From the Floodplain to the Woodland (and back): Baboon movement in the highly seasonal and heterogeneous ecosystem of Gorongosa National Park

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Abstract

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Movement ecology, or the study of how organisms move within their environments, has long been studied in multiple taxa, including primates. Within primates, the wide-ranging, terrestrial, group-living baboon has been studied both for insight into the primate clade, as well as a proxy for early hominins, with their behaviour and decisions presumed analogous to those of our human ancestors. Previous studies on these baboons have established the role of topographic mental maps, group decision making, habitat structure, and episodic memory on the movement ecology. However, Papio clade is made up of multiple species and subspecies across sub-Saharan Africa, inhabiting a diverse range of ecosystems and environments, and shows a wide range of behavioural plasticity. Here, I study how baboons inhabiting a low predator-density, high baboon-density, highly seasonal area compare in their movement decisions between adjacent but structurally different habitats, and to other study sites. Focusing on GPS collar data from four monkeys from two baboon troops in Gorongosa National Park, Mozambique, I answer questions of where, how, and why these baboons move through their environments. I compare baboons ranging in a stable, densely wooded area to baboons in the low-density, seasonally inundated alluvial floodplain, and compare their movements across the year from the rainless dry season, through the flooded wet season and back into the beginning of the next dry season. I begin by establishing the ranging data of the baboons, and use machine learning to group each home range into basic habitat types. I use step-selection analysis to determine predictors of movement and habitat choice amongst both troops, and find that they vary not only between seasons and troops, but also between monkeys within the same troop; however, all monkeys' movements are predicted by the angle to their sleep site in all seasons. I then use hierarchical clustering to establish the location of resources used by each baboon, and apply the Travelling Salesperson Problem to the movement paths between resources, showing that the baboons perform better than the nearest neighbour route, and on occasion use the optimal route. Next, I examine the use of sleep sites relative to these resources, and find that the baboons prefer to sleep in the centre of their home ranges, and reuse sleep sites throughout the year, including sites that are periodically inaccessible due to flooding. I further find that the baboons use sleep sites closer to their last resource of the day, rather than the first resource. Finally, I apply nearest neighbour analysis to the baboon GPS tracks, and identify reused routes within the home ranges. I find that while these routes are used throughout the year, routes in areas vacated during seasonal changes are not reused within the study period, providing inconclusive results on the baboons' long-term memory. Overall, I present the first study of the drivers and mechanisms of movement behaviour in Gorongosa baboons, showing how they compare to other long-term study sites and helping to further disentangle the role environment plays in movement decisions.

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Author Contributions

All work in this thesis is primarily my own.

This thesis consists of four independent data chapters formatted for publication in peer-reviewed journals, with an additional introduction and discussion. Currently all chapters are in preparation for submission to peer-reviewed journals.

Dora Biro and Susana Carvalho contributed ideas, feedback, and to the design and analysis of each study, and contributed to manuscript preparation and edits for each chapter. Both also contributed to collar deployment and the design of collar data collection protocol.

Philippa Hammond provided demographic and behavioural data for the Woodland Troop. Philippa Hammond had equal contribution to collar deployment and design of collar data collection protocol. She also contributed to the manuscript preparation and edits for each chapter.

COVID-19 Impact Statement

The research done in this thesis took place before, during, and after the events of the COVID-19 pandemic. I began my DPhil in October 2017, and completed my first field season in Gorongosa National Park (GNP), Mozambique from April 2018-November 2018. During this time, I completed daily follows of the Floodplain Troop of baboons, gathering baseline movement data with a handheld device, that was eventually to be coupled with hormone data from faecal samples, as well as behavioural data. I planned on returning to the field in April 2019, equipped with collars and a faecal sample collection protocol, and ready to start data collection on semi- to fully-habituated baboons. However, Cyclone Idai struck Gorongosa in March 2019. This massive weather event killed hundreds of people in Mozambique and Zimbabwe, and the decision was made to delay my return to GNP until June and have an additional field season in 2020. In October 2019, the Mozambique national election occurred, sparking a series of events leading to shootings around GNP. As the roads were unsafe to travel, I was unable to organise a visa to stay longer in Mozambique or permits to export my faecal samples, and so I was relying on my 2020 field season to ensure I had all the data I needed.

Unfortunately, the COVID-19 pandemic prevented my 2020 field season, leaving me unable to complete my thesis as originally planned. I naively assumed that I would be able to return to the field in late 2020 or at worst early 2021; however, this was not the case, and I was forced to change my thesis plans significantly. Fortunately, colleagues in GNP were able to download the remaining collar data for me when they were able to find the troops. Ultimately, of my originally planned thesis, only one chapter was able to be completed. Because of the delay in my thesis, I was not able to receive further funding, and instead worked part-time while finishing, an added stressor on top of lockdowns, sickness, and all the other implications of a pandemic.

While these issues were regrettable, I believe I have been able to produce a worthwhile thesis that demonstrates interesting analyses of remote sensing and GPS data, even in the absence of many covariates or ground truthing. However, when reviewing the research, these circumstances of data collection should be noted, particularly in regard to missing analysis or other factors.

To my family, blood or otherwise, and all the primates in Gorongosa National Park.

Table of Contents

1

Chapter 1: Introduction

CONTENTS

1.1 Introduction

Movement is integral to all living things, from single-celled organisms to mega-fauna (Greenwood & Swingland, 1983; L. Hansson & Åkesson, 2014; Nathan et al., 2008). While all living beings must move at some stage in their life cycles, the reasons they do so can vary: generally, they need to locate food and avoid predation, as well as find suitable growing or living environments, shelter, and mates (Greenwood & Swingland, 1983; Laundré et al., 2010). As such, the study of animal movement is at the core of understanding species' unique adaptations to their environments. Questions of when, where, how, and why movement occurs remain some of the most fundamental in organismal biology (Nathan et al., 2008).

When movement occurs is largely dictated by an animal's environment; they must move when the likelihood of obtaining food outweighs the risks of predation or competition. When space and resources are limited but competed for, interspecific competitors should still find ways to avoid each other to coexist, or risk conflict (Hardin, 1960). This temporal partitioning of species is limited by evolved endogenous rhythms and morphology, but various species still show flexibility in when they decide to move. This flexibility often occurs on a small scale, where local pressures force animals into a different movement schedule. For instance, in times of high heat and low wind, mouflon (*Ovis gmelini musimon x Ovis* sp.) were more active before dawn and after dusk compared to periods when it was cool and windy (Bourgoin et al., 2011). Chacma baboons (*Papio ursinus*) increased nocturnal activity when days were shorter, brighter and colder (Ayers et al., 2020); in the day, yellow baboons (*Papio cynocephalus*) spent more time overlapping when available food was more evenly dispersed and appeared to actively avoid other troops (Markham et al., 2013).

On a large scale, animals globally are becoming more nocturnal in response to human movement patterns, affecting even top-level carnivores and other predators (Gaynor et al., 2018; Haswell et al., 2020). For instance, lions (*Panthera leo*) were shown to temporally partition themselves from humans using bomas or grazing livestock, travelling in these areas only when human activity was low, i.e., overnight (Oriol-Cotterill et al., 2015). Thermoregulation and ease of movement also impact when animals decide to move. Pygmy rabbits (*Brachylagus idahoensis*) alter their movement patterns seasonally based on climate and predation risk, moving more in warmer periods to reduce thermal stress and resting in areas of low predation (Milling et al., 2017). Finally, despite evolution towards a particular niche, some animals can alter their behaviour significantly in order to occupy a different temporal niche. One instance of this is the golden spiny mouse (*Acomys russatus*): despite evolving an eye structure that is most suited to nocturnal behaviour, competition by the common spiny mouse (*Acomys cahirinus*) led it to adopt a diurnal activity pattern, preferring darker microhabitats such as below boulders (Kronfeld-Schore et al., 2001).

Where an animal moves is largely dictated by the same drivers and constraints as when they move, with animals striking a balance between biological needs, such as necessity for food, water, shelter, and increasing fitness, and the risk of predation or conflict with conspecifics (Greenwood & Swingland, 1983). Throughout their day, animals must maintain homeostasis through their energy budget, as well as meet any social needs; therefore, they must choose where to go based on how much energy it will take to get there, what they are able to get by staying in an area, the risks of approaching an area, and whether a better option exists (Charnov, 1976; Laundré et al., 2010; Pontzer & McGrosky, 2022). When food is involved, animals must further take into account the process of finding, obtaining, and processing the food compared to their

chances of equal calories in the wider environment (Charnov, 1976). Other factors that impact health, such as inhospitable temperatures, low water availability, and human incursion further complicate movement decisions (Atkins et al., 2019; Branco et al., 2019; Gesquiere et al., 2011; Long et al., 2016; Stelzner, 1988; Thompson et al., 2016). Particularly as habitat destruction increases and farmland becomes more abundant, crop-raiding behaviour and water shortages increase the risk of human-animal interaction, adding an increased risk when foraging for food above natural predators (Branco et al., 2019; Paietta et al., 2022; Taylor et al., 2016).

In an optimal world, individuals would not only incorporate the costs and benefits of going to the next resource, but further plan the energetic expenditure of an entire journey, a task that requires spatial and temporal reasoning as well as memory of previous movements across days, weeks or even years (D. J. Anderson, 1983; Boyer & Walsh, 2010). This task becomes even harder when the food is ephemeral or mobile, and over long time periods, animals must remain flexible in their foraging strategy to account for changes in the environment (Trapanese et al., 2019).

There are many ways an animal can decide where to move. For solitary species, movement generally relies entirely on the needs of the individual. For instance, leopards (*Panthera pardus)* living in a highly anthropogenic environment, preferred to stay away from human settlements and closer to high-density environments such as tea plantations and forests in the wet season when there was more wild food available. However, they stayed further from protected areas and closer to tea plantations, where domestic animals were abundant, during the dry season, seasonally striking a balance between the need for food and avoidance of open areas, consistent with their landscape of fear (Naha et al., 2021). While group-living animals also make independent decisions, these decisions are strongly influenced by those around them. Some groups follow a single leader, who makes decisions based on memory and experience, such as in

African elephants (*Loxodonta africana*), who choose to follow the matriarch as a leader (McComb et al., 2001). Other species, such as meerkats (*Suricata suricatta*), try to influence group members into their own preferred movement, with dominant individuals often showing the most influence (Averly et al., 2022). Still others, including chimpanzees (*Pan* spp.), live in fission-fusion societies, where the group fissions into smaller groups or individuals as a response to time constraints and food availability, but fusion back with those groups when conditions allow, thus satisfying individual requirements while also reaping some of the benefits of group-living (Lehmann et al., 2007).

How movement happens can be approached through two complementary angles. First, we can ask what the physical mechanism is by which an animal propels itself through space; second, we can probe the navigational strategies it implements. Physical movement is both enabled and constrained by physiology, as well as by the area through which the animal is moving (Biewener & Patek, 2018; Halsey, 2016). Navigation, on the other hand, is a combination of intrinsic capacities and experience. When travelling repeatedly through a familiar area, such as a home range, a representation of the spatial relationships between locations of interest can make it easier to repeatedly travel between fixtures (Tolman, 1947). This "map" is generally thought to be one of two types: landmark, also known as topographic or topological, or Euclidean. Landmark maps allow an animal to orient between key locations in its environment, but without these being represented according to the distances and directions between them. Topological maps can allow animals to travel from point to point along known routes, but they do not allow for the computation of novel shortcuts, and if the animal encounters an obstacle or a fixture is removed, it may be unable to compensate (Di Fiore & Suarez, 2007; Janson & Byrne, 2007; Poucet, 1993). In contrast, a Euclidean map incorporates directional and distance information

between known locations, and while preferred routes may be used to travel, novel routes between previously "unconnected" points can also be computed (Poucet, 1993; Rolland & Trull, 2022). Both types of map rely on memory, and many species show evidence of one or the other.

For example, baboons (*Papio ursinus*) show little evidence of Euclidean mapping when forced to change routes due to intergroup encounters, but are more likely to use network or landscape maps to traverse the environment (Noser & Byrne, 2007a). On the other hand, there is some evidence that chimpanzees (*Pan troglodytes verus*) navigate between food resources without relying on habitual routes, and do so with more precision than if they were simply using a very dense landmark map, implying they use a Euclidean map (Normand & Boesch, 2009).

In social species, individuals less familiar with a given terrain can often rely on more experienced group members for navigational information. However, for a range of migratory animals, including numerous species of birds, movement over long distances must commence without prior experience. There is now extensive evidence that migratory vectors are genetically encoded in these species, complemented by the use of magnetic, visual, olfactory, and potentially even auditory cues (some of which need to be calibrated prior to the start of migration) (Mouritsen, 2018). Subsequently, more experienced navigators will alter their migration routes based on terrain features and weather patterns, while others become vagrants, ending up in a place far removed from their typical migratory destination (McDuffie et al., 2022; Zawadzki, 2021). While such long-distance movements place a different set of demands on animals than travel related to daily activity, understanding the mechanisms of long-distance travel can also contribute to our understanding of short-distance navigation.

Why animals move is the key to where, when, and how they move. Animals may employ different movement strategies based on their end goals, or choose not to move at all.

Understanding what drives animals to move requires understanding where they are going, for what reason, and how/if they get there.

The study of movement in primates has developed significantly since the earliest such studies in the 1960s, with focus both on why primates move and how they move. Early captive studies established that chimpanzees *(Pan troglodytes)* are capable of generating efficient movement paths between resources distributed around an enclosure, forming a mental map of the least-distance path, and remembering which food sources were depleted or already checked (Menzel, 1973). A later study on wild chimpanzees found that, in locating tools for nut cracking, they were similarly able to locate nearby appropriate stones even if they were out of sight, suggesting the use of a precise mental map (Boesch & Boesch, 1984). Around the same time, the now longest-running baboon research site, the Amboseli Baboon Project, was beginning to create a baseline understanding of yellow baboon (*Papio cynocephalus*) foraging and movement patterns (Altmann & Altmann, 1970). Considered dietary generalists, baboons could be expected to forage at random on any available food. However, baboons in this study site were found to forage on more varied patches of food in different habitat types during the wet season, when there was greater food abundance, and minimise travel distance to food, indicating risk avoidance and the balancing of energy expenditure and travel costs (Post, 1978, 1982). Temperature also affected the movement of Amboseli baboons, with the baboons mitigating high temperatures by travelling slower and resting more often, rather than seeking shade, giving another angle to movement decisions (Stelzner, 1988).

More recently, the study of primate movement through direct observation has been increasingly complemented by the use of remote monitoring approaches such as the deployment of Global Positioning System (GPS) devices on animals (Dore et al., 2020). With the use of new

technology came the need for new methodologies, leading to the development of novel approaches across species for analysing habitat selection and decision making, including step selection functions (Fieberg et al., 2010, 2020; Thurfjell et al., 2014), route analysis (Di Fiore & Suarez, 2007), change-point tests (Byrne et al., 2009), and circuity index, or path tortuosity (Garber & Hannon, 1993) (for a full review, see Rolland and Trull (2022)).

As long-term data-sets grow, the need to unify our approach to studying movement and cognition between study sites, species, and genera also does, particularly as movement data becomes more precise and widely available (Janmaat et al., 2021; Kays et al., 2023). In this thesis, I will present some of the first studies of primate movement data coming from Gorongosa National Park, Mozambique. I attempt to establish a baseline data set of grey-footed chacma baboon (*Papio ursinus griseipes*) movement in GNP, using both previously tested and novel methods of analysing ranging data. My thesis aims to contribute to our understanding of movement ecology by using a seasonal, heterogeneous environment as a model for how animals have been – and may continue to be – forced to adapt in a frequently changing world. I test methodologies that allow for continuous data collection with or without human monitoring, and show how they can be used retrospectively to compare data across time periods. Using the model of the highly adaptive, widespread baboon, I investigate what drives movement decisions, how they vary across time and seasons, and how memory aids flexibility in adapting to seasonal shifts.

Although this thesis only addresses a subset of the questions that could be answered by the data, it further aims to fill a gap in the mammal data collected in GNP, and to help create models to monitor shifts in animal behaviour throughout the Anthropocene.

1.2 Technology and Movement Ecology

Movement can take many forms, from movement across a petri dish to flying around the world; it is influenced, and limited, by physiology, energetics, and the environment in which the mover exists (Biewener & Patek, 2018). How movement is studied is highly dependent on the study subject, the questions being asked, and the area in which the subject lives. Early studies of movement relied on direct observation, with small-scale movements of captive species or observable wildlife being recorded on a paper representation of the environment, and large-scale movements relying on tagging and observation or recapture of the subject. Later, radio-telemetry allowed for more continuous, but less accurate observations of movement without the need to lay eyes on the subject (Joo et al., 2022). As technology progressed, scientists' ability to study free-ranging wildlife's movement did as well, allowing more in-depth studies on movement from minute-by-minute to year-to-year studies (Kays et al., 2015; Nathan et al., 2022). However, as large amounts of data become available, often collected to answer a specific question, the inability to process and compare data can become a hindrance to understanding key questions of animal movement.

There is currently a push to unify movement studies and ensure that the wealth of data available is used, often beyond its original purpose (Fehlmann et al., 2023; Janmaat et al., 2021; Kays et al., 2023). Repositories such as MoveBank (movebank.org) allow researchers to share raw or cleaned GPS and accelerometer data, as well as the context in which it was collected, promoting further studies and allowing collaborations between groups studying similar subjects or habitats.

As the amount of data grows, so do new methods of studying it. With low resolution GPS data, analysis of movement was often limited to linearity of movement, basic resource selection functions, and change-point analysis to understand decision making and navigation in animals.

Large-scale migration tracks were often limited by error bars of tens of metres if not kilometres, and the movement of smaller subjects relied on camera traps and intensive observation (Joo et al., 2022). With some GPS trackers able to log data at sub-second temporal resolution and high spatial precision, scientists can now identify individual decision points in a daily path, pinpoint key resources that may not be apparent to human observers, and look at group cohesion and leadership empirically in situations beyond human access (Byrne et al., 2009; Farine et al., 2017; Strandburg-Peshkin et al., 2015a). Analysing these data has led to an increase in new models and techniques, such as integrated step selection analysis on top of traditional resource selection functions, tagging of multiple animals in the same habitat or entire social groups, and finding ways to integrate data beyond GPS such as accelerometer, remote sensing, and proximity tags (Alavi et al., 2022; Avgar et al., 2016; Fehlmann, O'Riain, Hopkins, et al., 2017; Thurfjell et al., 2014).

Despite the benefits of real-time tracking beyond what is possible with direct observation, there are constraints on what GPS loggers can manage. GPS trackers are limited in size to what an animal can safely carry, which will itself vary according to the animal's lifestyle (e.g. flying animals can accommodate a much smaller percentage of their body weight in biologgers than terrestrial species). This limitation in turn affects battery life, storage capacity, data precision and durability, while studies are often limited by the longevity of the device, the effort of tagging animals, the risks associated with capture and tagging procedures, and the ethical questions surrounding GPS tagging, such as potentially higher risk of predation and ostracism by group members (Dore et al., 2020). If a GPS device can be safely deployed, researchers must decide whether they should be able to download the data remotely, or if they will be able to retrieve the collar; whether to combine it with other dataloggers (such as an accelerometer); how to optimise

logging frequency against battery life given the aims of the study; and which individual animals are best to place the device on (Dickinson et al., 2020; Kölzsch et al., 2016; Nathan et al., 2022). Devices may malfunction after considerable time, effort, and funding to deploy them, or the environment may not be suitable for connecting with satellites (Dore et al., 2020; Matthews et al., 2013). Data that are collected must then be retrieved, either from a satellite or the device itself, cleaned of failed or incorrect fixes, and transformed to match the other data being used.

Alongside GPS, another form of remote data collection, remote sensing, has also increased in use as technology progresses. Defined as "the collecting of information about the earth using aircraft and satellites" (Cambridge Dictionary, 2024), here I refer exclusively to satellite imagery, which is used widely in ecology for identifying habitats, seasonal changes, cloud cover, and other large-scale atmospheric and vegetation changes (Stark et al., 2018). Combined with GPS data, the growing field of remote studies has grown to the point of having its own journal, to share methodologies and insights to analysing the wealth of data available (Tibbetts, 2017).

The excess of data can be a blessing and a curse. Subject to satellite position, time of day, atmospheric conditions, and even the age and type of satellite, what is shown in an image both physically and in the data can vary wildly, so standardising images to extract data can become a massive undertaking. Once the data is cleaned, it then needs to be matched with the GPS data collected, which can have varying format in terms of the timestamp, coordinate projection, and timescale; if the GPS data is taken at a different interval to the satellite imagery, decisions have to be made about which images to use, making it hard to accurately apply the data collected to the research questions (Tibbetts, 2017).

