetem *et al.*, 2014; Fuller *et al.*, 2016). This includes shifts in behaviour, physiology, and phenology, allowing individuals to regulate body temperature, conserve water, and adjust activity patterns. However, these adaptations have limits, particularly in increasingly arid environments where rising temperatures and reduced water availability exacerbate physiological stress (Hetem *et al.*, 2014). Many large mammals, including baboons, lack specialized mechanisms such as selective brain cooling, making them more dependent on behavioural thermoregulation and access to water sources (Brain and Mitchell, 1999; Maloney *et al.*, 2007). Furthermore, habitat fragmentation and human development restrict the ability of populations to shift their ranges in response to climate change, increasing their risk of extinction — particularly in regions like South Africa, where up to 69% of mammal species could be lost by 2050 (Thomas *et al.*, 2004).

Future studies

Future studies should assess how perceived predation risk interacts with the energetic and thermal landscape, and what trade-offs in behaviour, movement and habitat selection arise. The landscape of fear may further exacerbate already strained energy budgets and thermoregulatory activity with

increasing temperatures as microhabitats that have optimal thermal properties or resources may be avoided due to this perceived risk (Cowlishaw, 1997b; Coleman and Hill, 2014). Furthermore, the role of the anthropogenic environment should be assessed as, along with increasing aridity, human interaction poses a significant threat to primate survival (Hoffman and O'Riain, 2012). The threat of human-primate conflict is seen with the increase in habitat fragmentation, primate injury, urban development and the introduction of alien species (Henzi *et al.*, 2011; Hoffman and O'Riain, 2012; Slater, Barrett and Brown, 2018). With limited energy budgets, baboons may be driven into human-modified areas in search of high-quality forage, particularly as models predicting suitable baboon habitats show these areas are becoming more developed (Hoffman and O'Riain, 2012).

Conclusion

This study demonstrates that baboon movement, behaviour, and habitat selection are shaped by the interaction between thermal and energetic landscapes, with individuals adjusting their ranging and activity budgets to balance energy acquisition with thermoregulatory demands. These findings underscore the complex trade-offs that occur as environmental temperatures and resource availability fluctuate.

Understanding these thermal and energetic trade-offs is increasingly important as primates face rising temperatures, habitat fragmentation, and resource scarcity (van Doorn, O'Riain and Swedell, 2009; Korstjens, Lehmann and Dunbar, 2010; Hetem et al., 2014; Hill and Winder, 2019; Sha et al., 2020). Animals, particularly large mammals, face a risk of climate induced habitat loss and the indirect effect of climate change in reducing resources (Fuller *et al.*, 2016) or vegetation productivity (Henzi, Byrne and Whiten, 1992). The survival of large mammals, including baboons, will depend on their ability to exploit behavioural and physiological plasticity to buffer against habitat changes and thermal extremes (Hetem *et al.*, 2014). With increasing habitat fragmentation and resource scarcity, understanding these adaptive limits is critical for predicting future resilience of species and informing conservation policies. Conservation strategies should prioritise maintaining thermal heterogeneity, as microhabitats with

diverse thermal properties provide essential buffering against extreme temperatures (Fawcett *et al.*, 2019). This heterogeneity provides varying degrees of thermal properties alongside differences in resource and refuge availability, enabling spaces for various behaviours within the activity budget. By preserving landscape heterogeneity and enhancing habitat connectivity, primates, and other large mammals, can better balance thermoregulatory and energetic demands through informed movement, behavioural adaptations, and habitat selection decisions.