However, as new software and better computer processing make it easier to access remote-sensing data, the benefits of combining it with GPS data manifest. Animal tracking can be linked

with large- and small-scale climate-induced changes, the construction of roads, changes in land use, and other pressures that are harder to measure day to day, and which may not be recorded locally, which helps to mitigate the lack of observational data often associated with GPS studies. With many GPS collars able to send data remotely to the researcher via satellite, it is now possible for scientists to complete research on habitat selection, movement patterns and social patterns without direct observation following collar deployment (Arthur et al., 1996; Jonsen et al., 2005; Thurfjell et al., 2014).

1.3 Baboon Movement Studies

Studies of habitat selection and movement decisions in baboons date back to the 1970s (Altmann & Altmann, 1970; Post, 1978). Since then, using both direct observation and GPS collars, studies have established baselines for movement in, most often, chacma (*Papio ursinus*) (de Raad & Hill, 2019; R. Hill & Dunbar, 2002; Noser & Byrne, 2009) and yellow (*Papio cynocephalus*) (Markham et al., 2013; Pochron, 2001; Post, 1982; Stelzner, 1988) baboons. However, work has also been done on other species, such as olive baboons (*Papio anubis*) (Cheney & Seyfarth, 2007; Strandburg-Peshkin et al., 2015a, 2017a; Suire et al., 2021).

Both habitat selection and step selection models have been used to determine what habitats baboons prefer, and how that influences their travel decisions. Habitat, or resource, selection models examine relationships between an animal's locations over time and the environmental conditions of those locations (Morris et al., 2016). On the other hand, step selection models analyse the overall distribution of locations, including environmental and social covariates, before comparing possible areas an animal could physically be in with areas it was recorded as being in (Avgar et al., 2016; Michelot et al., 2019; Chapter 2) Strandburg-Peshkin et al. (2017) used step selection analysis to find that olive baboons (*Papio anubis*) were more likely to take

steps in areas recently used by troop mates and on roads; direction of sleep site was also a predictor depending on the time of day. Temperature and water availability have also been shown to influence habitat choice and movement. One study predicted that chacma baboons (*Papio ursinus*) are limited in their range across southern Africa by thermoregulation, avoiding higher temperatures above 35.1C, and rainfall above 1,081mms. However, chacma baboons were found outside of these ideal ranges (including in this thesis' study site) (Stone et al., 2013). Other studies have shown that baboons regularly range in areas of high heat stress, adjusting their behaviour and local habitat to thermoregulate (Barrett et al., 2004; Russell A. Hill, 2006; Stelzner, 1988).

With the need to simultaneously maintain homeostasis and avoid predation, efficient movement should be a priority for baboons. Pochron (2001) showed that yellow baboons (*Papio cynocephalus cynocephalus*) planned movement to certain food resources, as reflected in observation that baboons travelled more quickly and directly towards them than in movements to non-foraging locations. A later study looked at speed and directness in chacma baboons (*Papio ursinus*) travelling between fig trees in Blouberg Nature Reserve, South Africa. This study found that, while these baboons also increased speed and directedness when approaching some fig trees on a repeatedly used path, they did not do so for all fig trees, implying that their directedness was more related to a limited mental map that contained select fig trees, rather than an expansive model of their environment (Noser & Byrne, 2009).

In the same population, Noser and Byrne also found evidence for route planning to out-of-sight resources, showing evidence for goal-directed movement towards distant resources, bypassing resources that they then returned to and exploited later in the day (Noser & Byrne, 2007b). This implies a flexible prioritisation in resource choice and planning, as well as the use of memory to

track resources utilised previously. However, in a further study, the same authors found no evidence that baboons were using a Euclidean map – instead they appeared to rely on a topological network map of known resources, given the longer waiting time and smaller detours in areas without prominent landscape features (Noser & Byrne, 2007a). De Raad and Hill (2012) found similar results: chacma baboons (*Papio ursinus*) in the Soutpansberg Mountains, South Africa approached resources from limited directions, and took more roundabout routes to subsequent resources. Interestingly, they used similarly linear travel in all parts of their home range, suggesting that the core and peripheral areas were equally well-mapped.

Sleep sites have also been shown to influence movement linearity, speed, and direction in baboons. Baboons have been shown to utilise cliff faces, emergent and canopy trees in both continuous and open forest, as well as caves as sleep sites (Hamilton III, 1982). The choice of sleep site, however, is limited by the availability of suitable sites relative to both competition and resource distribution. It has been postulated that moving sleep sites frequently will reduce the risk of predation, parasites, and competition in primates (Chapman, 1989; Hausfater & Meade, 1982). However, the reuse of sleep sites in baboons is variable across sites. At the Mpala Research Centre in Kenya, a troop of olive baboons showed a clear preference for a single sleep site, spending the majority of nights there, while at Amboseli, yellow baboons showed preference for sleep sites at the population level, but individual troops moved sleep sites frequently, leading to almost continuous occupancy of preferred sleep sites by different troops (Loftus, 2022; Loftus et al., 2022; Markham et al., 2016).

Regardless of how it is chosen, the size of the angle from the baboon troop's trajectory to the sleep site has been shown to influence movement decisions in baboons (Strandburg-Peshkin et al., 2017b). Chacma baboons with a variety of sleep site choices exclusively chose to sleep in

exotic trees near food sources in Cape Peninsula, South Africa, and also foraged almost exclusively in plantations and vineyards rather than indigenous vegetation (Hoffman & O'Riain, 2011), showing the influence of resource distribution on sleep site selection, but utilised multiple sleep sites every season.

Baboons' resources, including sleep sites, occur as part of a larger topographic map (de Raad & Hill, 2019). Repeated route networks have been found in multiple arboreal primate species (black howler monkeys, *Alouatta pigra*, (De Guinea et al., 2019); spider and woolly monkeys, *Ateles belzebuth* and *Lagothrix poeppigii*, (Di Fiore & Suarez, 2007); orangutans, *Pongo pygmaeus morio*, (Bebko, 2021)), owing largely to limited connectivity in the forest canopy, meaning routes are often followed within a few metres of each other. Primates in less constricted ecosystems have also been shown to use repeated route networks. Green et al., 2020 used line density analysis to find route network use in chimpanzees (*Pan troglodytes*), while de Raad (2012) found a route network in baboons by visually identifying routes on a map. Noser and Byrne (2009) found repeated routes between known fig trees when using a handheld GPS device, but thus far no studies on baboons have used GPS data and advanced route comparison methods to identify and characterise route networks.

This thesis attempts to fill gaps in the current baboon literature, while also establishing methods that can be further used in terrestrial animal studies. I begin by establishing habitat preference using step selection analysis, in an environment where the risk of predation is relatively low but the density of baboons is very high, circumstances not seen in other study sites. I further evaluate whether baboons have a route network at this study site, using nearest neighbour analysis developed to evaluate route similarity in animal movement data. By applying the Travelling Salesperson Problem to full-day travel routes and using GPS data to identify resources in the

environment, I give insight into the efficiency of day-long paths. Finally, I examine how seasonal flooding affects the use of routes, sleep sites, and resources when the availability of dry terrain plummets and the baboons are forced to temporarily move outside of their normal ranging area, helping to understand the long-term role memory plays in baboon movement strategies.

1.4 Study Site

Gorongosa National Park (GNP) is a 4,000 km^2 protected area located in Sofala Province, central Mozambique. This area was the site of conflict pre-dating and including the Mozambique Civil War (1977-1992), with major impacts on the abundance and diversity of wildlife in GNP. For some, particularly predators, the conflict and the period following caused a major decline in numbers due to poaching for bushmeat and trophies, while certain species at lower trophic levels thrived (Bouley et al., 2018; Pansu et al., 2019; Stalmans et al., 2018). The lack of predators may have led to a rise in the baboon population, with a higher than usual density of troops located within GNP, filling one of the meso-predator roles (Stalmans & Peel, 2016; Taylor et al., 2016).

GNP itself consists of a mosaic ecosystem, varying from dense miombo woodland to open floodplain, and sparse acacia woodland to montane rainforest (Stalmans & Beilfuss, 2008). Central in GNP is Lake Urema, with seasonal distributaries branching out onto alluvial floodplain surrounding it, varying from deep rivers to oxbow lakes and dry riverbeds depending on the season. The entire Park also has an abundance of termite mounds and seasonal water pans, which provide shade and water through much of the year. To the north of the main park is Mount Gorongosa, and villages surround the park itself (Figure 1.1).

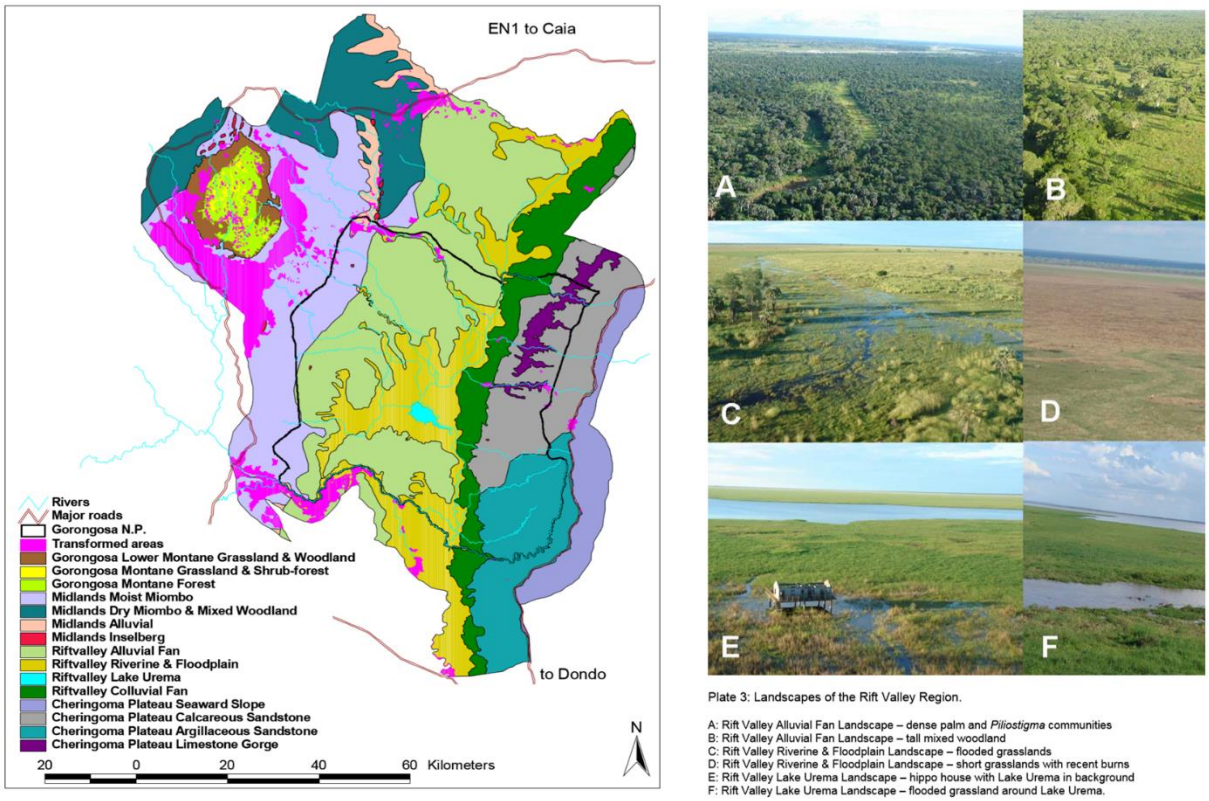

Figure 1.1 Landscapes of Gorongosa National Park, Mozambique. Figure from Stalmans and Beilfuss (2008)

The seasonality in GNP is marked, with significant rains occurring from November to April, and a dry season with little to no rain occurring from May to October (Tinley, 1977). Temperature minimum and maximum averages across seasons vary from around 15C to over 30C (min 9C; max 43C), while humidity hovers between 70-80% (Figure 1.2). At the peak of wet season, around 40% of GNP is inundated as Lake Urema and the pans expand from flooding, rendering many of the roads impassable and necessitating travel by boat.

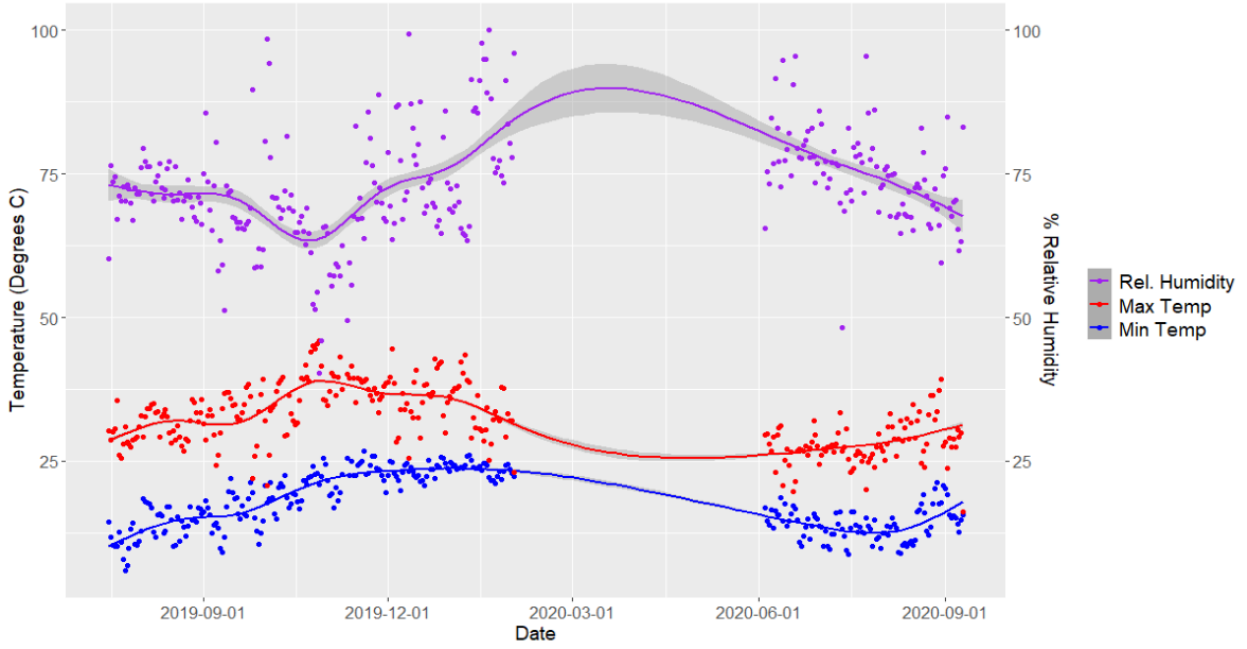

Figure 1.2. Daily average relative humidity, minimum and maximum temperature across the study period, taken using Kestrel Drop D3 devices placed in shaded areas around the study range and recording temperature and humidity hourly. Points are shown only when data is available; curves are otherwise extrapolated from available data.

Gorongosa is an ideal site to study the movement decisions of baboons, given its cyclical climate patterns and diversity of environments. In areas with high seasonality, complex or rapidly changing environments, navigation may be more cognitively demanding than in a homogeneous environment. While many animals display various levels of behavioural and cognitive flexibility in novel situations, this flexibility often results in a trade-off between adapting to new situations and retaining old information (Tello-Ramos et al., 2019). In environments where seasonality causes landscape changes such as flooding, animals need to track not only where and when food is, but also the accessibility of the food source, alongside other temporal resources such as sandbank bridges across water (Abrahms et al., 2021; Trapanese et al., 2019). Indeed, major weather changes can also cause behavioural changes that indirectly impact movement, such as altering when animals get up, how often they rest, how far they can travel in a day, and even

their levels of survival and reproduction (Bartlam-Brooks et al., 2013; Cheney et al., 2004; R. Hill & Dunbar, 2002; Van Lawick-Goodall, 1968).

Since 2006, the Gorongosa Restoration Project has worked to restore pre-war wildlife populations to GNP, by increasing the number of rangers, promoting humanitarian efforts and job availability for local people, and reintroducing predators to GNP (Daskin et al., 2016). This has led to a major increase in the number of predators in GNP, with over 100 lions, a troop of wild dogs, and a transient leopard present in GNP at the time of the study. Since data were collected, hyenas and leopards have further been reintroduced, while the lion and wild dog populations continue to grow (Atkins et al., 2019; Bouley et al., 2018).

1.5 Study Subjects

To explore movement strategies in a complex environment, this thesis relies on data collected from two groups of grey-footed chacma baboons (*Papio ursinus griseipes*) located in the southern portion of GNP. A likely hybrid between chacma and yellow baboons, the baboons of GNP live in a mosaic environment that is subject to annual flooding, creating an ideal area to study movement strategies in different environments (Martinez et al., 2019).

Baboons (*Papio sp*.) are a well-studied clade across southern Africa, known for their wide range, flexible behaviour, and generalist diet across many species, including chacma baboons (*Papio ursinus*), yellow baboons *(Papio cynocephalus*), and olive baboons (*Papio anubis*) (S. A. Altmann, 1974; S. A. Altmann & Altmann, 1970; Cheney & Seyfarth, 2007) (Figure 1.3). They live in multi-male, multi-female groups in a variety of habitats, from open savannah to dense woodland, and are often observed exploiting human areas through crop raiding, scavenging rubbish, and living in human-populated areas, often making a nuisance of themselves (Fehlmann,

O'Riain, Kerr-Smith, et al., 2017; Lodge et al., 2013; Schweitzer et al., 2017). They are female philopatric with exclusive maternal care, although males have been observed carrying infants and there is evidence for paternal care and fitness effects (Buchan et al., 2003; Charpentier et al., 2008). Males disperse from their groups as adolescents, and have been observed to commit infanticide in their new groups (Cheney & Seyfarth, 2007; Zipple et al., 2017). They generally eat a diet of fruit, leaves, subterranean foods, small animals, invertebrates including shellfish and snails, and bird eggs (Kitchen & Bergman, 2016); in GNP, they have been observed eating all of these things. They occupy large home ranges that often overlap with other troops, partitioning themselves temporally rather than spatially (Hamilton, 1985; Markham et al., 2013). However, when two troops do interact, intergroup encounters vary from "wahoo" competitions, or increasingly loud, threatening vocalisations, to violence (Cheney et al., 2004; Kitchen et al., 2004; Kitchen & Bergman, 2016).

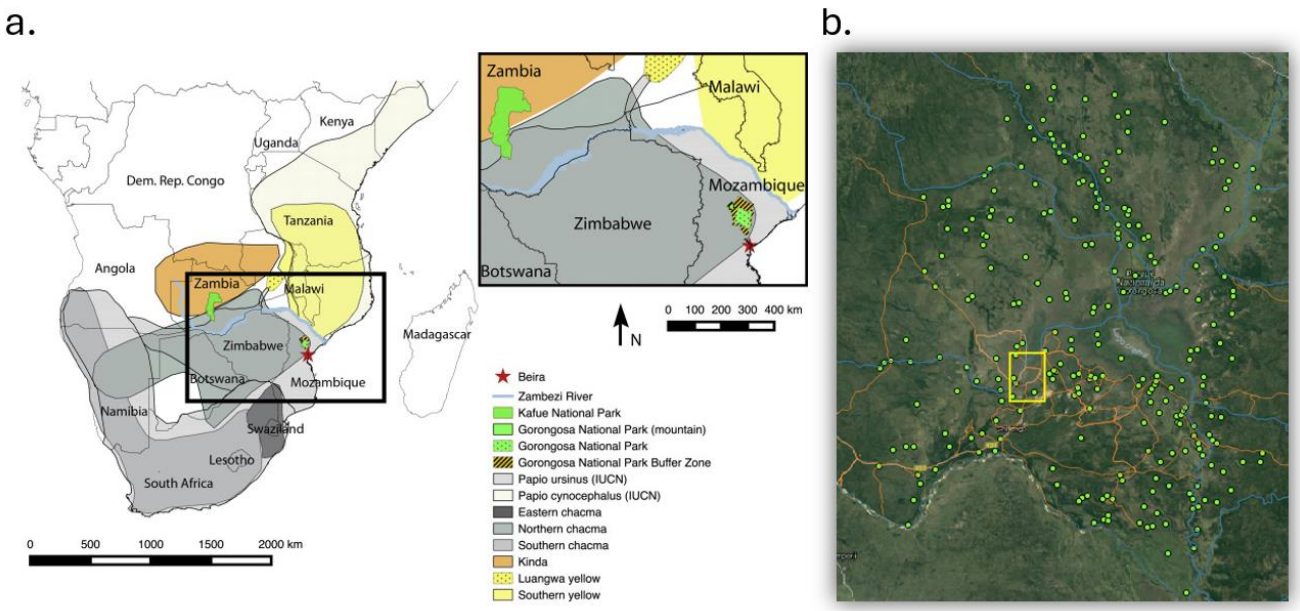

Figure 1.3. Reference for placement of Gorongosa baboons. (a) Range of baboons in southern Africa, taken from Martinez et. al. (2019). Gorongosa is indicated in bright green in central Mozambique. (b) placement of study subjects' home ranges within Gorongosa National Park, indicated by yellow box; green dots represent baboon troops observed during 2016 aerial survey. Image courtesy of Dr. Marc Stalmans.