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Appendix

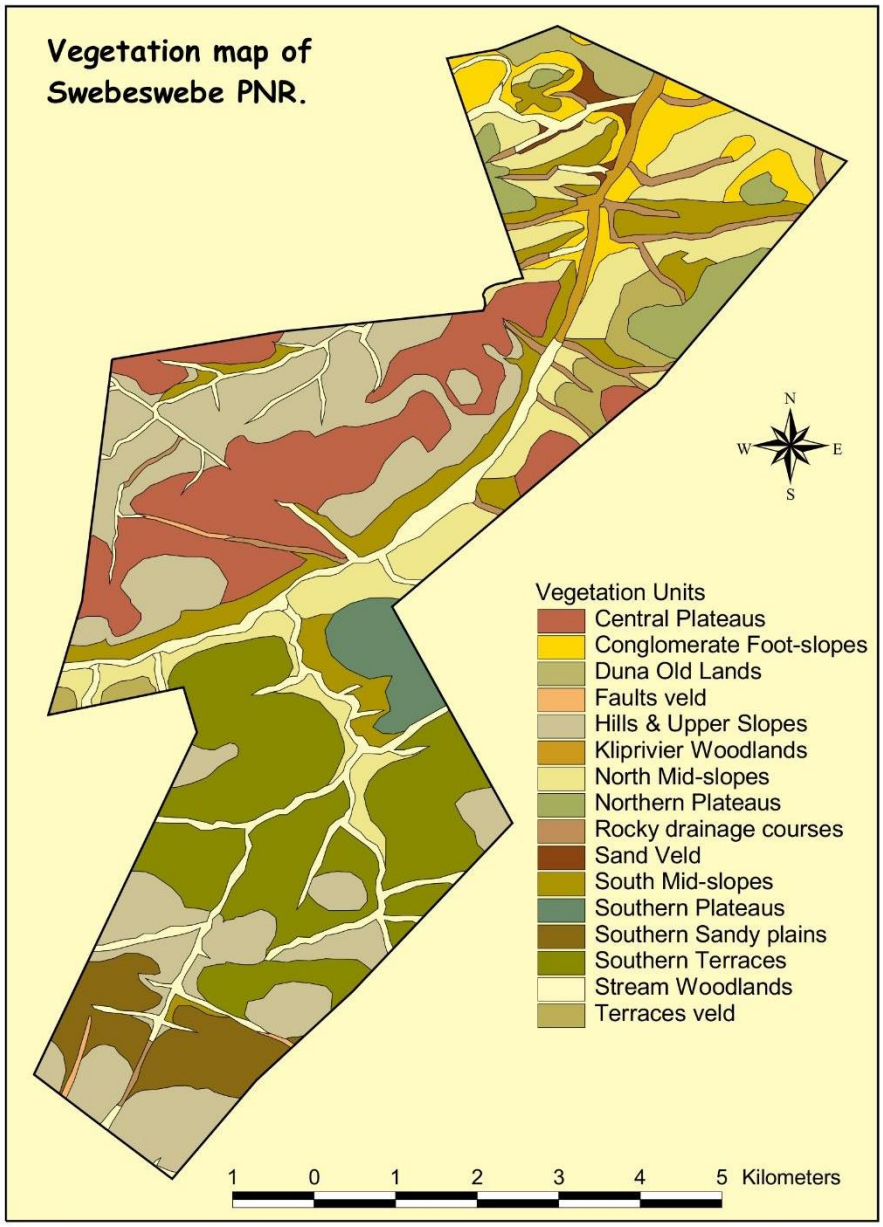


Figure S1: Vegetation map of Swebeswebe wildlife estate categorising vegetation types

Table S2: Top five and null model for daily travel distance (m) of the troops

	Intercept	NDVI	NDWI	Macroclimate Temperature	Photoperiod	Log-Likelihood	AIC	Delta AIC	Weight
16	2007.528	-815.6099	-222.6644	706.1808	425.6906	-2655.259	5324.923	0.00000	0.9954513
12	3196.440	-920.9569	NA	732.0868	325.0047	-2662.083	5336.469	11.54536	0.0030973
15	7071.342	-944.7041	-107.0013	1028.4404	NA	-2662.980	5338.262	13.33896	0.0012633
8	-4116.452	-684.7071	-270.6665	NA	941.3742	-2664.929	5342.161	17.23765	0.0001799
14	-2372.519	NA	-572.3129	471.9117	797.0800	-2668.006	5348.314	23.39045	0.0000083
Null	7143.602	NA	NA	NA	NA	-2713.705	5433.496	108.57239	0.0000000

Table S3: Top five and null model for daily travel rate (m/s) of the troops

	Intercept	NDVI	NDWI	Macroclimate Temperature	Photoperiod	Log-Likelihood	AIC	Delta AIC	Weight
Null	0.1860933	NA	NA	NA	NA	307.7988	-609.5121	0.000000	0.8223285
2	0.0560927	-0.0208680	NA	NA	0.0107864	307.9353	-605.6555	3.856585	0.1195635
6	0.2216983	-0.0239070	NA	0.0197849	-0.0031543	307.6421	-602.9821	6.529981	0.0314107
3	-0.0390002	NA	-0.0176787	NA	0.0188717	305.8602	-601.5053	8.006854	0.0150099
1	0.0263692	NA	NA	NA	0.0133257	304.1738	-600.2046	9.307473	0.0078335
4	0.0092663	-0.0159898	-0.0107706	NA	0.0147584	305.5441	-598.7860	10.726114	0.0038539

Table S4: Top five and null model for daily travel directedness of the troops

	Intercept	NDVI	NDWI	Macroclimate Temperature	Photoperiod	Log-Likelihood	AIC	Delta AIC	Weight
Null	0.2265782	NA	NA	NA	NA	-225.8631	457.8117	0.000000	0.8343769
1	0.2273967	NA	NA	NA	NA	-227.8771	461.8396	4.027933	0.1113545
9	0.2310014	NA	NA	0.0705938	NA	-228.0072	464.1573	6.345579	0.0349492
2	-0.3392457	NA	NA	NA	0.0479523	-229.1638	466.4704	8.658727	0.0109937
5	0.2279284	NA	-0.0250197	NA	NA	-230.0967	468.3362	10.524516	0.0043251
3	0.2296866	-0.0202957	NA	NA	NA	-230.1747	468.4922	10.680493	0.0040006

Table S5: Top five and null model for two-weekly home range size (km^2) of the troops

	Intercept	NDVI	NDWI	Macroclimate Temperature	Photoperiod	Log-Likelihood	AIC	Delta AIC	Weight
6	-6.940535	NA	-1.499679	NA	1.1779353	-784.2954	1578.807	0.0000000	0.3709271
8	-8.467693	0.4571197	-1.690991	NA	1.3066401	-783.2917	1578.887	0.0800463	0.3563746
14	-4.778761	NA	-1.505047	0.2559319	0.9982981	-784.1616	1580.627	1.8199213	0.1493130
16	-7.456944	0.4338675	-1.683579	0.1103882	1.2225705	-783.3466	1581.099	2.2925075	0.1178900
13	7.260591	NA	-1.362124	1.0455542	NA	-788.5075	1587.231	8.4242583	0.0054952
Null	7.313515	NA	NA	NA	NA	-808.0570	1622.200	43.3930777	0.0000000

Table S6: Top five and null model for daily travel behavioural counts of the troops

	Intercept	NDVI	NDWI	Macroclimate Temperature	Photoperiod	Log-Likelihood	AIC	Delta AIC	Weight
16	0.0166771	-0.0289629	0.0782651	0.0383462	-0.0639238	-1857.407	3729.060	0.000000	0.5929445
15	0.0891094	NA	0.0748825	0.0365594	-0.0709164	-1859.208	3730.600	1.539944	0.2745488
12	0.1394278	-0.0266890	0.0923504	NA	-0.0750875	-1860.404	3732.991	3.930866	0.0830687
11	0.2004242	NA	0.0885189	NA	-0.0809922	-1861.949	3734.029	4.968818	0.0494366
13	-0.0699179	NA	NA	0.0685684	-0.0563882	-1872.445	3755.021	25.961050	0.0000014
Null	4.4864573	NA	NA	NA	NA	-2434.156	4874.364	1145.303645	0.0000000

Table S7: Top five and null model for daily rest behavioural counts of the troops

	Intercept	NDVI	NDWI	Macroclimate Temperature	Photoperiod	Log-Likelihood	AIC	Delta AIC	Weight
15	-3.461869	NA	0.1029750	0.2020097	0.1036205	-1454.837	2921.858	0.000000	0.6877901
16	-3.474696	-0.0168181	0.1073756	0.2009331	0.1047936	-1454.605	2923.455	1.597204	0.3094763
13	-3.642048	NA	NA	0.2431190	0.1199991	-1461.700	2933.530	11.672238	0.0020085
14	-3.649805	-0.0034452	NA	0.2432395	0.1206992	-1461.692	2935.568	13.709699	0.0007252
11	-3.047892	NA	0.1787029	NA	0.0688613	-1479.390	2968.911	47.053467	0.0000000
Null	2.908397	NA	NA	NA	NA	-1762.600	3531.252	609.394383	0.0000000

Table S8: Top five and null model for daily forage behavioural counts of the troops

	Intercept	NDVI	NDWI	Macroclimate Temperature	Photoperiod	Log-Likelihood	AIC	Delta AIC	Weight
15	-1.674365	NA	-0.1208835	-0.1155921	0.0406467	-1788.849	3589.882	0.000000	0.6321370
16	-1.613862	0.0214262	-0.1230432	-0.1176210	0.0349108	-1788.360	3590.965	1.082797	0.3678618
11	-2.053024	NA	-0.1667469	NA	0.0751553	-1803.409	3616.948	27.066079	0.0000008
12	-2.026737	0.0104226	-0.1680120	NA	0.0726429	-1803.294	3618.772	28.890164	0.0000003
13	-1.360148	NA	NA	-0.1689159	0.0129150	-1806.478	3623.087	33.204916	0.0000000
Null	3.962365	NA	NA	NA	NA	-2202.268	4410.588	820.705377	0.0000000