Due to their larger body size and marked sexual dimorphism, with chacma baboons ranging from 14.8kg (female) to 29.8kg (male) (Smith & Jungers, 1997), their ability to inhabit various environments, and their social living, baboons can be used as a proxy to better understand early hominins' movement decisions (G. E. King, 2022). For this reason, the study of living baboons is part of the Paleo-Primate Project Gorongosa, a multidisciplinary study on human origins based in GNP, which these studies were a part of (https://gorongosa.org/paleo-primate-project/).

Given they struggle to generate novel routes or adapt to unforeseen obstacles, baboons are thought to use topological or landmark maps rather than Euclidean maps (de Raad & Hill, 2019; Noser & Byrne, 2009). They use democratic decision making to plan when and where to move, although certain individuals emerge as leaders more often than others based on social status and age (Strandburg-Peshkin et al., 2017a; Cedric Sueur & Petit, 2008).

However, democratic decision making does not mean that all decisions are made at the group level (Pyritz et al., 2011); on the other hand, in baboons, movement decisions come from the combined decisions of every individual in the troop, each of which can influence the decision, or even fission from the group to make separate decisions (King et al., 2008, 2011; Pyritz et al., 2011). In all group-living animals, disparity between mental maps, as well as individual wants and needs, can impact the route taken (L Conradt & Roper, 2003; Larissa Conradt & Roper, 2005). While the role of group decision making and the associated benefits and consensus costs, should not be discounted individual movement decisions within the same group also can give valuable insight into group-level decision making.

Movement data for this thesis were collected from four GPS/accelerometer collars deployed on four baboons in two troops in the southern portion of GNP. The Woodland Troop (WT) ranges in *Vachellia-Combretum* woodland in the southern portion of GNP, relying on two major pans for

water and relying on a diet of a mix of leaves, berries, and other plant material (Hammond et al., 2022). The Floodplain Troop (FT) range in the southern portion of the alluvial floodplain, residing in fever tree woodland and on the open floodplain during the dry season, and retreating south into the denser woodland during the floods. They consume primarily *Vachellia xanthophloea* seed pods, *Cyperaceae* sp. corms, palm nuts, and *Chrozophora plicata*, although they have also been observed feeding on a number of other tree species, small birds, eggs, mussels, water plants, and hunting small mammals. Their home range overlaps during the peak of dry season with WT, as both troops rely on the Mussicadzi River for water as the pans dry out; for most of the year, however, they are spatially separated. Both troops overlap with numerous other baboon troops, other primates including vervets, and elephants, lions, wild dogs, crocodiles, and multiple species of antelopes. Both troops had been followed since 2018, and were semi-habituated by 2019 by myself and Philippa Hammond (Hammond et al., 2022).

Data for this thesis was collected in the year following 2019's Cyclone Idai, one of the worst cyclones to ever affect the southern hemisphere, which moved directly through GNP (Walker et al., 2023) (Figure 1.4). This led to a major humanitarian crisis in Sofala Province, a marked decline in several small-bodied species, shifts in vegetation and water availability, and long-term changes to population density, although data on baboons has not yet been released (Beardmore-Herd et al., in review; Walker et al., 2023; Warren, 2019). In the season following the cyclone, census of FT indicated that multiple infants, juveniles, and subadults were absent, as well as multiple adult males and one adult female, resulting in a loss of approximately 30% of the group, although it is not known how many of these baboons were lost as a direct result of the cyclone (Lewis-Bevan, Hammond, et al., 2019). A full census before and after the cyclone was not available for WT.

Collars (model 1D, e-obs Digital Telemetry, Grünwald, Germany) were placed on four cycling adult female baboons between 31 July 2019-14 August 2019. Baboons were drawn to an open area using maize for a month prior to collaring, and habituated to manually controlled traps. One monkey was trapped and sedated using a trap, while three were free-darted from a vehicle. All baboons were sedated, monitored, collared and handled exclusively by trained veterinarians, and were sedated using ketamine at 15mg/kg. They were placed in recovery cages until sufficiently awake to be released, on average 1-2 hours later. Collars were equipped with a fabric strip at the connection point, designed to wear through and remove the collar after at least two years and ideally after no more than four to five years. Because of the nature of the collar removal, collars were not expected to be retrieved, and data were downloaded from the collars monthly from August 2019-November 2019, then again in February 2020, May 2020, and June 2020, using the e-obs BaseStation II connected to a Yagiantenna (868 MHz 10E) from a distance of 10-50 metres. Downloaded data were then processed using e-obs decoder_v10s1.

Figure 1.4 Camera-trap photos of flooding from Cyclone Idai in FT's home range. While the water height from this event was unusually high, the floodplain is similarly inundated annually. Photos from Dr. Piotr Naskrecki.

1.6 Behavioural and Contextual Data Collection

Data analysed in this thesis were collected via GPS collars from August 2019-June 2020. However, this thesis also incorporates anecdotal and previously analysed behavioural data, which give context to the behaviour, habitat, and ranging patterns of both troops, as well as assisted in ground-truthing the GPS data.

Data collection for the Woodland Troop began officially in April 2018, and the troop was followed by myself, Philippa Hammond, and Zoe Melvin, as we standardised behavioural collection protocols. Shortly thereafter, Zoe Melvin and I began habituating the Floodplain Troop in May 2018. Data collection on both troops continued until August 2018, and a one-month break was taken until Philippa Hammond and I returned to continue data collection on the

Woodland and Floodplain troops respectively, in September 2018. Behavioural data collection continued almost continuously until mid-November 2018, and resumed in June 2019. WT was then followed intermittently from June 2019-September 2019, while FT was followed almost daily for the same period, except for collaring from mid-July 2019 to mid-August 2019. Follows ceased from the beginning of September 2019 until late September 2019, and resumed only for FT until the end of November 2019.

Daily follows consisted of a census of all present group members (when visible), instantaneous scan sampling of the entire visible troop every 15 minutes, including what habitat type they baboons were in, the type, density and height of vegetation, other species present, and all behaviours and their directionality. Social interactions were also collected ad hoc, as well as records of food types and locations, hunting events, interactions with predators and other troops, and water sources and whether or not they contained water.

Based on data collected during the 2018 field season, the baboons in both troops spent the majority of their time foraging, either in a single patch or moving slowly while also consuming food items. Due to habituation, they also spent a significant amount of time vigilant to the observers (Hammond et al., 2022). In FT, the baboons spent more time travelling on hotter, dryer days, and more time resting on cooler, wetter days. They tended to use open areas for foraging, and closed habitats for resting and socialising. However, in 2019, baboons in FT spent more time resting during hotter days, and more time in general in closed habitats; this is likely linked to the consistent water availability, which allowed baboons to remain near the river rather than travelling to further pans or streams to drink. Comparable behavioural data was not available for WT in 2019.

1.7 Thesis Structure

This thesis is comprised of four self-contained chapters followed by a concluding discussion.

In Chapter 2, I apply a step selection function to the daytime GPS tracks of the four collared baboons to understand how their habitat preferences changed seasonally, and if they had preferred areas in which to spend time, given the range and distribution of those available. I also examined what predicted baboon movement, taking into account not only habitat type but also direction of the sleep site and proximity to water.

In Chapter 3, I create a novel approach for assessing the efficiency of daily travel routes in Gorongosa's baboons, by invoking the classic Travelling Salesperson Problem. I use hierarchical clustering to find areas where baboons spent significant portions of their time across the year, and track which of these sites' baboons travelled to each day. I compare their daily routes between these areas to routes generated by different kinds of algorithms: both a simple "nearest neighbour" heuristic and a much more complex route optimiser that finds the shortest-distance path between the rising sleep site, each visited area, and the evening sleep site. Findings allow me to hypothesise the involvement of some degree of planning in the baboons' daily movement.

In Chapter 4, I look at the distribution of sleep sites in both the dry and wet seasons for each troop. I use the methodology I developed in Chapter 3 to find the first and last resource used each day, and compare travel distance from the rising sleep site to the first resource of the day and the last resource of the day to the evening sleep site, to test whether either resource predicted sleep site selection. I also examine whether baboons had preferred sleep sites, compare sleep sites before and after the seasonal displacement, and assess if these remained consistent following the baboons' return once the flood had receded.

In Chapter 5, I examine whether baboons in GNP navigate using habitual routes. I apply nearest neighbour analysis to rolling segments of the data to quantify similarities between routes and route segments, and compare the routes from the sequential dry seasons to examine the extent to which routes remained the same after a period of displacement.

In Chapter 6, I provide a general summary and discussion of the findings from my thesis and suggest potential avenues of further research. I also discuss the limitations of the methodology and data used, and their implications for my findings. I explain how my thesis answers questions about drivers of baboon movement and provides novel methods for interrogating GPS data without behavioural covariates, as well as the implications of both of these developments for current and future research.

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2

Chapter 2 : Step Selection Functions Reveal Seasonal Drivers of Baboon Ranging Patterns

CONTENTS

2.1 Abstract

Habitat choice is a key component of movement ecology across species. As habitat complexity increases, both in habitat structure and seasonality, so does the complexity of choosing where to

go. One of the most widespread primate genera across southern Africa, *Papio,* is known for its high adaptability, occupying multiple habitat types ranging from arid desert to seasonally flooded gorges. Numerous studies have examined how baboons at different sites adapt to their specific environments, but few have touched on how strategies may vary within a single site. Here, we examine the ranging patterns and movement decisions of two troops of grey-footed chacma baboons, *Papio ursinus griseipes*, occupying two adjacent but different habitats in Gorongosa National Park, Mozambique. Using GPS collars deployed for between 293-322 days on four adult female monkeys across two troops with proximate but compositionally different habitats, as well as remote sensing data, we compare ecological covariates with movement data to identify predictors of movement in each monkey. We use step-selection functions to compare the influences on individual movement between the two home ranges and across the two contrasting seasons (wet and dry) in Gorongosa. We find variation in movement predictors between sites and seasons, and individuals. We find that, in the dry season, distance to water and the presence of trees predicted steps for both troops, while in the wet season, a higher NDVI (a proxy for vegetation type, density and phenology) at the end of the step was more predictive. Across seasons, a lower angle between the direction of travel and the end-of-day sleep site was predictive for all monkeys, but individuals within the same troop were differently influenced by angle to water and habitat type. We further find that, despite the spatial proximity of the two troops, predictors varied between troops and seasons. These findings indicate that movement strategy varies even within a single study site and study troop, and lay the groundwork for further studies assessing the drivers of spatial decision making and intra-troop variation within a single field site.

2.2 Introduction

Understanding how animals adapt to variability and changes in their habitat is a key question for movement ecology. Several species have been shown to adjust their movement patterns in response to climatic changes, predation risk, and human influence (Alho & Silva, 2012; Cain et al., 2008; Nielsen et al., 2004; Prokopenko et al., 2017; Tufto et al., 1996). However, understanding how various factors combine to shape an animal's behaviour can be difficult, as such factors range from small-scale interactions to large ecological shifts (Bartlam-Brooks et al., 2013; Latombe et al., 2014; Thurfjell et al., 2014). Further, it can be difficult to compare the same species at different study sites to understand how individuals select their ranging area, given differences in access to behavioural and movement data in different habitats (Janmaat et al., 2021).

In Africa, one of the most behaviourally plastic and adaptable taxa is the *Papio* genus. Baboons show their adaptability to various and changing environments through the wide range of habitats they occupy, and the use of human-dominated habitats (Fehlmann, O'Riain, Kerr-Smith, et al., 2017; Fischer et al., 2019; Gesquiere et al., 2008; Van Doorn et al., 2010). However, despite their flexibility, baboons are still impacted by changes in their environment. Physiologically, baboons are endocrinologically affected by changes in season, temperature, and access to water (MacLarnon et al., 2015; Mitchell et al., 2009; Pochron, 2000). For example, in the Amboseli Basin, male baboons (*P. cynocephalus*) were found to have higher faecal glucocorticoids (fGC), a presumed measure of stress, and lower faecal testosterone in the dry season compared to the wet season (Gesquiere et al., 2011). Similarly, females in the same area had high fGC levels in the dry season compared to the wet season, which also correlated with months with higher maximum daily temperatures (Gesquiere et al., 2008). Despite this, the baboon clade is well-

known for its ability to breed year-round, a relatively rare trait in non-human primates (Beehner et al., 2006; Bercovitch & Harding, 1993; Cheney et al., 2004; Polo & Colmenares, 2016).

These changes in stress level may also link with how predators react to seasonality. In one study, lions (*Panthera leo*) were found to increase their time in areas rich with prey species for not only themselves, but also smaller predators, during periods with lower food availability (Vanak et al., 2013). This study further showed that other carnivore species, such as leopards (*Panthera pardus*) and wild dogs (*Lycaon pictus*), actively chose to avoid areas where lions spent their time, thus avoiding intraguild competition, but influencing their own hunting prospects. Seasonality also affected mortality by predation in baboons (*P. ursinus griseipes*) in the Okavango Delta, a highly seasonal environment, with death due to predation at its highest during the flooding season when movement was constrained by the water (Cheney et al., 2004). Since it is accepted that baboons modify their behaviour based on perceived predation risk, it is reasonable to assume that seasonal changes in predator threats will have some influence on baboon vigilance, ranging patterns, and activity budgets (Cowlishaw, 1997; Hammond et al., 2022; Russel A Hill & Cowlishaw, 2009; Markham et al., 2016).

To adjust to changes in physiological stress and predation risk, baboons may alter their ranging patterns (Coleman & Hill, 2014; R. Hill & Dunbar, 2002). Because baboons thermoregulate via cutaneous water loss, access to drinking water is important to maintain a suitable body temperature, which is often preferentially sought during the hottest part of the day (Stoltz & Saayman, 1970). Similarly, baboons preferentially seek shade during the hottest part of the day, and Pochron (2000) found a seasonal difference in sun avoidance in yellow baboons (*P. cynocephalus cynocephalus*), showing that they avoided it as much as possible in the wet season,

but only sought shade while resting in the dry season (Pochron, 2000; Stelzner, 1988). This behaviour was also observed among chacma baboons (*P. ursinus griseipes*) in Gorongosa National Park, Mozambique (L.L-B & S.C., pers. obs.). In De Hoop Nature Reserve in South Africa, various studies found that temperature, humidity, and windspeed, which often fluctuate seasonally, change the perceived environmental temperature for baboons (*P. cynocephalus ursinus*), and influence their ranging and behavioural patterns (Hill et al., 2004; Hill 2006). Baboons (*P. ursinus*) in Cape Peninsula, South Africa, increased feeding, socialising and travelling in the summer, and resorted to raiding farms for ostrich feed pellets in winter (Van Doorn et al., 2010). In Sukerbosrand Nature Reserve, South Africa, baboons (*P. ursinus*) were shown to travel further distances in the wet season than the dry season, although this did not influence their seasonal home range size (Slater et al., 2018).

Human influence also impacts baboon behaviour, particularly in human-modified environments. For instance, Strandburg-Peshkin *et al.* (2017) found that olive baboons (*P. anubis*) dramatically change their movement patterns on and around roads (Strandburg-Peshkin et al., 2017a). Crop raiding, or exploiting human food stores and waste sites, both in response to food shortages and as a general foraging strategy, has also been observed in a number of human-modified habitats (Hoffman & O'Riain, 2011; MacLarnon et al., 2015; Strum, 2005).

When quantifying how baboons adjust their movement patterns, habitat selection and ranging behaviour in the face of environmental changes or in complex environments with extensive variation in habitat types, there has been an increase in the number of studies relying on remote data collection such as GPS collar deployment, with a push to also utilize these data to answer wider questions linking behaviour and cognition (Janmaat et al., 2021; Kays et al., 2015). One

recent review compiled a set of 179 collar deployments across 16 primate research teams, further demonstrating the vast wealth of data available from remote sensing studies (Dore et al., 2020). Such studies have already been attempted across a number of species (see Thurfjell et al. (2014) for a review of recent studies), with step-selection functions (SSFs) or matched conditional logistic regressions moving to the forefront of habitat use analysis.

SSFs have many of the characteristics of biased correlated random walks (BCRWs). BCRWs are a type of parametric random walk model used to model organism's movements in its environment by using characteristics of its steps (Codling et al., 2008). Both BCRWs and SSFs presume there will be movement in a general direction (bias), with the direction of each step influenced by the direction of the previous one (correlation) (Codling et al., 2008; Duchesne et al., 2015). SSFs, unlike BCRWs, are non-parametric, and model movement by comparing areas where the animal chose to be with areas that were available, but rejected (Duchesne et al., 2015; Prima et al., 2017). These analyses take GPS data of an organism recorded at consistent time intervals and treat each temporally sequential pair of points as a "step". Based on the distribution of the characteristics of all observed steps (e.g. step length, turning angle compared to prior step), random steps are created to represent areas where the organism could have hypothetically chosen to go. It then compares the characteristics of each observed step with its matched random steps, and determines which characteristics are most predictive of an actual step being taken. These characteristics range from purely mechanical, i.e., step length and angle, to purely environmental, e.g., road presence, proximity to water, elevation, etc. The steps are compared using a conditional logistic regression; models incorporating both mechanical and environmental characteristics have recently been referred to as integrated Step Selection Functions (Avgar et al., 2016).

Such studies have already made significant headway into understanding the movement decisions of a number of species. For instance, SSFs have helped show that polar bears (*Ursinus maritimus*) exhibit a difference in ice use between seasons, while wolves (*Canis lupus*) not only adjusted their ranging behaviour based on road presence in one study, but in another affected the movements of prey species such as moose (*Alces alces*) and woodland caribou (*Rangifer tarandus caribou*) (Arthur et al., 1996; Latombe et al., 2014; Zimmermann et al., 2014). Similarly, wolves have been shown to influence elk (*Cervus canadensis*) movement, as the prey species chose denser woodland in high predator-density areas (Fortin et al., 2005).

While SSFs have been used less often in primates, they lend themselves to answer questions similar to those that have been posed for other species. In primates, behavioural studies have shown that baboons (*Papio* sp.) use familiar paths to navigate their environment rather than choosing new paths daily, but when and how they move can be impacted by predators, thermoregulation, and access to novel or ephemeral resources (de Raad & Hill, 2019; Fehlmann, O'Riain, Kerr-Smith, et al., 2017; Pochron, 2000).

This study aims to use SSFs to understand the diversity of movement strategies that can be used by the same species by focusing on habitat selection and movement influences in the baboons of Gorongosa National Park (GNP), Mozambique. GNP offers a unique resource for studying baboon habitat selection due to high seasonal variation in temperature, rainfall, and water availability, caused in part by the seasonal flooding of the southern portion of GNP (Figure 1.2). The encroaching water displaces a number of species that range on the floodplains, forcing them to higher ground for the duration of the rainy season (Beardmore-Herd et al., in review; Walker et al., 2023). It also has one of the highest densities of baboon populations in southern Africa,

with baboons scattered across most of the southern portion of GNP through the multitude of landscapes available (Stalmans et al., 2018; Stalmans & Beilfuss, 2008). Because of this, it is possible to compare baboon troops living in areas of similar large-scale ecological variables (i.e. temperature, humidity, season), but varying in small-scale habitat types.

GNP is a well-established research site for multiple species, and baboons have been studied by the Paleo-Primate Project Gorongosa since 2017. Research on mammals in GNP previously determined, through camera trapping, that primates in GNP tend to stay closer to roads, and to inhabit areas ranging from dense trees to open landscapes; however, they prefer areas with high termite-mound density, with termite mounds acting as a source of shade, cooler temperatures, and often food (Gaynor et al., 2020). This site is further remarkable in its status as a recovering ecosystem, following devastation and the massive decline of vertebrate species after the Mozambique Civil War (1977-1992) (Daskin et al., 2016). Since the end of the war, efforts have been made to protect existing species to allow their recovery and to reintroduce lost species in GNP. As a result, many species, in particular the ungulate and predator populations, have been rapidly recovering and diversifying, and there has been a steady growth in lion and elephant numbers, as well as the reintroduction of wild dogs, leopards, and hyena into GNP (Atkins et al., 2019; Bouley et al., 2018; Gaynor et al., 2020; Pansu et al., 2019).