Table S9: Top five and null model for daily social behavioural counts of the troops

	Intercept	NDVI	NDWI	Macroclimate Temperature	Photoperiod	Log-Likelihood	AIC	Delta AIC	Weight
12	-2.412496	0.1444133	-0.0805154	NA	0.0016171	-1542.389	3096.962	0.000000	0.5323218
16	-2.321625	0.1471366	-0.0704747	-0.0251700	-0.0067164	-1542.172	3098.589	1.627426	0.2359300
14	-2.169973	0.1361525	NA	-0.0531176	-0.0200130	-1543.864	3099.911	2.949005	0.1218445
10	-2.346291	0.1252368	NA	NA	-0.0036330	-1545.015	3100.161	3.198785	0.1075392
11	-2.732737	NA	-0.0524242	NA	0.0337783	-1548.832	3107.795	10.833460	0.0023644
Null	2.703548	NA	NA	NA	NA	-1696.074	3398.200	301.238483	0.0000000

Table S10: Top five and null model for daily shade use counts of the troops

	Intercept	NDVI	NDWI	Macroclimate Temperature	Photoperiod	Log-Likelihood	AIC	Delta AIC	Weight	Family	Degrees of Freedom	Scans
16	-1.776847	0.1258898	0.0937008	0.1989230	0.0309849	-1980.347	3974.940	0.000000	0.6574782	Negative Binomial(1.4912,log)	7	+
14	-2.003072	0.1280982	NA	0.2361205	0.0514628	-1982.309	3976.801	1.861411	0.2592275	Negative Binomial(1.4912,log)	6	+
15	-2.075937	NA	0.1045490	0.2086441	0.0608965	-1983.699	3979.582	4.642729	0.0645246	Negative Binomial(1.4912,log)	6	+
13	-2.330991	NA	NA	0.2486719	0.0840674	-1985.978	3982.087	7.146814	0.0184489	Negative Binomial(1.4912,log)	5	+
12	-0.895243	0.1457807	0.1704440	NA	-0.0473075	-1989.004	3990.191	15.251409	0.0003207	Negative Binomial(1.4912,log)	6	+
Null	3.748350	NA	NA	NA	NA	-2152.032	4310.116	335.176047	0.0000000	Negative Binomial(0.6785,log)	3	NA

Table S11: Top five and null model for troop level and top elevation sparse microhabitat temperature differences

	(Intercept)	scale(NDVI)	scale(NDWI)	Season	TimeCat	scale(Weatherair)	df	logLik	AICc	delta	weight
28	-0.2842277	-0.9105070	0.7551560	+	+	NA	8	-1935.899	3888.027	0.0000000	0.3530327294
32	-0.3400746	-0.9096925	0.7359931	+	+	0.4756319	9	-1935.200	3888.687	0.6593656	0.2538841246
20	-0.7526224	-0.8539055	0.6136187	NA	+	NA	7	-1937.785	3889.748	1.7208645	0.1493255057
26	-0.5908128	-0.6529952	NA	+	+	NA	7	-1937.886	3889.949	1.9217563	0.1350550729
30	-0.6426476	-0.6588186	NA	+	+	0.5122713	8	-1937.078	3890.385	2.3581717	0.1085786659
Null	0.1206617	NA	NA	NA	NA	NA	3	-1948.950	3903.937	15.9096582	0.0001239015

Table S12: Model output for Ivlev's electivity index with microhabitat type (eleveg) time category (Timecat) and season as interacting terms

	Ivlev's Index		
Predictors	*Estimates*	*CI*	*p*
(eleveg [highopen] × Timecat [Midday]) × Season [Wet]	-0.12	-0.69 – 0.44	0.659
(eleveg [middense] × Timecat [Midday]) × Season [Wet]	-0.18	-0.70 – 0.34	0.487
(eleveg [midopen] × Timecat [Midday]) × Season [Wet]	-0.04	-0.57 – 0.49	0.881
(eleveg [lowdense] × Timecat [Midday]) × Season [Wet]	0.05	-0.48 – 0.58	0.856
(eleveg [lowopen] × Timecat [Midday]) × Season [Wet]	0.05	-0.51 – 0.61	0.851
(eleveg [highopen] × Timecat [Afternoon]) × Season [Wet]	0.08	-0.58 – 0.74	0.814
(eleveg [middense] × Timecat [Afternoon]) × Season [Wet]	0.04	-0.48 – 0.56	0.866
(eleveg [midopen] × Timecat [Afternoon]) × Season [Wet]	-0.05	-0.57 – 0.47	0.849
(eleveg [lowdense] × Timecat [Afternoon]) × Season [Wet]	0.07	-0.47 – 0.60	0.798
Random Effects			
σ^2	0.02		
$\tau_{00\ Troop.ID}$	0.00		
ICC	0.00		
$N_{Troop.ID}$	4		
Observations	97		
Marginal R^2 / Conditional R^2	0.866 / 0.866		