Our principal goal was to understand how changes in seasonality affect not only the ranging patterns and home range size of baboons, but also how predictors of baboon movement and habitat choice vary seasonally. We combine GPS collar data from four baboons in GNP with remote sensing data such as satellite imagery and established maps of GNP to compare two troops ranging in very different but proximate habitats to understand how the differences in

habitat type, and the seasonal displacement caused by the annual flooding, cause variation in movement predictors. By doing this, we hope to not only contribute to the baseline data of a recovering ecosystem, but also shed light on how genetically and spatially proximate troops in different habitats vary in their movement strategies, and what that might mean for other baboon study sites, particularly with the rising unpredictability of climatic changes and seasonal variation.

2.3 Methods

2.3.1 Study Area & Subjects

Data were collected in GNP, Sofala Province, Mozambique. GNP covers an area of approximately 4000 km^2, and comprises a mosaic habitat, with a diversity of herbivores and a growing lion population (~200 lions as of 2021). During the study, GNP also contained three rapidly expanding packs of reintroduced wild dogs, but no known resident leopards (Stalmans et al., 2018; Stalmans & Beilfuss, 2008). Given that leopards are typically baboons' primary predators, and the low-density of lions in GNP were known to predate antelope rather than baboons, baboons in GNP face very little predation, and themselves were observed to hunt young herbivores such as ducklings, antelope, and warthogs (L.L-B, pers. obs.). GNP also undergoes seasonal flooding, with the wet season inundating about 40% of GNP from November-April, and the rainless dry season lasting May-October (Tinley, 1977). Temperature and humidity also vary according to season. In the wet season, the mean daily maximum temperature is 35.5C, while the average minimum is 23.5C; in the dry season, this shifts to a maximum of 31.1C and a minimum of 15.4C. The average relative daily humidity in the wet season is 76.7%, and 71.5% in the dry season (Figure 1.2). GNP is also subject to volatile rains during the beginning and end of the

rainy season, interspersed with some dry patches, as well as annual cyclones, thus causing periods of flooding and drying.

The data collected in this study came from the ranging area of two troops of chacma baboons (*Papio ursinus griseipes*, but see ref. (Martinez et al., 2019) for evidence of potential hybridization with *P. cynocephalus*) in the southern portion of GNP. The Floodplain Troop ("FT", *n* ~32 individuals; range 25-38 over course of study) ranged in the southern portion of the GNP's alluvial floodplain, an area comprised mostly of open grass- and sedge-land, as well as fever tree (*Vachellia xanthophloea*) woodland and dense riparian woodland. The main water sources in this area are the seasonal Mussicadzi and Tsungue rivers. Baboons in this troop had a diet that, during the dry season, comprised large quantities of the seed pods and underground storage organs of *Cyperaceae* sedges, and the seeds of *Chrozophora plicata*. While *Cyperaceae* sedges were available year-round, *V. xanthophloea* and *C. plicata* are widespread but seasonal resources. Notably, this troop was forced to change ranging area annually due to seasonal flooding, moving away from the floodplain area and into the fever tree woodland.

The Woodland Troop ("WT", *n* ~ 90 monkeys; range unknown over course of study) ranged in moderate to dense *Vachellia-Combretum* savannah woodland, comprised primarily of *Vachellia robusta*, interspersed with large, seasonal water pans and bordered in the north by the Mussicadzi River (Hammond et al., 2022). These baboons foraged on *Vachellia* seed pods and engaged in bark-stripping of *Vachellia robusta* (Hammond et al., 2022; Muschinski et al., 2020). They also foraged on available fruits, berries, honeycomb, insects, and other items in the leaf litter. Both troops were seen to engage in the hunting and consumption of vertebrates, such as juvenile birds, warthogs, and antelope.

As with all *P. ursinus* troops, both troops were multi-male, multi-female, and generally moved as a group within their home ranges, although subgrouping was also observed.

2.3.2 Baboon Movement Data

Individual baboons (n = 4, all adult cycling females with no dependent offspring) were captured either using a baited cage with a manual door release (n = 1), or through free darting from a vehicle (n = 3). In both cases, baboons were attracted to an area using human-provided maize scattered around the cage or near the vehicle, and, once in a safe position, they were sedated by a licensed veterinarian using ketamine and medetomidine. The baboons were then fitted with collars (model 1D, e-obs Digital Telemetry, Grünwald, Germany) equipped with GPS and tri-axial accelerometers, placed in a shaded recovery cage, and observed until the veterinarian deemed them sufficiently recovered to be released, approximately 1-2 hours later. Collars were equipped with a fabric strip designed to wear down and remove the collars without further human intervention after at least two years and ideally after no more than four to five years.

Two of the collared baboons were from FT ("Eve" and "Abacaxi") and two from WT ("Acacia" and "Kigalia"). All four GPS units were programmed to sample baboon location once a second for ten seconds every 15 minutes (i.e., a burst of up to 10 fixes at 1Hz at 15-minute intervals). GPS data were downloaded from the collars monthly from August 2019-November 2019, then again in February 2020, May 2020, and June 2020, using the e-obs BaseStation II connected to a Yagiantenna (868 MHz 10E) from a distance of 10-50 metres. Downloaded data were then processed using e-obs decoder_v10s1.

During analysis, only the final fix out of each 10-second burst was used to allow for satellite connection . Although the collars continued to record GPS fixes at night, we filtered the data to

only include movements occurring before the monkeys had reached their evening sleep site and after they had left the next morning (see "Sleep Site Locations & Angles" below). Collaring took place between 28 July 2019 and 16 August 2019, and spatial data were collected from 30 July, 2019 to 24 June, 2020, with the number of GPS days (i.e., days where a GPS collar was active) varying across monkeys due to the timing of collar placement and the end of the collar's battery life (*min* = 232, *max* = 311, *mean* = 282).

2.3.3 Environmental Data

To assess which environmental factors predicted baboon movement, several variables were quantified for the two troops' home ranges. These included NDVI, measured as a continuous variable; habitat type, classified into one of three habitats; the presence of roads, classified as 'present' or 'absent'; and the presence of permanent and temporal water bodies such as rivers, streams and pans, also classified as 'present' or 'absent' (Figure 2.2). Although not strictly environmental, the location of the sleep site was also included to account for the inevitable movement towards the area where the monkeys would spend the night, and the previously shown role of sleep site in movement decisions (Barton et al., 1992; Strandburg-Peshkin et al., 2017a).

2.3.3.1 NDVI

NDVI data were collected using Planet 4-scope satellite imagery, downloaded from the Planet website between every 2-5 weeks, depending on the availability of usable data (P. Team, 2017). Data were used at the pre-calculated Surface Reflectance levels, and NDVI was calculated for each image using R Studio Version 1.3.959 (R Core Team, 2020), using the package raster (Hijmans, 2020). The NDVI formula used the near-infrared [NIR] and red [R] bands: [NIR-R] / [NIR+R]. This created a spatial raster for every satellite image, with a pixel resolution of 3m.

Data were then extracted using the extract function of the same package, using the date of the NDVI raster most proximate to the date of a given GPS fix. Due to limitations in data, plant phenology and surface water were not accounted for in the calculation of NDVI.

2.3.3.2 Habitat Type

Habitat type was categorised from a single Planet 4-scope satellite image (pixel resolution of 3m), taken on 01 December 2019, using QGIS version 3.14.0-Pi (Q. D. Team, 2023) and the SemiAutomaticClassificationPlugin (SCP), version 7.10.4 – Matera (Congedo, 2021). Known areas from on-the-ground observation in GNP, as well as areas inferred from satellite imagery, were marked with polygons as one of four habitat types: Trees, Bare Ground, Water, or Low Vegetation, which included areas of grassland and sedges. Each habitat type contained at least eleven polygons of example imagery. The SCP then used information from the pixels within these polygons to infer the remaining pixel values as either one of the habitat types or a non-classifiable category. Classification was done using a maximum likelihood classification with a threshold of 0, with all bands weighted equally. Following this, to remove noise and improve accuracy of the final raster, a class sieve was run across the entire image. This identified any habitat areas that were less than four connected pixels and reclassified them based on the surrounding eight pixels. Although this may have removed smaller patches or single trees, it also removed much of the random noise associated with this type of classification due to the seasonality of water in GNP; for this analysis, all water was subsequently reclassified as "Bare Ground", with fixed water bodies being used as representation of waterways (see "Water Bodies" below). Examples of habitat type can be found in Figure 2.1.

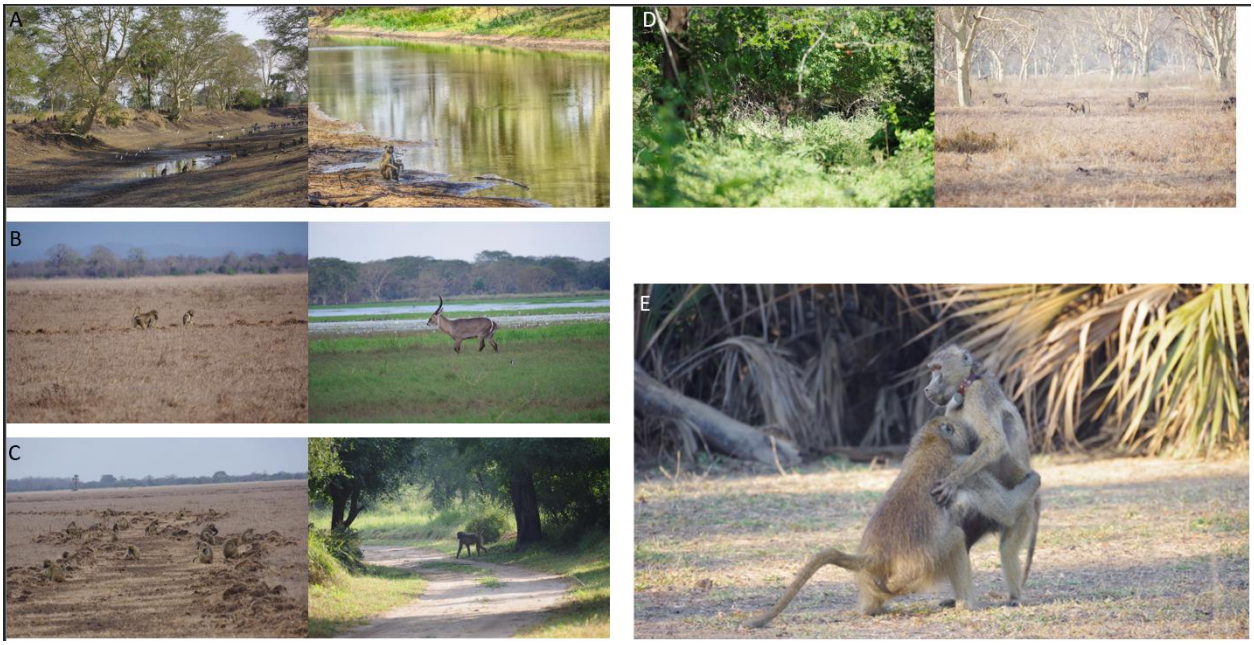

Figure 2.1. Examples of different habitat types and seasons in GNP. (A) the Mussicadzi river empty during the dry season and full during the wet. (B) Low vegetation area (floodplain) in the dry and wet season. (C) Examples of a road in the floodplain and woodland areas. (D) Examples of Vachellia and Acacia woodland (trees). (E) An example of a collared monkey embracing another monkey on bare ground.

2.3.3.3 Road Data

Road data were obtained from Dr. Marc Stalmans (Gorongosa National Park) and was up to date as of 2018. Data was obtained by driving the main road network with a Garmin GPS device and using the recorded track as a line for the road. To create a polygon from the road line, a 2-metre buffer was added to either side of each road, to create a 4-metre-wide road. Determining whether or not a GPS point fell on or off a road was done using raster::extract (Hijmans, 2020).

2.3.3.4 Water Body Locations & Angles

The locations of water bodies were determined based on two sources. GPS locations of temporary pans within GNP were provided by Dr. Marc Stalmans, identified via satellite imagery. Other waterways, such as rivers and streams, within GNP were taken from publicly available data via the Humanitarian Data Exchange (HOT OSM Contributors). Within GNP, although the amount of water available fluctuates, water bodies were treated as year-round

resources as they are utilised both for the water they provide as well as the plants that grow in them during the dry season. During this study, most water bodies remained full with at least some water, following the effects of Cyclone Idai in May 2019, based on ground truthing and monitoring of water bodies from July-November 2019.

The two data-sets were combined, and each water body was given a 10m radius buffer, to give dimension to the data which were originally logged as points and lines. Distance between each GPS position of the monkeys and the nearest water body was calculated as the two closest points of the geometries using rgeos::gNearestPoints (R. Bivand & Rundel, 2020).

Angle to the nearest water body was determined using the baboon's location and the nearest geometry of the closest waterbody as the destination point. For each pair of consecutive GPS points in the day, two vectors were calculated: one vector from the first point to the subsequent point, and one vector from the first point to the nearest water body The angle between these two vectors was calculated in radians (0 to π). 0 represented moving directly towards the water body, and 1 moving directly away from it. This gave an angle relative to the water body, but did not account for cardinal direction (*i.e.,* bearing relative to North). Water bodies were not adjusted based on seasonality, due to the inconsistency in water availability throughout the year. Furthermore, dried pans and streams may still represent a significant resource for Gorongosa baboons in the dry season, as they are the main areas where a major dry-season food source, *C. plicata*, grows (L. L-B., pers. obs.).

2.3.3.5 Sleep Site Locations & Angles

Sleep site on any given day was determined to be the location of the collared individuals at 0200 hours of that day. A 50-metre radius was placed around this point, and we determined the

monkeys had entered the sleep site when they entered this radius in the evening and did not leave it again until the following morning. If the monkeys entered the area during the day but subsequently left it without remaining overnight, it was not counted as entering the sleep site. Angle to the sleep site was calculated as with angle to the nearest water body (see above), using the angle to the evening sleep site of each day.

2.3.4 Ground-truthing and Daily Follows

L.L-B and P.H. observed the troops in their natural habitats from April-November 2018 and L.L-B observed the troops July-November 2019. The observational data taken supplemented this study and aided in the classification of remote-sensing data.

2.4 Statistical analysis

All statistical analysis was carried out in R version 4.0.2 (2020-06-22).

2.4.1 Home Ranges

Home ranges were calculated using the adehabitatHR package, using the minimum convex polygon (MCP) of 95% of the available GPS points (Calenge, 2006). This percentage was chosen based on visual examination. Starting with the 50% most central points, the MCP was calculated for each addition of 5% more peripheral points. This led to a line increase of home range size until the last 5% of points were added, at which point the MCP increased logistically, implying the 5% least central points were outliers. The MCP was used to define a home range which included areas where the baboons could have reasonably gone to but chose not to, rather than limiting analysis to only the areas the baboons spent the most time in, as in other methods of calculating home range size.

Data for each monkey was divided into seasons based on fixed dates, with the wet season lasting from November 15-April 15, and the dry season from April 16-November 14 (Figure 2.2).

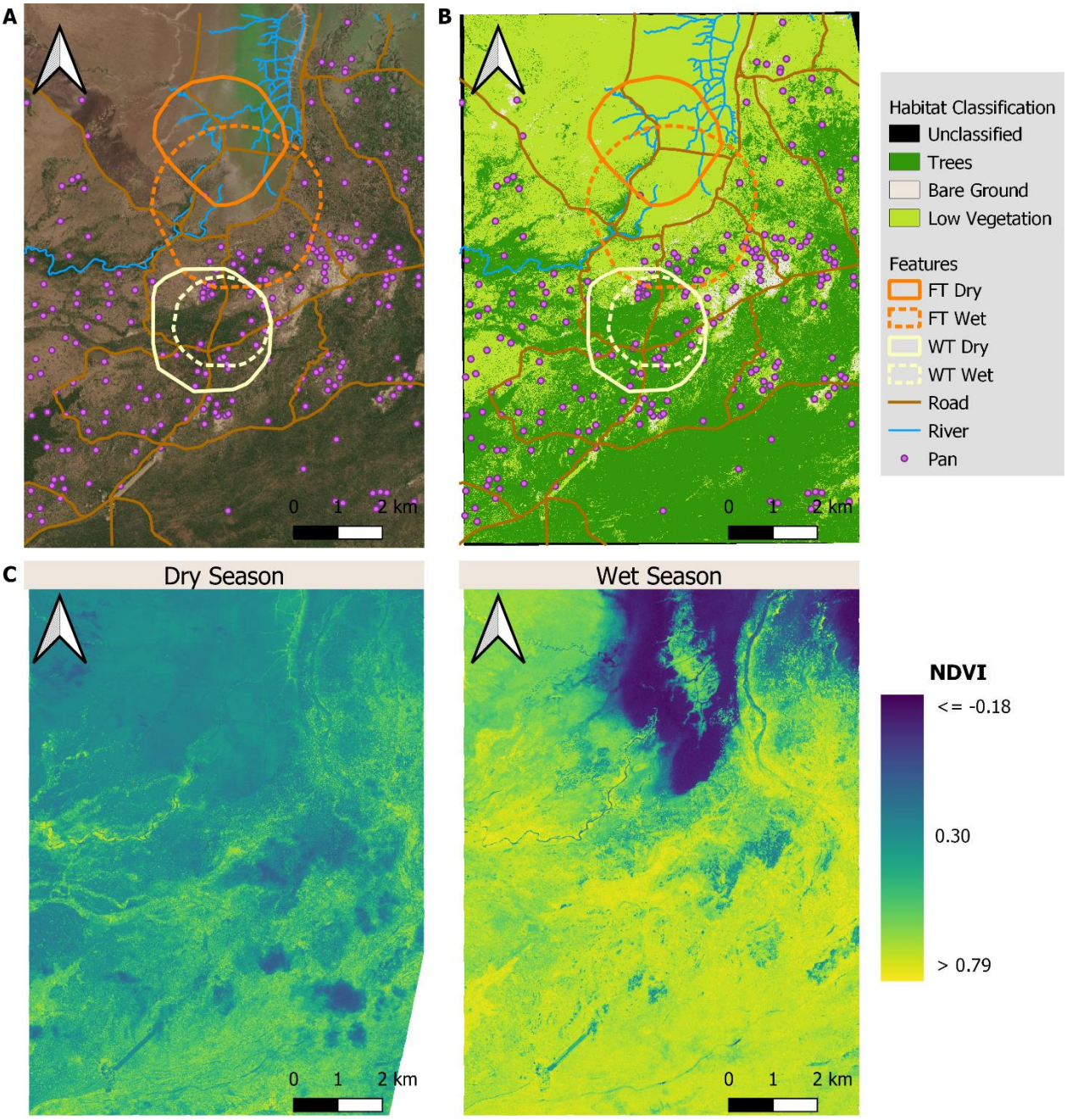

Figure 2.2. A comparison of satellite imagery and habitat classification of the baboons' main ranging areas. (A) Satellite imagery of the wet and dry season home ranges of both troops, downloaded from Planet image repository (Planet Team). Dry season home range is illustrated with a solid line, while wet season is illustrated with a dotted line. FT home ranges are in orange, while WT are in beige. Roads, rivers, and water pans are also marked. (B) The result of the habitat classification of the area shown in panel A. Landscape features are illustrated as in panel A. Water bodies are shown as blue lines (rivers/streams) and purple dots (pans). Habitat is divided into trees (dark green), bare ground (cream), low vegetation (light green), and unclassified areas (black). (C) A comparison of NDVI taken from two days in the year, representing the end of dry season (left) and the end of wet season (right).

2.4.2 Movement Drivers and Habitat Use

To analyse what covariates influenced our collared baboons' movement decisions, a step-selection function was used. This compared a series of observed steps, defined as travel from one GPS fix to another, against a set of randomly generated "hypothetical" steps.

For each observed step, five random steps were created using the amt package (Signer et al., 2019). These steps were based on the distribution of step distances and directions throughout the true GPS data, and so represented realistic steps the animal could have chosen to take (see Singer et al. (2019) for further information). Steps that occurred within 50m of a sleep site at the start and end of the day were excluded. Then, for each observed and random step, several environmental covariates were determined. These were based on covariates found to influence baboon movement in other studies, and included the NDVI at each end of the step, whether or not each step started or ended on a road, the proximity of each end of the step to the nearest water body and that evening's sleep site, the angle of each step compared to the angle towards the nearest water body and that evening's sleep site, and the habitat type at the start and end of the step. The additional covariates of the length of the step and the turning angle of the step relative to the previous step were also added to account for baboons' typically inerratic movement across the landscape. The observed and random steps were then contrasted using conditional logistic regression, using the coxph() function of the survival package (Therneau, 2020). For this analysis, data were divided into seasons as described above, and each monkey was analysed individually (Prima et al., 2017). Of the available analysis methods, the Efron method was selected to reduce the computational time of each model (Gail et al., 1981). Each model was also evaluated with the day serving as the cluster. This meant that while steps within each cluster were temporally, and presumably spatially, auto-correlated due to their sequential

nature, clusters themselves were less likely to be correlated as steps were not recorded while the animal was approaching, resting at, or leaving a sleep site (Fleming et al., 2014; Prima et al., 2017).Thus, the final model used was *clogit(case_ ~ NDVI_end + as.factor(Road_End) + sleep_angle + as.factor(hab_End) + water_dist_end + water_angle + strata(step_id_), method = "exact")*.

2.5 Ethics Statement

This work was carried out with ethical clearance from Oxford University (APA/1/5/ACER/23Jan2018) and from the Ministry of Tourism and the Gorongosa Restoration Project in Mozambique (permit numbers PNG/DSCi/C114/2018, PNG/DSCi/C93/2018, PNG/DSCi/C147/2019 and PNG/DSCi/C142/2019). All handling of the study subjects was performed by professional staff, and following collar deployment all subsequent data collection was completed remotely and in the animals' natural habitat.

2.6 Results

2.6.1 Ranging Data

Collars failed to acquire, or failed to download, preprogrammed fixes <1% of the time for all monkeys except Acacia (WT), whose collar failed to acquire fixes or acquired an impossible fix around 4% of the time. Over the course of the study, there were 299 GPS days with enough successful fixes collected from Eve (FT), 290 from Abacaxi (FT), 266 from Acacia (WT), and 314 from Kigalia (WT). Distance travelled per day, once points within 50m of the sleep site were excluded, also varied per monkey. Eve (FT) travelled 4160m ± 1588m (mean ± SD) a day; Abacaxi (FT) 4219m ± 1620m/day; Acacia (WT) 2393m ± 1077m/day; and Kigalia (WT) 3368m ± 1035m/day. For all monkeys except Acacia, horizontal accuracy was measured as roughly 5m ± 5m; for Acacia, accuracy was measured at 10m ± 8m.

For FT, the mean home range size of both monkeys changed in size from approximately 6.2km^2 (± 0.1km^2) in the dry season to approximately 11km^2 (± 0.1km^2) in the wet season, with a physical shift in location to the south. For WT, home range size was approximately 6.0km^2 (± 0.3km^2) in the dry season but only 3.4km^2 (± 0.2km^2) in the wet season, with WT remaining in just the central portion of their home range during the wet season. Home range composition also changed slightly between the dry and the wet season. For FT, trees were more available in the wet season home range than the dry season, and for both troops trees were preferentially used over low vegetation or bare ground, compared to their availability.

In both troops, the two collared monkeys moved largely in the same directions, and to the same areas at the same time, although the mean distance between them varied by troop. The FT monkeys were on average 82m ± 90m apart, with a maximum distance of 1081m. However, the WT monkeys were on average 226m ± 244m apart, with a maximum distance of 1922m. Due to the variation in when and precisely where the baboons chose to move, each monkey was further analysed individually rather than as a group.

2.6.2 Step Selection Functions

The results of the Step Selection Functions are presented in Table 2.1, and their key conclusions are summarized below. We present results for the wet and dry seasons separately, given the considerable shifts in home range size and location, as well as in climatic variables, at these times of year.

2.6.3 Dry Season

For both individuals in WT, NDVI at the end of the step, angle to the sleep site and distance to water were predictive of a step being observed. Steps towards an area with a higher NDVI were

more likely to be observed, but steps with a higher angle relative to the sleep site were less likely to be observed (i.e., movement towards the sleep site was predictive). The distance to water was also negatively correlated with a step being observed: the greater the distance to water, the less likely an observed step.

In FT, sleep angle, angle to water, distance to water, and habitat at the end of the step were predictive of a step being observed for both monkeys. As with WT, a lower sleep angle increased the likelihood of a step being observed. For both monkeys, a step ending in low vegetation, all else being equal, was less likely to be observed than a step ending in trees; for Eve, the same could be said for a step ending in bare ground. For both monkeys, an increase in water angle made the step more likely to be observed, but an increase in the distance to water made the step less likely to be observed (Table 2.1).

2.6.4 Wet Season

For both WT individuals, NDVI and sleep angle continued to predict observed steps in the wet season as well, with a higher NDVI and a lower sleep angle being predictive of an observed step. However, no other covariates were found to be significant in the wet season.

For FT, NDVI was predictive for both monkeys, with a higher NDVI being predictive of a step being observed. A lower sleep angle was also predictive of an observed step for both monkeys. For Eve and Abacaxi, a step ending in low vegetation was less likely to be observed than the same step ending in trees; for Abacaxi, a step ending in bare ground was also less likely to be observed than the same step ending in trees. Water angle was also predictive for Abacaxi, with an increase in water angle increasing the likelihood of a step being observed.

Table 2.1. Results of Step-Selection Functions, separated by wet and dry season. Columns show Odds Ratio, Confidence Interval, and p-value of each covariate for each monkey. Covariates in first column are taken from the end of each step. Significant findings (p<0.05) are highlighted in grey.

Dry Season												
	Abacaxi (FT)			Eve (FT)			Kigalia (WT)			Acacia (WT)		
Covariate	**OR[1]**	**95% CI[1]**	**p-value**	**OR[1]**	**95% CI[1]**	**p-value**	**OR[1]**	**95% CI[1]**	**p-value**	**OR[1]**	**95% CI[1]**	**p-value**
NDVI	2.72	0.83, 8.93	0.10	1.28	0.67, 2.48	0.5	1.98	1.14, 3.46	0.016	5.21	2.12, 12.8	<0.001
On road												
0 (Intercept)	—	—		—	—		—	—		—	—	
1 (On Road)	1.01	0.66, 1.54	>0.9	1.23	0.84, 1.80	0.3	1.08	0.69, 1.70	0.7	1.24	0.87, 1.78	0.2
Relative angle to sleep site	0.85	0.82, 0.88	<0.001	0.85	0.83, 0.88	<0.001	0.86	0.84, 0.89	<0.001	0.85	0.81, 0.89	<0.001
Habitat type												
1 (Intercept)	—	—		—	—		—	—		—	—	
2 (Low Veg)	1.28	0.87, 1.88	0.2	0.41	0.28, 0.62	<0.001	0.76	0.56, 1.03	0.080	1.39	0.73, 2.65	0.3
4 (Bare Ground)	0.71	0.55, 0.91	0.007	0.47	0.37, 0.61	<0.001	0.90	0.81, 0.99	0.040	1.19	0.96, 1.46	0.11
Distance to closest water	1.00	1.00, 1.00	<0.001	1.00	1.00, 1.00	<0.001	1.00	1.00, 1.00	0.028	1.00	1.00, 1.00	<0.001
Angle to closest water	1.13	1.07, 1.20	<0.001	1.08	1.05, 1.12	<0.001	0.98	0.95, 1.02	0.3	1.03	0.99, 1.07	0.11

[1]OR = Odds Ratio, CI = Confidence Interval

Wet Season												
	Abacaxi			Eve			Kigalia			Acacia		
Covariate	**OR[1]**	**95% CI[1]**	**p-value**	**OR[1]**	**95% CI[1]**	**p-value**	**OR[1]**	**95% CI[1]**	**p-value**	**OR[1]**	**95% CI[1]**	**p-value**
NDVI	21.9	11.9, 40.4	<0.001	27.2	15.3, 48.5	<0.001	3.00	1.63, 5.51	<0.001	3.14	1.55, 6.37	0.001
On road												
0 (Intercept)	—	—		—	—		—	—		—	—	
1 (On Road)	1.34	0.92, 1.96	0.13	1.09	0.78, 1.53	0.6	1.27	0.86, 1.89	0.2	1.09	0.74, 1.60	0.7
Relative angle to sleep site	0.86	0.83, 0.89	<0.001	0.85	0.82, 0.88	<0.001	0.87	0.85, 0.89	<0.001	0.88	0.85, 0.91	<0.001
Habitat type												
1 (Intercept)	—	—		—	—		—	—		—	—	
2 (Low Veg)	0.80	0.65, 0.99	0.039	0.82	0.67, 1.01	0.068	1.24	0.93, 1.64	0.14	0.96	0.69, 1.33	0.8
4 (Bare Ground)	0.73	0.65, 0.83	<0.001	0.74	0.66, 0.83	<0.001	1.00	0.90, 1.12	>0.9	0.94	0.84, 1.06	0.3
Distance to closest water	1.00	1.00, 1.00	0.7	1.00	1.00, 1.00	0.5	1.00	1.00, 1.00	0.5	1.00	1.00, 1.00	0.9
Angle to closest water	1.04	1.00, 1.08	0.039	1.02	0.99, 1.06	0.2	0.99	0.94, 1.03	0.5	0.98	0.93, 1.02	0.3

[1]OR = Odds Ratio, CI = Confidence Interval

2.7 Discussion

What drives animal movement and how individuals decide when, where and how to travel during their daily or seasonal ranging activities are central questions in the field of movement ecology (Nathan et al., 2008). Multiple studies have examined such questions across different species and study sites, or even across different species at the same study site, to understand the drivers of movement decisions across species (Fortin et al., 2005; Roffler et al., 2018; Zimmermann et al., 2014). In this study, we attempted to determine how the unique ecosystem in GNP influenced movement decisions in two groups of baboons living in proximate but compositionally different environments. GNP exhibits a range of not only habitat types, but also temperatures and rainfall, leading to ephemeral resources including sleep sites, food, and water. We set out to determine how movement strategies shifted between the dichotomous seasons, and what factors influenced these strategies.

We compared GPS points taken from real collar data with hypothetical points to which monkeys could feasibly have travelled, but did not. We then set out to determine what drove the monkeys' choices, by quantifying variation in a suite of environmental variables at the actual and at the hypothetical destinations. In doing this, we found seasonal, inter-troop and individual variation in predictors of movement decisions.

First, while we found differences in predictors of movement for each troop by season, a low sleep angle was predictive of both troops' movement regardless of season. This echoes the findings of Strandburg-Peshkin et al. (2017) in Mpala baboons, and may indicate some degree of planning on the part of the troops (this suggestion will be further addressed in Chapter 3) (Strandburg-Peshkin et al., 2017a). A low sleep angle indicates a general movement towards a

sleep site; this being a significant predictor of daily movement may indicate that the baboons were heading towards a certain location to sleep well before sunset. Visual inspection of the data indicates that this pattern was more prominent in the latter half of the day, when steps towards the sleep site were most likely to be observed. However, in the middle of the day, steps towards the sleep site were unlikely to be observed. This means that a single sleep site coefficient within the model cannot fully capture this complex relationship. Instead, this pattern may indicate that in the beginning and middle of the day, factors other than the sleep site may be more predictive of where the baboons will move, but near the end of the day, the sleep site became the most prominent predictor of movement. However, it is difficult to disentangle this effect from the effect of defining the daily path as ending at the sleep site, whether or not it was chosen ahead of time or opportunistically. Further analysis is needed to fully understand how sleep site choice influences movement decisions throughout the day, and whether and when such choices are made during the day.

Seasonality also affected home range size and location, which may have further influenced a difference in decision drivers between seasons. We found that the two troops showed differences in the effect on their home range caused by flooding. WT, which normally inhabits a relatively large area, lost over a third of its home range in the wet season. On the contrary, FT, a troop that is normally constrained to a home range on the floodplain with little access to *Vachellia* woodland, almost doubled its ranging size in the wet season and moved further into the trees south of the floodplain. These changes likely signal a larger seasonal population shift in GNP. WT, normally located on higher ground less prone to flooding, appear to shrink their ranging area as other baboon troops and mammals compete for the dry space. They are aided in this by having a multitude of resources available in a very small area, and are not forced to travel for

food, water, sleep sites, or dry land. By contrast, FT, which has returned to its dry season ranging area annually since observation of the troop began in 2018, may be displaced multiple times throughout the rainy season (Chapter 5). The area in which they range is lower ground and more volatile, and the inconsistent rains and intermittent annual cyclones may lead to more than one displacement until the waters fully recede.

In both troops, we found that the distance to water and angle to the sleep site predicted the baboons' choice in the dry season, with a lower angle towards the sleep site (*i.e.,* movement towards), and a lower distance to water being predictive. In the wet season, angle to sleep site and NDVI were predictive, with areas with a higher NDVI being preferred. In FT, trees were preferred over low vegetation in both seasons, but vegetation type was not predictive for WT. Between the two FT monkeys, Eve was more likely to choose bare ground over low vegetation, but Abacaxi showed no preference between the two.

However, while a high NDVI was predictive of movement for WT in both seasons, it was only indicative in the wet season for FT. This may be for a few reasons. First, NDVI was calculated for the entire study area, encompassing both troops' ranging areas, every 1-3 weeks of the study. Therefore, low and high are relative to other steps the baboons may have taken in that period, sampled from the area that they could access in the next 15 minutes between fixes. For WT, which inhabits a densely tree-covered area, relative NDVI would have seen the baboons moving to greener areas as the seasons changed, given their propensity to feed on tree products, including leaves. FT, however, feeding on underground storage organs, would have been fully surrounded by dry vegetation for much of the dry season; further, the *Vachellia* species found in their dry-season home range has very small leaves; therefore, it is very similar in NDVI to that of

the floodplain sedges, and so it is unlikely a difference would have been detected to the point of being predictive.

In the wet season, however, FT moved into areas with a much higher contrast in NDVI, due to the difference in tree species, and the onset of the annual flooding, with water, and particularly dirty water, generally being represented with a very low NDVI. Thus, to avoid water and move to where there was available food, FT would have had to select for the higher NDVI areas of tree stands rather than the inundated grasses.

Finally, it should be noted that NDVI is not a perfect reflection of phenology, and that different plants will vary in reflectiveness throughout the year. Particularly for food items where baboons utilise underground storage organs, rather than external plant parts, NDVI is unlikely to be an indicator of food availability; further, the presence of standing water is also likely to influence NDVI. Therefore, future studies should examine the utilisation of areas with different levels of NDVI, and record plant phenology periodically in order to fully interpret the link between NDVI and baboon habitat use.

The differences in the predictiveness of proximity and angle to water may also be explained by behavioural differences between the troops. Distance and angle to water were not generally predictive of observed steps in WT; however, in the dry season, they were both predictive for FT. The direction of the effect, with a low distance but high angle to water being predictors of movement, implies that baboons in FT may move along water bodies rather than towards them (this was also observed during on-the-ground data collection by LLB as the baboons were often seen to move along the Mussicadzi river). This difference to WT may be driven by a difference

in habitat type, with WT not having an equivalent water body in their home range, or it may reflect a difference in ranging strategy.

Within the same troop, we found some individual variation in movement predictors. In the dry season, Kigalia's observed steps were predicted by a step ending in trees rather than low vegetation, but Acacia's steps were not. Abacaxi's steps were predicted by angle to water in the wet season while Eve's were not, and a step ending in bare ground lowered the chances of a step being true for Abacaxi, while Eve's steps were not predicted by bare ground. These differences imply differences in movement strategies between monkeys in the same troop, despite *P. ursinus* troops typically moving as a group and previous studies indicating that movement decisions are democratic (S. A. Altmann, 1974; King et al., 2008; Strandburg-Peshkin et al., 2015b). However, in both troops and at any point during the day, the two collared baboons could be over 100 metres apart; additionally, the two monkeys in each troop did not necessarily travel together and use the same resources (Chapter 3). Thus, a difference in small-scale movement strategy may explain these discrepancies in the predictiveness of the model.

While this study was able to examine many of the movement predictors of baboons in GNP, future studies may be able to incorporate additional information to further develop these results. This study was not able to include complete information on water bodies, and at what periods of the year they were flooded, due to lack of data. It further did not include predator or detailed foraging patch data, which are also expected to impact movement decisions. Such data would expand on the results of this study by including more relevant predictors; however, by using NDVI as a proxy for foraging patches, vegetation type as a proxy for risk and physiological stress, and records of known water bodies in the ranging areas, we were able to make a

predictive model of baboon movement in GNP. This adds to the baseline dataset of mammals in GNP, as well as adding to the already established body of baboon data in southern Africa. Further, this study took place in the months following a major cyclone, where the behaviour and activity budgets of the baboons were markedly different than in the previous study year. Future studies should compare the same analysis over multiple years, to fully understand how weather patterns impact not only habitat choice, but also the link between habitat and behaviour.

Our results show that even on a relatively small scale, there can be significant variation in baboon movement strategy and decision making. Our study also illustrates the adaptability needed to cope with large-scale changes, such as seasonal flooding, and indicates a strategic shift in movement choice between seasons. As climate change causes more volatile weather and creates more distinct and prolonged periods of flooding, understanding how species adapt to these changes is crucial for helping to conserve them and their habitats. Further work is needed to understand how other animals in areas like Gorongosa National Park adapt to seasonal changes, and how these adaptations might influence their large-scale ranging behaviour.

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3

Chapter 3: The Travelling Salesbaboon: Chacma baboon route efficiency in multi-stop daily travel routes

CONTENTS

3.1 Abstract

The ability to navigate through both familiar and unfamiliar environments is of critical importance for foraging efficiency, safety, and energy budgeting in wild animals. For animals that remain in the same home range annually, such as grey-footed chacma baboons (*Papio ursinus griseipes*), movement efficiency is expected to reflect familiarity with the home range as well as the nature of the resources within it. For example, resources that are patchy, transient, or seasonal present a greater spatial cognitive challenge, and travel between them may be less efficient than for more consistent or predictable resources. Here, we analyse daily route efficiency in adult female grey-footed chacma baboons at Gorongosa National Park, Mozambique. We use GPS data taken at 15-minute intervals from collars deployed on four baboons of two different troops to identify resource patches used during daily ranging periods (sleep site to sleep site). We then compare the length of the route taken between a given day's patches to routes calculated by two alternate optimisation heuristics: the nearest neighbour method, in which the subject repeatedly travels to the next most proximate patch and then back to the end point, and the Concorde algorithm, which calculates the shortest possible route connecting the day's patches. We show that baboons travel more efficient routes than those yielded by the nearest-neighbour heuristic, but less efficient routes than the Concorde method, implying some degree of route planning. We discuss our novel method of resource patch identification using only remote GPS data, as well as the implications of our findings for primate movement and cognition.

3.2 Introduction

Understanding how animals employ spatial memory, decision-making and planning during daily ranging activities is a key question in the field of movement ecology (Nathan et al., 2008). In

wild primates, this question has been the subject of burgeoning scientific interest, particularly as technological advances increasingly allow researchers to overcome the challenges of accurately tracking these animals through complex landscapes (Janmaat et al., 2021). However, the role of spatial cognition in shaping foraging paths is hampered by gaps in our understanding as to how primates use past and present experiences to make movement decisions (Janson & Byrne, 2007). Multiple factors drive primate movement, including the distribution and profitability of foraging patches in terms of nutritional value per cost of search and travel ('Optimal Foraging Theory') (Amato & Garber, 2014; Charnov, 1976; De Guinea et al., 2019), the cost of traversing the 'Landscape of Fear' (Atkins, 2020; Cowlishaw, 1997; Laundré et al., 2010; Noser & Byrne, 2007a; Rhine & Tilson, 1987), and other short-term considerations such as thermoregulatory impactors (R. Hill & Dunbar, 2002; Russell A. Hill, 2006).

Various mechanisms have been identified that may help primates resolve the sometimes conflicting demands of these factors, such as spatial and temporal mapping of risks and resources (Di Fiore & Suarez, 2007; Garber & Hannon, 1993; Hopkins, 2016; Noser & Byrne, 2007a; Valero & Byrne, 2007), episodic memory (Boyer & Walsh, 2010; Martin-Ordas et al., 2010; Noser & Byrne, 2015), and relying on knowledgeable leaders (Couzin et al., 2005; Stueckle & Zinner, 2008) or on the pooling of individual competences through collective decision making (King & Sueur, 2011; Petit et al., 2009; Strandburg-Peshkin et al., 2015a). Quantifying the influence of these mechanisms allows researchers to better understand how primates make in-the-moment decisions, relying on information from the current state of the physical and/or social environment and, sometimes, prior experience. However, less work has been done to understand how primates link sequential movement decisions over longer timeframes (e.g., over the course of a day of travel), and the extent to which they plan these decisions. Due to the propensity of

previous research to use captive primates to study memory, decision-making and planning, the link between resource-driven movement and cognition remains unclear, leaving open the question whether primates can use multi-step route planning in the wild (Janson, 2014).

Various studies have, nonetheless, sought to examine wild primates' ability to plan and remember locations of interest (such as resource patches) and the paths that connect them, with apparent route planning being identified in several cases. De Guinea et. al. (2019) measured landscape variables such as elevation and canopy density while observing wild black howler monkeys (*Alouatta pigra*), which showed that the routes they used were located in areas of higher food-density than routes not used, implying they may have chosen those routes to monitor feeding trees. A study on mantled howler monkeys (*Alouatta palliata*) also found that they targeted mature fruits in long-distance movements (Hopkins, 2016). Other arboreal monkeys, such as spider monkeys (*Ateles belzebuth*) and woolly monkeys (*Lagothrix poeppigii*) have also been shown to re-use routes to travel in areas with a high-density of food items (Di Fiore & Suarez, 2007).