Table S13: Top five and null model for dry season habitat selection model

	cond((Int))	disp((Int))	cond(daily_cave)	cond(daily_fence)	cond(daily_microhab)	cond(daily_river)	cond(daily_waterhole)	cond(daily_anthro)	cond(daily_NDVI)	cond(daily_NDWI)	df	logLik	AICc	delta	weight
207	1.6401312	+	-0.0004283	0.0001489	+	-0.0004738	8.37e-05	NA	NA	NA	12	-7025.722	14075.56	0.0000000	3.069113e-01
208	1.6239379	+	-0.0004283	0.0001466	+	-0.0004732	7.25e-05	1.95e-05	NA	NA	13	-7025.083	14076.30	0.7413505	2.118511e-01
255	1.6156797	+	-0.0004297	0.0001470	+	-0.0004718	8.22e-05	NA	0.144195	-0.1458605	14	-7024.244	14076.64	1.0829831	1.785855e-01
223	1.6267522	+	-0.0004286	0.0001484	+	-0.0004730	8.29e-05	NA	0.054627	NA	13	-7025.277	14076.69	1.1289113	1.745311e-01
256	1.5983357	+	-0.0004296	0.0001446	+	-0.0004711	7.07e-05	2.01e-05	0.146740	-0.1461441	15	-7023.565	14077.31	1.7471666	1.281210e-01
Null	0.7878217	+	NA	NA	NA	NA	NA	NA	NA	NA	3	-7224.990	14455.99	380.4281585	7.552450e-84

Table S14: Top five and null model for wet season habitat selection model

	cond((Int))	disp((Int))	cond(daily_anthro)	cond(daily_cave)	cond(daily_fence)	cond(daily_microhab)	cond(daily_NDVI)	cond(daily_NDWI)	cond(daily_river)	cond(daily_waterhole)	df	logLik	AICc	delta	weight
256	1.1206473	+	-0.0001046	-0.0002250	8.32e-05	+	-0.1510050	-0.1741017	-0.0004591	5.03e-05	16	-4856.561	9745.372	0.000000	5.735338e-01
128	1.1165148	+	-0.0000623	-0.0002230	8.32e-05	+	-0.1402939	-0.1655081	-0.0004555	NA	15	-4858.852	9747.925	2.553055	1.600185e-01
224	1.0768175	+	-0.0001033	-0.0002232	8.38e-05	+	-0.1503654	NA	-0.0004523	4.78e-05	15	-4858.962	9748.146	2.773525	1.433163e-01
252	1.1788237	+	-0.0001039	-0.0001743	NA	+	-0.1627816	-0.1759075	-0.0003908	5.04e-05	15	-4859.635	9749.490	4.117941	7.317447e-02
96	1.0750423	+	-0.0000631	-0.0002214	8.38e-05	+	-0.1401963	NA	-0.0004492	NA	14	-4861.030	9750.254	4.881314	4.995687e-02
Null	0.6910037	+	NA	NA	NA	NA	NA	NA	NA	NA	3	-4950.124	9906.258	160.885805	6.647378e-36

Table S15: Top five and null model for distances from river model

	Intercept	NDVI	Macroclimate Temperature	Microclimate Temperature	Season	Photoperiod	Log-Likelihood	AIC	Delta AIC	Weight
16	619.6012	-45.72301	14.413390	12.29783	+	-30.01800	-20212.17	40440.38	0.000000	0.9448214
14	649.9480	-45.75536	21.231915	NA	+	-32.80606	-20216.52	40447.09	6.701262	0.0331275
8	545.9784	-44.72947	NA	19.56221	+	-23.61463	-20216.93	40447.91	7.523138	0.0219645
15	284.5173	-39.85083	1.498058	18.31496	+	NA	-20222.78	40459.60	19.216369	0.0000635
6	536.1499	-43.74178	NA	NA	+	-23.09626	-20224.80	40461.62	21.238031	0.0000231
Null	271.1626	NA	NA	NA	NA	NA	-20263.34	40532.69	92.306770	0.0000000