In terrestrial primates, Noser and Byrne (2007) mapped out the most-used resources of wild chacma baboons (*Papio ursinus*) and examined their ability to navigate between them when they were forced to detour from their normal routes. They found that the baboons made larger detours in areas with a conspicuous landmark such as a hill when compared with areas without prominent landmarks, implying that they navigate using a route network rather than Euclidean mapping (Noser & Byrne, 2007a). Another study compared the movement patterns of humans and chimpanzees (*Pan troglodytes*) in a foraging context, using linearity and speed to measure spatial knowledge of the area and food locations, finding that while humans travelled at a constant speed but with higher linearity in familiar areas, chimpanzees decreased both speed and

linearity in familiar areas (Jang et al., 2019). This indicated that, while both species used spatial knowledge to navigate, chimpanzees appear to travel in a more 'relaxed' way in familiar areas, potentially due to an increased sense of safety, thus demonstrating that linearity and speed are not always suitable proxies for spatial knowledge as found in other studies on chacma baboons (*Papio ursinus*) (Noser & Byrne, 2007b). A further study showed that, in areas with highly seasonal resources, home ranges and daily routes shift to preferentially utilise the available resources, representing a much larger shift in foraging strategy and route planning (Green, Boruff, Niyigaba, et al., 2020).

Despite extensive evidence that wild primates can establish, remember, and use travel routes, these routes and their networks may reflect the accumulation of past individual and collective experiences, rather than being the most optimal routes given the current state of the environment. Furthermore, studying the efficiency of travel paths in wild animals poses a challenge when the relevant destinations and/or intermediate stopping points are opaque to researchers. An oft-used method of testing travel efficiency and planning in animals is distilled in the Travelling Salesperson Problem (TSP). This long-standing optimisation problem invokes a travelling salesperson who must start at a given point, travel to a specific number of other points, and then return to the starting point by travelling the shortest cumulative distance; for foraging animals, this translates to visits to multiple resources while minimising travel costs and thus maximizing calorie gain (D. J. Anderson, 1983). This method to test the efficiency of foraging and an animal's ability to compute and plan multi-step routes has been studied in particular depth in bees (*Bombus impatiens* and *Bombus terrestris*) using artificial setups of flowers over an observable area. Studies showed that bees, given time and multiple trials to learn the best route, can take efficient routes between flowering plants and within inflorescence, trading off the

distance between resources and their caloric benefits; however, *Bombus impatiens* that were not given a chance to optimise their route through repeated trials failed to do so spontaneously (Lihoreau et al., 2011; Saleh & Chittka, 2007). Similar abilities to compute efficient routes between a set number of resources have also been found in pigeons (*Columba livia*) travelling between artificial goals (Baron et al., 2015). Artificially created resources have also been used to study the TSP in primates. Captive chimpanzees (*Pan troglodytes*) were shown to be able to use near-optimal routes to recover food items that had been hidden within the past hour within their enclosures, thus obtaining them before their cage-mates (Menzel, 1973). Similarly, captive vervet monkeys (*Chlorocebus pygerythrus*) were able to solve the TSP, although only with up to six locations in a 5x5 grid of feeding stations spaced 1.53m apart (Cramer & Gallistel, 1997).

Although the resources in these studies were artificially placed across a small area, they showed that non-human animals are able either to plan their routes in advance or to learn to refine their routes through experience by gradually minimising the energy expended on travel between a fixed set of resources. Crucially, the former scenario implies that multiple steps of a route are planned prior to initial departure, rather than successive decisions being made as the animal progresses along the route. Demonstrating that such skills are employed also by wild animals, however, poses additional challenges.

Studies on wild vervet monkeys (*Chlorocebus pygerythrus*) used an artificially established foraging patch to test route planning, showing that the vervets used relatively simple algorithmic processes, or heuristics, such as cluster strategy or convex hull, to solve the problem of connecting multiple resources, with variation in individual foraging strategy but a lack of ability to find the optimal route (Teichroeb, 2015; Teichroeb et al., 2012). Without the use of artificial resources, it becomes considerably harder to measure route optimality, unless both a full

resource distribution and the animals' intended destination(s) are known in advance. Nonetheless, several studies have successfully tackled such challenges. For example, wild tamarins (*Saguinus mystax* and *Saguinus fuscicollis*), which travel on average only 2km daily, were shown to be able to take efficient travel routes based on knowledge of the prior 1-21 days' available resources more often than expected by chance (Garber & Hannon, 1993). In species that range over larger distances, track linearity has also been used as a measure of route planning when all resources cannot be known; Valero and Byrne (2007) postulated that spider monkeys (*Ateles geoffroyi yucatanensis)* can plan multiple resources to visit in a single day, based on the assumption that linearity of travel reflected spatial memory (but see Jang et al., 2019; Noser & Byrne, 2007b), which indicate linearity does not always correlate with spatial knowledge). Chacma baboons (*Papio ursinus*) showed some evidence of planning for out-of-sight resources based on the same premise of linearity reflecting planning, but not the ability to plan visits to multiple resources in advance, nor the ability to adjust when their plans were interrupted (Noser & Byrne, 2007b, 2007a, 2009). It is worth noting that the latter studies all relied on handheld GPS devices carried by researchers during follows, thus human influence on the recorded routes cannot be ruled out.

Although several of these studies claim to have found evidence that individuals were able to solve the TSP, a more recent review showed that in multiple studies the distance travelled was no better than if the individual had used a relatively simple process, the nearest neighbour heuristic, in which the individual always travels to the resource most proximate to its current position (Janson, 2014). This is a common issue with captive primate studies, as the limited space available for experiments means that there is little consequence to sequentially choosing the next nearest resource, whether or not this optimises the distance to return to the starting point from the

final resource visited. However, in wild primates, where returning to sleep sites can add considerable cost to daily travel (and can be further constrained by predation risk and even conspecifics in cases of sleep-site competition), ensuring that the final resource visited is located near the sleeping site will be beneficial, even it if means not following the nearest neighbour heuristic. Unfortunately, the analysis of wild primate ranging data is often hampered by a lack of thorough knowledge regarding the distribution, location, and availability of resources in the environment, as well as the challenges of accurately tracking wild primates' movement paths for the duration of entire days over an extended period.

Recent advances in biologging technology have improved our ability to tackle both of these problems. GPS tracking devices attached to individual primates in the wild can be used to collect data on primate groups' ranging patterns, their proximity to other groups, the speed, structure and length of movement paths, and resource selection, such as the location of sleeping sites or foraging patches (Kays et al., 2015; Markham et al., 2013, 2016; Strandburg-Peshkin et al., 2015a). In this study, we introduce a novel technique to use GPS data to study foraging efficiency in wild chacma baboons (*Papio ursinus griseipes*) in Gorongosa National Park, Mozambique. We analyse GPS fixes taken at 15-minute intervals from four individuals from two different troops over a period of 332 days. Using cluster analysis to identify the most-used areas in a primate's day, we remotely identify resource patches without the need for on-the-ground observations (de Raad, 2012). We quantify the efficiency of the route travelled between a given day's resources and compare it with two hypothetical routes derived from (i) the nearest neighbour heuristic and (ii) the optimal (least distance) route. By calculating the difference in distance travelled between the actual and the two hypothetical routes, we evaluate how efficiently baboons solve the TSP in their own environments, and how we can use current and

historic GPS data to answer questions about primate movement even in the absence of direct observational data.

3.3 Methods

3.3.1 Study site and subjects

Data were collected from four GPS collared grey-footed chacma baboons (*Papio ursinus griseipes*) from two different troops in Gorongosa National Park (GNP), Mozambique. GNP consists of a heterogeneous, mosaic landscape, with distinct dry (April-October) and rainy (November-March) seasons (Stalmans & Beilfuss, 2008). Although the Mozambique Civil War decimated the mammal wildlife of GNP, the Gorongosa Restoration Project has managed to largely recover much of the herbivore population, as well as an increasing number of lions and crocodiles, and a high density of baboons (Bouley et al., 2018; Gaynor et al., 2020; Stalmans et al., 2018). Additionally, during the study period, two packs of wild dogs were introduced into GNP, although no resident leopards (the baboons' main predators) were known to range within GNP.

Two cycling, adult female baboons with no dependent offspring were collared from each of two study troops, the Floodplain (FT) and Woodland (WL) troops, which have been followed on foot and studied periodically since 2017 as part of the Paleo-Primate Project Gorongosa. The collared monkeys were named Acacia (Woodland), Kigalia (Woodland), Eve (Floodplain) and Abacaxi (Floodplain). The systematic habituation of the Woodland troop began in July 2017, and of the Floodplain troop in May 2018.

FT (n = approx. 30 individuals) ranges on the floodplain in the southern-central portion of GNP, covering around 15 km^2 based on the minimum convex hull of 95% of their ranging points

(Figure 2.2a). This area consists primarily of alluvial floodplain with some fever tree (*Vachellia xanthophloea*) woodland. Their ranging area is bordered by the Tsungue River to the east and bisected by the Mussicadzi River to the west and south. These rivers are seasonal, and at most points of the year can be crossed via wading, jumping, fallen trees, or sand banks, except during seasonal floods. FT's diet consists primarily of sedges, *Vachellia* seed pods, and some palm fruits, with opportunistic hunting of small birds, shellfish, and mammals.

WT (*n* = approx. 90 individuals) ranges in approximately 7.5 km^2 in the woodlands directly south of the Floodplain troop's home range. This area is primarily made up of medium-to-dense *Vachellia-Combretum* woodland, interspersed with seasonal water pans and termite mounds. WT's diet consists mostly of leaves and fruits, with opportunistic hunting of small mammals (Hammond et al., 2022). The extreme north of the WT's home range is bordered by the Mussicadzi River.

FT's relatively larger home range can be explained by the seasonal flooding of GNP. From November-April, annual rains inundate the central area of GNP, forcing wildlife towards the edges into a virtually new home range (Beardmore-Herd et al., in review; Walker et al., 2023). During the dry season, FT utilises the northern half of their range, and they migrate to the southern portion during the wet season (Chapter 5).

3.3.2 Data collection

The four baboons were darted and collared between late July and mid-August 2019. Each baboon was fitted with a GPS/accelerometer collar (model 1D, e-obs Digital Telemetry, Grünwald, Germany) by an experienced vet following anesthetization via dart gun. Each collar was programmed to record a burst of 10 GPS points every 15 minutes UTC time, at the minute intervals of :00, :15, :30, and :45. Collars collected data until the end of their battery life, which

varied for each collar, ranging from 293 to 323 days. GPS data were downloaded from the collars monthly from August 2019-November 2019, then again in February 2020, May 2020, and June 2020, using an eObs BaseStation II connected to a Yagiantenna (868 MHz 10E) at a distance of 10-50m. Downloaded data were then processed using Eobs decoder_v10s1.

3.3.3 GPS data processing: daily resources and routes

For the purposes of our analysis, from each burst of GPS fixes at 15-minute intervals, only the last GPS fix in each burst was used. GPS records were split into discrete calendar days for analysis, containing the GPS points for that day including and between sleep sites, but discarding overnight GPS points. Within each GPS day, these GPS points were divided into 'waypoints', or areas where the baboons spent substantial time (>15 minutes; see below for more detail). The first and last waypoint of each day was automatically the sleep site, determined as the GPS location at 0200 hours UTC on the study day ("morning sleep site") and 0200 hours UTC on the next day ("evening sleep site"). When the collars failed to detect satellites at 0200 hours, 0230 was used.

Once sleep sites were identified, GPS data were first filtered for only points that were taken a minimum of 50m from either the morning or evening sleep site. This was to ensure that only the sleep site was considered a waypoint for that area, and not any areas used for basking or waiting for the rest of the group to emerge from the sleeping tree.

Through previous daily follows of baboons, areas were observed where the troops tended to forage or spend time napping or socialising (LLB, personal obs.). Areas where baboons spent a significant amount of time were therefore considered to be resources of some description, either for foraging, resting, sheltering or socialising. To find these waypoints, the filtered GPS points were ordered sequentially by date and time. The first GPS point was considered the "anchor"

point. The distance between each subsequent GPS point and this anchor point was compared. If the subsequent GPS point fell within 30m of the anchor point, which was roughly the spread of FT during a foraging bout (LLB, personal obs.), it was considered part of the same group of points (GoP). If a GPS point fell outside of the 30m radius, it became the anchor point of a new GoP. If there were no GPS points within the radius of a point, that point became its own GoP. This method was repeated sequentially through all points until no GPS points were left.

The created GoPs were then filtered to only include groups with two or more GPS points, as this signified that the monkey had remained in that area for at least 15 minutes. GoPs were then clustered using the hclust() function from the R package 'stats' (R Core Team, 2020), where any GoPs in the same month that fell within 40m of another GoP were combined to form a new waypoint cluster, or a polygon (de Raad, 2012). This was to increase the likelihood that waypoints indeed indicated a resource, i.e., the presence of something that could be exploited in that area multiple times, rather than the area acting as a one-off stopping point for hunting, predation avoidance, or other non-repeatable reasons. This aggregation also meant that resources which were in very large, continuous, depletable patches, such as areas with seasonal sedges or clusters of palm trees, would be counted as a single resource patch rather than multiple small ones. The geometric centre of each of these clusters was used as the defining GPS point for a waypoint.

To calculate daily routes between waypoints, each daily GPS track (generally 96 points/day per monkey) was compared to the waypoints of that month, and it was noted whether each GPS point in turn fell within the polygon of a waypoint. Waypoints were discarded if only one GPS point fell within a polygon, as this indicated the baboons had passed but not stopped to utilize the resource. The order of the final waypoints as they appeared in the daily GPS tracks was the order

of waypoints for that day, regardless of points that did not fall within a polygon, and this was defined as the day's route.

A day's route was defined as usable for analysis if the monkey had a) visited more than two waypoints while travelling between sleep sites and b) did not revisit any waypoint. This was to ensure that calculating an optimal route was neither trivial (in the case of too few waypoints) nor too complex (if allowing for revisits to waypoints on the same day). In identifying days that matched the criteria for usability, we found that around or just over half the days of each monkey were unusable for this type of analysis, mostly due to revisits to waypoints.

3.3.4 Comparison of actual travel routes to Nearest Neighbour and Branch-and-Cut (Concorde) route optimisation

All analysis was carried out using RStudio Version 1.3.95946. Once a daily route between waypoints was discerned from the GPS points, two types of route optimisation were used as comparison, the "Nearest Neighbour" (NN) and "Branch-and-Cut" (Concorde) methods. The NN method is considered a "greedy" but easy method: each sequential node is chosen based on proximity to the previous one, using only local information, without long-term planning regarding location of the start or end point of the route (i.e., the morning and evening sleep sites, respectively) (Janson 2014). This allows for short travel distances between consecutive waypoints, but often leads to long travel distances between the penultimate node and the final node.

The Concorde method is so named because it relies on the Concorde TSP solver (Cook, 2015) to select the most optimal route based on all possible routes, with the most optimal route being the one which requires the least distance travelled to cover all nodes and still return to the starting node. The comparison of all possible route distances was performed using the R packages sp

(Bivand et al., 2013; Pebesma & Bivand, 2005) and tspmeta (Mersmann et al., 2013). In the former, the function spDists() calculated distance matrices between each pair of waypoints, including sleep sites, in a day. These distances were calculated in Mercator projection (UTM), for precision across short distances, and were taken to be the beeline distance, without accounting for physical barriers or elevation changes (such changes were in any case negligible; the main barrier in the home range of either troop was the Mussicadzi river, which WT never attempted to cross and FT crossed with little diversion via sandbanks, fallen trees, wading, or jumping from tree crowns to the opposite bank). The latter package was used to determine the NN and Concorde routes for each day, using the same distance matrix each time.

Due to the constraints of the Concorde solver, it was necessary to manipulate the data such that the routes started and ended at designated points, specifically the morning and evening sleep sites. To accomplish this, within the distance matrix, distances to and from sleep sites were manipulated while maintaining the symmetry of the distance matrix. The distance between the first point, the morning sleep site, and the last point, the evening sleep site, was set to have negligible cost, at 0.000001m apart. However, the distance between the morning sleep site and all other points besides the evening sleep site was set to have extreme cost, by adding 10km to the total distance. This ensured that there would always be a high cost to returning to the morning sleep site, thus making it most optimal to start there, and that the model started and ended with each sleep site. For the NN analysis, because the chosen path depends on the start point, the start point was set as the evening sleep site. This forced the model to then choose to go to the morning sleep site and to pick the NN route from that point, before returning to the evening sleep site. Once the routes were created, the sequence of points were reordered to start with the morning sleep site and end with the evening sleep site, simply shifting the start and end

of the sequence (e.g., when the model produced the order "End-5-2-3-Start", this was translated to "Start-3-2-5-End" for analysis, with Start being the morning sleep site and End being the evening sleep site).

Once the Concorde and NN routes were determined, the cumulative distance of each day's modelled routes were compared to the actual route for that day, as described in the following section (see also Figure 3.1 for an illustrative example of a single day's actual, NN, and Concorde routes).

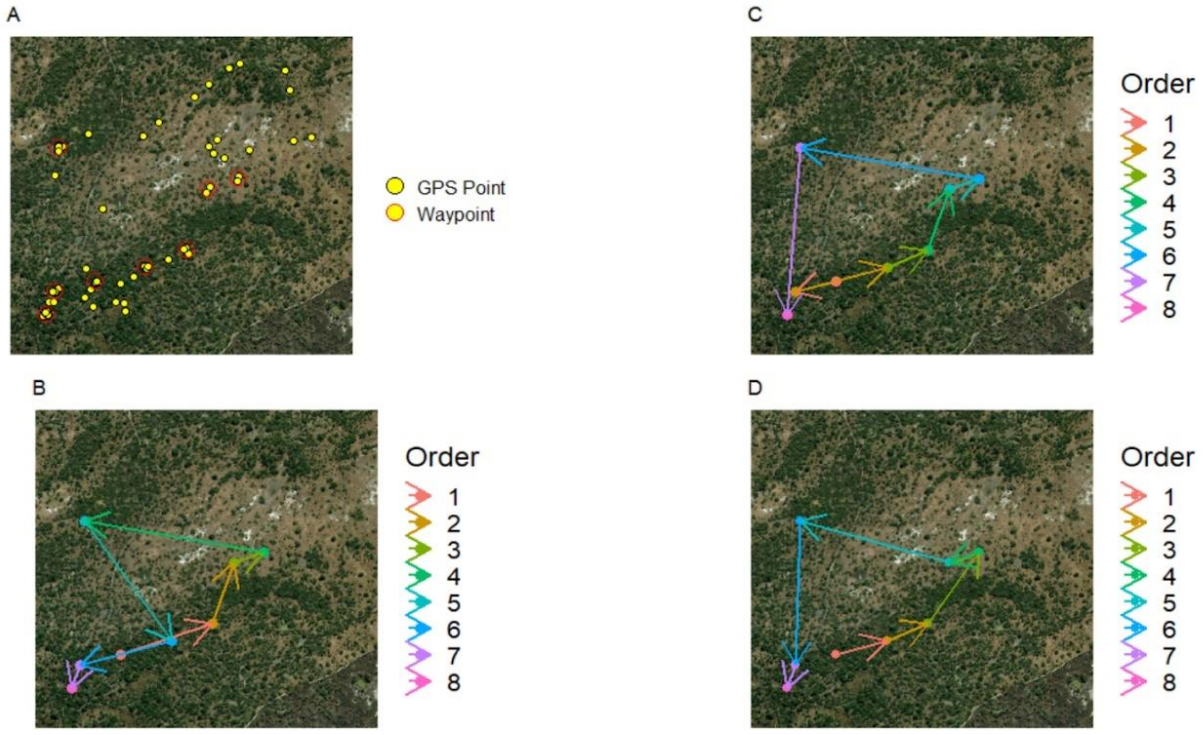

Figure 3.1 A single day's tracks taken from the Woodland Troop. ***(A)*** *Yellow dots show GPS fixes recorded for the day; red circles indicate clusters of points that were identified as waypoints.* ***(B)*** *The actual order in which the troop travelled between the waypoints identified in (A).* ***(C)*** *The hypothetical route calculated by the Nearest Neighbour heuristic for the same set of waypoints.* ***(D)*** *The hypothetical, maximally efficient route calculated by the Concorde optimiser.*

3.3.5 Statistical analysis

To compare the length of a given day's route produced by the NN heuristic to the length of the actual route recorded from that day, Wilcoxon Signed-Rank Test was used due to route length

differences being non-normally distributed, with long tails and a high peak near zero, precluding our ability to use a parametric test. For the difference between the length of the Concorde route and the actual distance travelled, a right-tailed Wilcoxon Signed-Rank Test was used due to it being impossible for the actual route length to be shorter than the optimal Concorde route.

To investigate what predicts differences in route length between the actual/observed routes, NN routes and Concorde routes, two linear models were used, with absolute distance travelled as the response variable, and with monkey ID, number of waypoints and type of route (NN, Concorde, or observed) as covariates. These models were run separately to compare actual and Concorde routes as well as observed and NN routes. A boxcox() function determined that the response variable should be transformed as the square root of the distances to ensure that the residuals were normally distributed (Venables & Ripley, 2002).

To examine the effect of the number of the day's waypoints on monkeys' ability to approximate the most efficient route, we calculated the percentage additional distance travelled by the monkeys compared to the shortest distance path (Concorde route) among the same waypoints. For example, a day with a 10% inefficiency, where the shortest possible route covered 1,000 m, would see the monkeys travelling 1,100 m. The square root of this measure of inefficiency was used as the response variable in a linear model, with monkey ID and number of waypoints as the covariates.

3.4 Ethics Statement

This work was carried out with ethical clearance from Oxford University (APA/1/5/ACER/23Jan2018) and from the Ministry of Tourism and the Gorongosa Restoration Project in Mozambique (permit numbers PNG/DSCi/C114/2018, PNG/DSCi/C93/2018,

PNG/DSCi/C147/2019 and PNG/DSCi/C142/2019). All handling of the study subjects was performed by professional staff, and following collar deployment all subsequent data collection was completed remotely and in the animals' natural habitat.

3.5 Results

Across the four GPS-collared monkeys, 714 travel days were available for analysis once unusable days had been discarded (Table 3.1). Note, however, that these figures almost certainly underestimate the real distances travelled since the distances between consecutive GPS fixes are calculated as straight-line distances. Collars failed to acquire, or failed to download, preprogrammed fixes <1% of the time for all monkeys except Acacia (WT), whose collar failed to acquire fixes or acquired an impossible fix around 4% of the time. For all monkeys except Acacia, horizontal accuracy was measured as roughly 5m ± 5m; for Acacia, accuracy was measured at 10m ± 8m.

Table 3.1 Summary data of individual monkeys' daily statistics for analysed days. Min and Max waypoints indicate the minimum and maximum waypoints each monkey visited in a day. Days matching Concorde indicates how many days analysed the monkeys travelled on the same route as the Concorde solver, and the minimum and maximum waypoints on those days.

Monkey	Total GPS Days	Usable Days	Min Waypoints	Max Waypoints	Mean ± SD Waypoints	Mean ± SD Travelled (metres)	Days matching Concorde (min:max waypoints)
Eve	*302*	*171*	*2*	*11*	*5.54 ± 1.78*	*3476.6 ± 1270.4*	*41 (2:9)*
Abacaxi	*293*	*193*	*2*	*11*	*5.52 ± 1.67*	*3474.8 ± 1307.1*	*48 (2:8)*
Acacia	*322*	*158*	*2*	*10*	*6.45 ± 1.70*	*2659.9 ± 743.4*	*64 (2:10)*
Kigalia	*318*	*192*	*3*	*11*	*6.22 ± 1.8*	*2792.2 ± 727.4*	*64 (3:11)*

Comparisons of daily route lengths calculated for the actual, NN, and Concorde routes are shown in Figure 3.2 and Figure 3.3. A paired, two-sided Wilcoxon Signed-Ranks Test for each monkey

showed significant evidence that for all monkeys except Abacaxi, there is a difference between the length of the NN route and the actual route length taken.

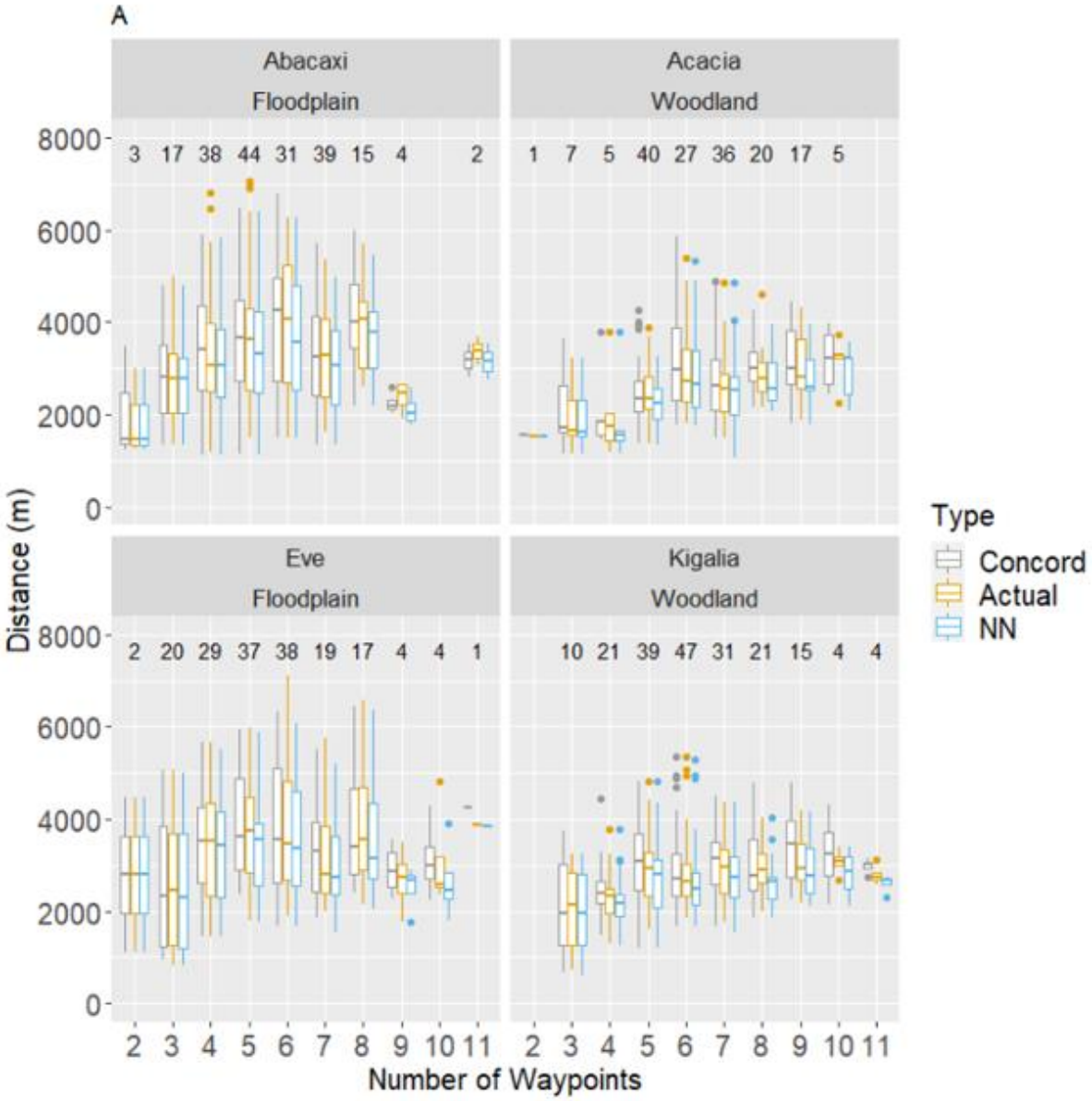

Figure 3.2 Comparison between actual daily travel paths recorded from wild baboons and hypothetical paths derived from two different path optimisation procedures (NN and Concorde) connecting daily waypoints. Distance travelled per day shown as a function of the number of waypoints visited that day. Numbers above each box indicate how many days with the number of waypoints on the x-axis was analysed for each monkey.

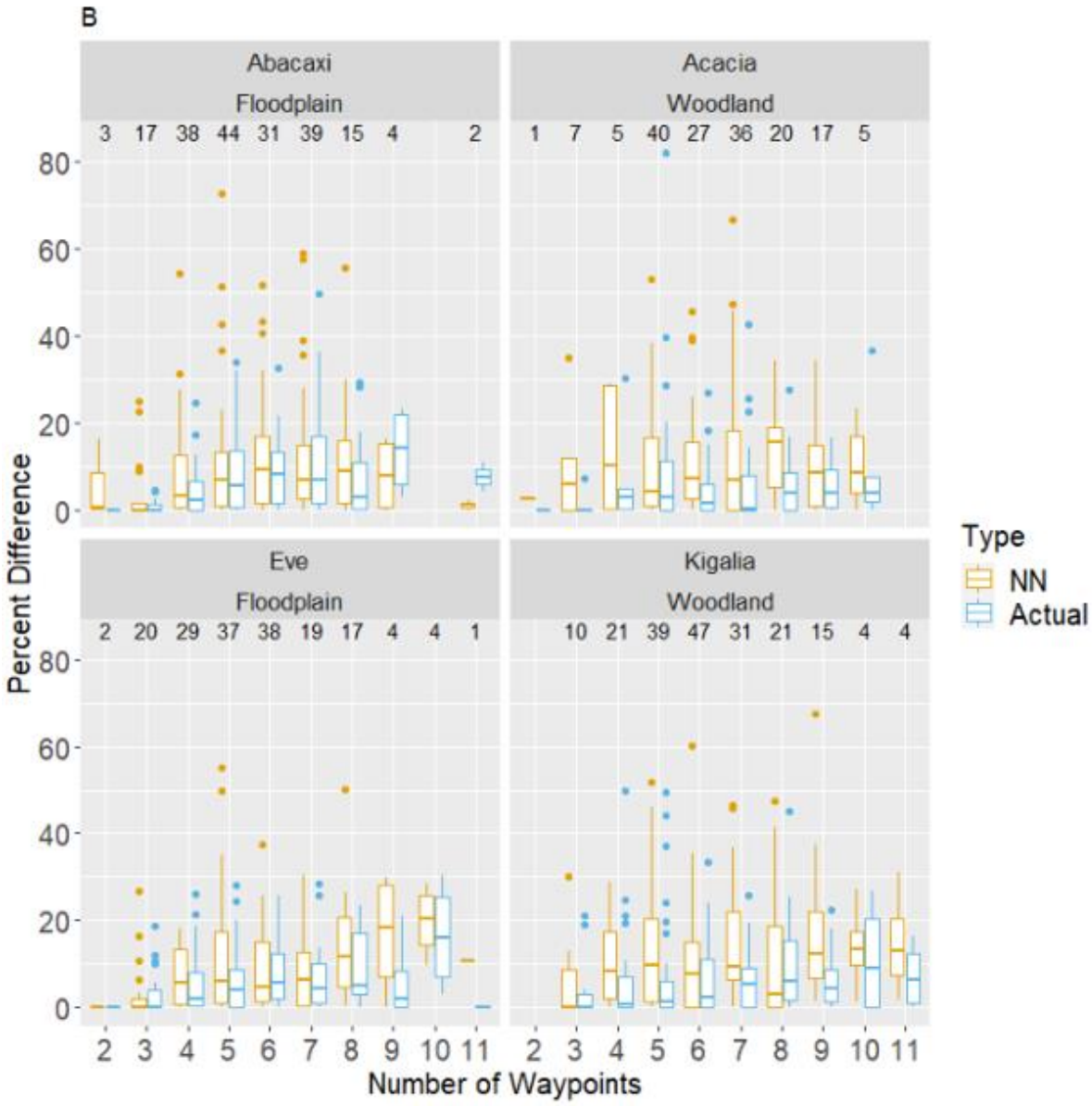

Figure 3.3. The additional distance travelled, expressed as a percentage of that day's optimal (Concorde) distance, for both NN and actual route distance, as a function of the number of waypoints visited that day. Each panel corresponds to data from one of the four subjects, with troop also labelled. Boxplots show quartiles and range, with points plotted individually if they are above or below the lower quartile by at least 1.5 times the interquartile range. The number of days with each number of waypoints is shown above the boxplots.

Further analysis using a paired, two-sided Wilcoxon Signed-Rank Test showed evidence that for all monkeys, the actual route taken was more likely to be shorter than the NN route. By contrast, a paired, one-sided Wilcoxon Signed-Ranks Test showed evidence that all monkeys' routes were longer than the Concorde route of each day. Results of these tests can be found in Table 3.2.

Table 3.2. Summary of paired, one-sided Wilcoxon Signed-Rank Tests comparing the lengths of route types. Column one shows that the length of the nearest neighbour route is significantly different from the length of the actual route for all monkeys except Abacaxi. Column two shows that for all monkeys, the actual route was statistically longer than the Concorde route, while column three shows that the actual route was statistically shorter than the nearest neighbour route.

Monkey	**Nearest Neighbour (two-sided)**		**Concorde (H: Actual > Concorde)**		**Nearest Neighbour (H: Actual < NN)**	
	V	**p-value**	**V**	**p-value**	**V**	**p-value**
Eve	*4818*	*0.04**	*8515*	*<0.01**	*4818*	*0.02**
Abacaxi	*6740*	*0.1*	*10585*	*<0.01**	*6740*	*0.05**
Acacia	*2215*	*<0.01**	*4464*	*<0.01**	*2215*	*<0.01**
Kigalia	*3876*	*<0.01**	*8256*	*<0.01**	*3876*	*<0.01**

In examining how inefficient the baboons' routes were, the number of waypoints emerged as a significant predictor of inefficiency, where relative to an average route of 5 waypoints, each additional waypoint increased inefficiency by about 0.82 percentage points (DF = 709, F-stat = 8.74, $p < 0.01$; see Figure 3.3). However, each monkey matched the Concorde route multiple times on days with routes ranging from 2-11 waypoints. The highest number of waypoints matched varied by monkey; Kigalia matched the Concorde solver on one day with 11 waypoints, while Acacia was able to match it on a day with 10 waypoints, Eve on a day with nine, and Abacaxi on a day with eight.

3.6 Discussion

Close to half a century ago, Altmann (1974) emphasised that a primate's movement decisions should be expected to be based, in part, around obtaining the most calories for the least distance

travelled, leading to further research inspired by optimal foraging theory and foraging efficiency. Therefore, understanding how well primates solve the TSP daily - that is, how they set out from their sleep site in the early morning, travel to enough resources throughout the day to fulfil needs for food, water, shelter, and sociality, and then return to the same (or different) sleep site in the evening while being as energetically efficient as possible - is key to understanding primate memory, decision-making and spatial planning.

The TSP has been used in previous studies with mixed results, with claims of individuals of some species succeeding at finding the most efficient route and others not (Cramer & Gallistel, 1997; Janson, 2014). Previous studies on baboon route planning showed that baboons were able to use some (albeit limited) level of multi-step route planning, based on observational and experimental data (Noser & Byrne, 2007a, 2007b). In this study, we made use of a different technique to build on these findings: we used remotely collected data, applied to a linear TSP, to develop a new method of measuring route efficiency using location data taken from GPS-collared chacma baboons. By clustering points into areas where the study subjects remained for at least 30 minutes, we were able to identify areas of interest to the monkeys, which we have called “waypoints” (the likely location of resources such as food, shade, or shelter). The number of these waypoints each group visited in a day varied between 3 and 19 over the course of 332 days of data collection, although the two collared monkeys in each group did not necessarily both visit each waypoint identified for a given day. We then compared the monkeys’ daily routes connecting these waypoints with hypothetical routes computed using two different algorithms: the NN heuristic and the Concorde optimiser.

Our results show that the baboons performed better than the NN model, but worse than the Concorde optimal model. The NN heuristic is a simple but greedy heuristic, wherein it seeks to

travel between waypoints as quickly as possible without regard for the efficiency of the overall route. Performing better than this model implies that the baboons did not simply choose always to travel to the next nearest resource from their current one, but instead were able to sacrifice some immediate gain for benefits later in the day (i.e., they may have travelled past possible resources to a distant resource and then returned to stop at them on their approach to a sleeping site). This is seen in the data particularly on days where the NN distance travelled was more than a kilometre longer than the actual route (n = 27 days), and in one case the difference was as much as 3 km. This may imply some degree of planning, given that the baboons were able to travel between a given set of waypoints in a more efficient manner than by repeatedly moving to the next nearest waypoint.

On the other hand, the baboons performed significantly worse than the Concorde model, which is to be expected given the computational demands of calculating the optimal route. However, on 218 days across all four monkeys, the baboons were able to find the most efficient route with days ranging from two to 11 waypoints (Table 3.1). While it is expected for subjects to find the optimal route by chance on days with fewer waypoints, their ability to find the optimal route on days with a greater number of waypoints makes a much stronger case for the involvement of planning. Indeed, while we found that overall route efficiency decreased as the number of waypoints increased (which is not surprising given that the difficulty of the task increases greatly with the addition of extra waypoints), the baboons were able to find the optimal route at least once on a day with 11 waypoints and used the optimal (i.e., Concorde) route on about 20% of days with 4-10 waypoints. Nonetheless, there are several explanations we can propose to account for the observation that on the majority of days the baboons' routes were suboptimal.

First, the baboons may be constrained by their own abilities to map space and/or to plan. One study found that baboons may not be able to form Euclidean map-like representations (Noser & Byrne, 2007a), which makes the task of finding the shortest route between points more difficult. However, another study suggested that baboons may use episodic memory and a cognitive map to plan their routes in advance (Noser & Byrne, 2007b). Second, since baboons travel in groups, any movement that an individual performs will result from a combination of their personal preference and those of the others in the troop. As such, the group consensus is likely to be a compromise between multiple individuals' preferences, meaning that even a hypothetical perfect route optimiser may need to compromise on the route travelled. The effect of group decision making is compounded in the baboons studied here, as their group spread is often hundreds of metres, potentially allowing them to exploit multiple resources at the same time (Chapter 1). Third, because resources are heterogeneous in nature (food, shade, etc), the order of waypoints may not be random or free as it is in the case of the NN and Concorde algorithm. For example, baboons may pass a shady patch without stopping in the early, cooler part of the day, only to return there later when temperatures soar, leading to what appears to be a suboptimal path purely from the perspective of path length. Fourth, and perhaps most crucially, we cannot be sure how many of a day's waypoints are 'fixed' at the beginning of the day, and hence how many waypoints ahead we can expect baboons to plan.

Besides these theoretical considerations, our results are also complicated by the nature of our data. We used remotely collected data – a method of studying primate, or indeed any animal, movement without the need for on-the-ground observation of the subjects. In doing so, we also established a novel method for identifying locations of interest ('waypoints'), but this technique has several limitations. In particular, the time-based definition of a waypoint means that some

"false" waypoints may have been identified. Pauses presumed to be for a stationary resource could have come about from an opportunistic hunt, an unexpected intergroup or predator encounter, a weather phenomenon such as rain or extreme heat, or even a newly discovered resource that the troop happened upon. Without knowing the exact nature of each identified waypoint, it is difficult to fully evaluate the subjects' capacity for route planning. However, stricter definitions of what constitutes a waypoint, integration of on-the-ground surveys, geographical and vegetation data, conspecific ranging data, and historical weather data could all help to clarify waypoints used in each model. Conversely, it is possible that our criteria for a waypoint are too restrictive, and that the monkeys are in fact visiting additional waypoints undetected by our analysis (which would render our comparisons with the calculated hypothetical routes less informative). Again, additional environmental data, as well as adjusting the parameters for what constitutes a waypoint for each study site, would help to minimise this issue.

Although the baboons observed in this study were seen to return to the same areas over multiple days to forage, it should also be noted that the patches varied in size and shape, particularly for FT, who tended to forage on patches of sedges rather than distinct trees. Parameters for a patch or waypoint were chosen based on the average observed size of food resources, including tree crowns. However, ground patches of food were more variable. As sections of the patch were depleted or became ready for consumption, the overall shape and in some cases location of the patch changed. The current method of identifying waypoints may be too coarse to account for these discrepancies. Weekly patch monitoring, either in person or using remote sensing, could help inform the best parameters of waypoint identification over time.

An additional limitation of our method is the uncertainty of how the primates chose these waypoints. Studies have shown that group movements in baboons, even when initiated by a single leader, are "voted upon" democratically (King & Sueur, 2011; Strandburg-Peshkin et al., 2015a; Cédric Sueur, 2011). While we interpret our results assuming that the baboons aimed to visit the patches we identified as waypoints, we cannot exclude the possibility that they opportunistically found patches over the course of their daily ranging, or simply picked a patch and then continued on to each subsequent patch as it was remembered or "voted upon" by the group. Nonetheless, our results show that this is unlikely, given the greater efficiency of the baboons' routes compared to those produced by the NN algorithm.

Another consideration of the study's limitations concerns the nature of the study site. At the time of the study, the density of predators in GNP was relatively low, and the number of resident leopards, the main predator of baboons, was presumed to be zero (although leopards were occasionally spotted transiting through GNP on camera traps) (Gaynor et al., 2020). Further, lions were not thought to hunt baboons in GNP, given the high number of preferred antelope. Therefore, there may have been less pressure on the baboons to find optimal routes, given they were less constrained by the threat of predation and the need to find a suitable sleeping site by dusk. The lack of predators may have also led to an increase in baboon density in GNP; troops were often seen to overlap home ranges, suggesting the avoidance of inter-troop encounters may have been prioritised over minimising daily travel distance (LL-B, personal observation). The high density of troops may lead to a prioritization by the baboons to travel more quickly to exhaustible resources, such as fruit trees, and return to more homogenous patches later in the day; this is discussed further in Chapter 4. However, in April 2021, leopards were reintroduced

to GNP, and a comparative analysis of similar data should be undertaken to understand the effects of increased predation on route planning and actual routes travelled.

Besides predation, the extreme seasonality of GNP was also not explored in this study, due to the majority of available data being collected in the wet season. This could be due to more unusable days (i.e., days where monkeys return to the same waypoint after visiting it the same day) occurring in the dry season. However, visual inspection of the distribution of the number of daily waypoints shows an emerging seasonal pattern. While the Woodland Troop exhibits no apparent change in the number of daily waypoints across seasons, the Floodplain Troop increases the number of daily waypoints in the wet season and decreases them in the dry season. The change in waypoints also, naturally, leads to the opposite change in efficiency, with days with more waypoints associated with lower efficiency and days with fewer waypoints associated with greater efficiency. This change in the number of waypoints in the Floodplain Troop may be the result of greater resource abundance in the wet season compared to the dry, physical barriers such as floodwater, or related to the seasonal change in home range size or physical shift in home range, with larger home ranges potentially being an artifact of fewer available resources (see Chapter 2). Further analysis, combined with future studies including on-the-ground data, may reveal more seasonal effects on route optimality in these baboons.

In sum, we aimed to study primate cognition through natural movement using only remote data, and in the process established a new method of studying spatial decision-making without the need for observational data. Our results provided evidence that baboons may be capable of some degree of planning of their daily travel routes, producing routes that are more efficient than a simple heuristic of iteratively moving to the next nearest location of interest. While these results come with caveats, they demonstrate a novel approach to examining primate decision-making in

the context of daily travel using remotely collected GPS data. This method can be further refined to include alternate remote sensing data, creating more robust results, and offering a new and practical way to utilise previously collected data or future data sets. The use and refinement of this method paves the way for further cognitive studies using historical GPS data across a variety of species and allows researchers to utilise their data sets for multiple purposes beyond the originally intended study.

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4

Chapter 4: Predictors of Baboon Sleep Site Selection in Gorongosa National Park

CONTENTS

4.1 Abstract

Sleep sites are a critical resource for all primates, providing shelter, safety, and a place to socialize. In Gorongosa National Park, Mozambique, the high density of baboon troops and seasonal flooding, coupled with the low availability of sleep sites in certain areas and rarity of

predators at the time of this study, create a unique setting to examine what drives baboons to select the sleep sites they do. Here we examine how resource use and seasonal flooding impact the baboons' sleep site choice. We find that unlike in other primate species, but similarly to baboons in other study sites, baboons in Gorongosa use sleep sites closer to their final resource of the day, rather than their first resource of the next day, leading to shorter end-of-day travel but longer morning travel distances. We further find that, despite the seasonal flooding causing displacement and changes in their home ranges, the baboons reuse the same sleep sites in two consecutive dry seasons, indicating some memory of the previous season. This study lays important groundwork for understanding the long-term effects of displacement due to weather events on affected baboons, as well as future studies on the role of predators in sleep site selection.

4.2 Introduction

Sleep has important functions in living creatures, contributing to homeostasis, attentiveness, brain development and long-term health (Cirelli & Tononi, 2008). Choosing a suitable sleep site is important for taxa which do sleep, with benefits that include predation avoidance, socializing, and access to food (Altmann, 1974; Burger et al., 2020; Butler & Roper, 1996; Caselli et al., 2014; Chapman, 1989; Savagian & Fernandez-Duque, 2017). Sleep site selection is particularly important for the short-term survival and long-term fitness of individuals, and in particular primates (J. R. Anderson, 1984). Where a primate or primate group sleeps can affect predation risk (Chu et al., 2018; Ellison et al., 2019; Feilen & Marshall, 2014a; Gazagne et al., 2020; José-Domínguez et al., 2015; Ogawa et al., 2014), (although this may not always be the case, even within the same species (Koops et al., 2012)), thermoregulation (Chu et al., 2018; Ellison et al., 2019; Koops et al., 2012), proximity to resources such as food or water (Brividoro et al., 2019;

Gazagne et al., 2020; Ogawa et al., 2014; Teichroeb et al., 2012), pathogen avoidance (Brividoro et al., 2019; Feilen & Marshall, 2014a), or conspecific avoidance and range defence (Brividoro et al., 2019; Markham et al., 2016).

Traditionally, the study of sleeping patterns in primates has been restricted to behavioural follows or captive primate studies, but the rise of biologging devices, such as those incorporating GPS loggers, has made it feasible to study the behaviours of cryptic or difficult-to-follow primates, as well as nocturnal behaviours where visual contact may be limited (Ayers et al., 2020; Campera et al., 2022). While handheld GPS devices have been used to track the location of sleeping sites in primates (Chu et al., 2018; Ellison et al., 2019), studies that equip animals with GPS collars to remotely record the sleeping patterns of wild primates have come about more recently. The recent rise of smaller, more accessible biologgers and improved quantitative treatments have made it easier for studies to collect and interpret large volumes of the necessary data.

With this rise in technology, several previous studies have used collar-mounted biologgers to study primate sleep sites and nocturnal behaviours, showing a range of factors that influenced both. Amongst nocturnal primates, a review of Lorisiformes found that sleep site type and selection vary between sleep sites, and daytime predation played a role in sleep site selection (Svensson et al., 2018). Similarly, nocturnal lesser galagoes (*Galago senegalensis*) slept in areas with more forest cover and connectivity, in places lower mean temperature than other parts of the environment, suggesting thermoregulation and predation risk influence their sleep site choice (Ellison et al., 2019). Amongst diurnal primates, proboscis monkeys (*Nasalis larvatus*) picked sleeping trees that minimised insect molestation and predation (Feilen & Marshall, 2014b), while

howler monkeys (*Alouatta caraya*) also moved sleep sites to avoid parasites, as well as be close to their first morning feeding site (Brividoro et al., 2019).

The sleeping patterns of the genus *Papio* have been extensively studied, in part due to their large body size making the placement of biologgers more viable, and the number of widespread, long-term field sites. For example, using dual-axis accelerometers mounted on GPS collars, Ayers et al., 2020 found that three wild chacma baboons (*Papio ursinus*) did not strategically use moonlit nights to reduce human avoidance or make up for shorter day lengths. Suire et al., 2021 studied sleep site use in Anubis baboons (*Papio anubis*) in relation to rainfall and resource availability, and found that while sleep site choice was not influenced by rainfall on a short time-scale, on a longer time scale, baboons chose to sleep closer to the area they had spent time in during the day, thus travelling less distance to their nightly sleep site. Another study found that while baboon rising times varied with visits from predators, the monkeys did not move their sleep sites in response, nor did they change their sleep sites more frequently afterwards (Bidner, Matsumoto-Oda, et al., 2018). A recent study using accelerometers also found that baboons were more likely to experience lower sleep quality when sleeping in unfamiliar places, although time spent sleeping did not influence distance travelled the next day (Loftus et al., 2022). While these studies shed some light on the drivers of baboon sleep-site choice, they were not able to account for, for example, seasonality limiting access to sleeping sites, or the drivers of choice in a low-predator environment.

In this study, we use GPS data to examine the sleeping patterns of two troops of baboons in Gorongosa National Park, Mozambique (GNP). GNP is a unique study site to examine baboon behaviour due to the relatively low density of predators at the time of the study, and the extremely high density of baboons compared to other sites (Bouley et al., 2018; Gaynor et al.,

2020; Stalmans et al., 2018). During the study, aerial counts showed over 200 baboon troops in the central portion of GNP, with troop size ranging from less than 10 individuals to over 100, compared to between 100-150 lions, around 50 wild dogs, and no resident leopards or hyenas (Bouley et al., 2018; Gaynor et al., 2020; Hammond et al., 2022; Stalmans et al., 2018). Anecdotal reports from rangers in GNP also suggest that nocturnal movement is common, as are baboons sleeping on the ground. This could suggest that, due to the high baboon density, sleep sites may be harder to come by, and that range defence and conspecific avoidance may influence sleep site selection more than antipredation strategies (Markham et al., 2013). Alternatively, the relatively low density of predators may allow for more nocturnal movement, which has previously been identified in diurnal primates, and less pressure to find a suitable sleep site (Ayers et al., 2020; Isbell et al., 2017).

In addition to the relatively low terrestrial-predator-to-baboon ratio, with the exception of crocodiles, GNP is unique in being one of only two baboon study sites where a significant period of seasonal flooding occurs. Annual rains result in a displacement of animals from the floodplain, who then return weeks to months later when the water has receded (Beardmore-Herd et al., in review.). For a troop that usually ranges on the floodplain, this means that for part of the year, their normal home range, potentially along with preferred sleep sites, is largely or completely inaccessible. For the Woodland Troop, the onset of the floods meant a shrinkage of the home range, presumably as other animals and conspecifics move away from the flooding and towards higher ground (Chapter 2).

To date, no studies have examined the sleeping patterns of the baboons of GNP, nor any area combining such low predator and high troop density. Therefore, this study aims to compare the baboons' sleeping patterns at this mosaic ecosystem with other sites where troops have been long

studied, including sites with strong seasonality or high predation risk. We describe the sleeping sites in the two studied troops, the Woodland Troop (WT) and Floodplain Troop (FT); we then present data on the location and distances between sleep sites, how often and in what temporal patterns sleep sites are reused, the number of sleep sites per troop, and the variation in sleep sites between the wet and dry seasons, in order to establish a baseline for inter-sites comparisons, as well as to provide data that offers a snapshot in time during a phase when the Gorongosa Restoration Project was well underway but not yet concluded. As the reintroduction of predators progresses, with novel species (hyenas, leopards) being introduced in 2021-2023, it will be equally important to replicate our current results using data from 2020 onwards. This study aims to answer three main questions relevant to allow the above-mentioned comparisons: 1) Do baboons in GNP exhibit preferences for the location of sleep sites (e.g., centre vs periphery of their home range)? 2) What is the relationship between sleep site selection and resource use? 3) Do the baboons return to the same sleep sites following seasonal displacement by flooding?

We begin by taking a basic measure of sleep site location, relative to the home range, to compare with other studies. Other researchers have shown that, in areas of regular predation and intergroup encounters, baboons tend to sleep away from the peripheries of their home range, in presumably more familiar areas (S. A. Altmann, 1974; Cheney & Seyfarth, 2007; Loftus et al., 2022; Markham et al., 2016). This may be a product of avoiding inter-group conflict in overlapping home ranges, an effect amplified in periods where sleep sites may be limited (Markham et al., 2013). With the density of baboons in GNP, a large amount of overlap was observed in the home ranges of both troops, even within central areas (Ferreira da Silva et al., in review; Stalmans et al., 2018). The two study troops were also shown to have starkly different home range sizes, with WT having a home range approximately half the size of FT's (FT home

range ~ 15km^2; WT home range ~ 8km^2); however, when divided into seasonal ranging areas, the home range sizes were comparable (Chapter 2). Additionally, low predation risk and seasonal movement may expand the number of "familiar" areas available to both troops, but particularly FT. Therefore, asking this question allows us to establish whether the known behaviour of sleeping centrally in the home range in other baboons exists in Gorongosa baboons and, at the same time, it is an opportunity to assess potential variation that is not explained by differences in carnivore presence but may instead stem from unusually large home ranges that allow for more sleep site choice than the smaller home ranges in other sites.

We next test the hypothesis that there is a relationship between sleep site and resource locations. We do this by calculating the distance from the sleep site to both the last resource of the previous day and the first resource of the following day. A study on sleep site selection at the Amboseli Baboon Research Project found preliminary evidence that one factor of sleep site selection is proximity to a temporary or unexploited food resource (Markham et al., 2016). Another study on Anubis baboons (*Papio anubis*) found that, over longer periods (i.e., a year), baboons may change their sleeping patterns based on climatic factors such as rainfall, which influences both the amount of food and water in the environment (Suire et al., 2021). Studies of other primate taxa have also shown a preference for sleeping close to resources, in particular food (Brividoro et al., 2019; Chapman, 1989). As in other studies, we expect that the baboons will either travel a short distance from the last resource of the day to the sleep site, or a short distance from the sleep site to the first resource of the next day. However, we do not expect that the baboons will travel a long distance both from the last resource and to the first resource, instead conserving energy by minimizing travel distance between the sleeping site and an exploitable resource.

Finally, we examine whether the baboons reuse sleep sites across seasonal displacement. While other troops use the same sleep sites repeatedly throughout the year (Bidner, Matsumoto-Oda, et al., 2018; Markham et al., 2016), GNP is unique in that some sleep sites are physically inaccessible to some troops due to seasonal flooding. Observations on FT and WT across 2017-2019 show that the baboons return to their dry-season home range annually and spend time in similar areas, despite a period away from it (Chapter 5). To test whether the baboons also reuse sleep sites across seasons, we calculate the number of days between sleep site use. We expect to see baboons return to their dry season sleep sites after the wet season and return to sleep sites even after long periods of absence.

4.3 Methods

4.3.1 Study Subjects and Location

Data were collected in Gorongosa National Park, Mozambique (GNP). GNP is a 4000km^2 park located in central Mozambique. GNP is a highly mosaic, seasonal environment that experiences a distinct dry (April-October) and wet (November-March) season. The seasonality leads to the floodplain of GNP surrounding the central Lake Urema to become inundated annually, as well as causing seasonal rivers to fill up and often burst their banks; during the dry season, the floods recede, leaving behind seasonal rivers that eventually dry into small ponds or empty riverbeds before the next dry season (Herrero et al., 2020; Stalmans & Beilfuss, 2008). This pattern is further exacerbated by regular cyclones hitting the area, including Cyclone Idai six months prior to the study, which had long-term impacts on the fauna of GNP (Walker et al., 2023). During the Mozambique Civil War (1977-1992) the mammal population of GNP was decimated; however, the Gorongosa Restoration Project has since restored much of the herbivore population, as well as re-introduced and supported several predator species in GNP (Atkins et al., 2019; Bouley et

al., 2018; Gaynor et al., 2020; Pansu et al., 2019). At the time of the study, GNP had one of the highest densities of baboon troops in southern Africa, as well as a stable population of crocodiles and increasing numbers of lions and wild dogs (Stalmans et al., 2018).

Four chacma baboons (*Papio ursinus griseipes*), from two different troops, provided data. All four baboons were cycling, adult females with no dependent offspring, fitted with GPS/accelerometer collars (see below for details). The two troops – the Woodland Troop (WT) and Floodplain Troop (FT) – both reside in the southern portion of GNP. Both troops have been followed on foot and studied periodically since 2017 (WT) and 2018 (FT) as part of the Paleo-Primate Project Gorongosa. Two of the collared baboons were from WT (Acacia and Kigalia), and two from the FT (Eve and Abacaxi).

WT (n ~ 90 individuals) inhabits *Vachellia-Combretum* woodland, maintaining the same central home range throughout the year, with the overall size of the home range shrinking approximately 15% through the wet season, based on analysis of the minimum convex polygon. FT (n ~ 30 individuals) lives on the alluvial floodplain to the north and adjacent to WT's home range, an area comprised mostly of low grasses and sedges and edged with *Vachellia* trees. FT's home range shifts during the wet season due to the inundation of the Floodplain, forcing them to range in a part of their home range which they rarely travel to during the dry season.

Observational data taken on these troops in 2018 and 2019 show that they prefer to sleep in trees, often cyclically returning to the same areas of trees. However, the exact sleeping site of each troop was unable to be identified in-person due to constraints on working in GNP, which required a return to base before the baboons had ascended their sleep trees. Nevertheless, baboons in both troops were often seen resting and socialising in the same areas both in the evenings and first things in the morning, implying their sleep tree was nearby. However, within

GNP, baboons were often seen on the roads or walking around after dark, and were observed by rangers to sleep on the ground, indicating that baboons were not constrained by daylight or habitat to find a sleep site.

At the time of the study, lions and wild dogs ranged in both troops' home ranges. No resident leopards were known to inhabit the area. Home range overlap was observed with multiple other troops, and intergroup encounters occurred weekly in FT, although there is no evidence that WT and FT ever encountered each other.

4.3.2 GPS Collars

Baboons were collared in July-August 2019 using cage trapping (n = 1) and free-darting (n = 3). Each baboon was sedated and fitted with a GPS/accelerometer collar (model 1D, e-obs Digital Telemetry, Grünwald, Germany) by an experienced GNP vet (see "Ethics Statement" below). Collars were programmed to record a burst of GPS points every 15 minutes UTC time, and to collect accelerometer data at a rate of 20 Hz every minute, although 2/4 accelerometers failed soon after deployment. The collars then collected data through to the end of their battery life, which ranged from 293-323 days across the four monkeys. Data were downloaded monthly from August 2019-November 2019, then again in February 2020, May 2020, and June 2020, using an eObs BaseStation II connected to a Yagiantenna (868 Mhz 10E) at a distance of 10-50m and processed using eObs decoder_v10s1. Collars incorporated a fabric strap that would wear down after at least two years, removing the collar from the baboon; therefore, collars were not designed to be retrieved.

4.3.3 Identification of Sleep Sites

Sleep sites were identified based on the baboons' location at 0200 hours daily. In the event 0200 was not available due to collar failure, 0230 was used instead. Once all sleep sites were

identified, single-linkage cluster analysis was used with a distance factor 100m to identify a single sleep site. This methodology is similar to previous studies and gives a conservative estimate of the number of sleep sites used (Bidner, Matsumoto-Oda, et al., 2018). This method also helped to account for choice in large patches of trees utilized by baboons for sleeping, wherein a number of trees used in a single area could be construed as a single sleep site for a large troop. The geographic mean of this cluster of points was then used as the sleep site location for analysis of distance between sleep sites and between resources and sleep sites. Individual sleep sites, i.e., collared monkey location at 0200, was used for analysis of group spread.

4.3.4 Resource Proximity

We identified non-sleep site resources based on clustering analysis. For each burst of points, the last GPS point was taken from the data. GPS points were grouped by rolling 30 day period, and filtered for points that only occurred after the baboon had already left the sleep site in the morning, or before they entered their evening sleep site. If the baboon spent more than 15 consecutive minutes (2 GPS fixes) within 30m of the same spot, then those two fixes became a group of points (GoP). Each GoP was added to until a fix was taken >30m from the original GPS fix of the GoP. Any GoP that had points within 40m of a second GoP was combined with that GoP. A minimum convex polygon was then drawn around each final GoP, and this polygon was presumed to be a resource for the baboons, either for resting, socializing, or feeding. The last resource of the day was defined as the final resource the baboon utilized before entering the sleep site. The first resource of the day was defined as the first resource the baboon utilized after exiting the sleep site. Distance to each resource was calculated based on straight-line Euclidean distance from the sleep site to the first utilized point of the resource (i.e., first point stopped at in the GoP that makes up the resource).

The centrality of a sleep site in the home range was categorised seasonally. First, GPS points were visually examined for outliers. Concentric minimum convex polygons were drawn around the most central 5% of points, with each subsequent polygon adding another 5% of all points. The home range size of each polygon was plotted linearly. Visual examination showed a steep increase in home range size from 95% of points to 100% of points compared to every other increase, indicating that the least-central 5% of points were outliers. These points were therefore excluded from the analysis of the home range boundaries. Once the home range was calculated, straight-line distance from each sleep site to the closest edge of the home range was calculated; this number was used regardless of whether the point fell inside or outside of the 95% centrality polygon.

4.3.5 Seasonality

For analysis, the year was divided into seasons based on calendar dates. The wet season was defined as November 1 – March 31, while the dry season was defined as April 1 – October 31 (Tinley, 1977).

4.3.6 Group Cohesion

Given that each troop contained two collared monkeys, who were presumed to have slept in proximity each night, the distance between each troop's monkeys' sleep site was calculated for each night both monkeys had active collars (Floodplain $n = 293$, Woodland $n = 276$). The average distance and standard deviation were then calculated for the distance between monkeys in each group, as an indicator of group spread, or cohesion, while sleeping.

4.3.7 Statistical Analysis

To test if distance from home range edge significantly predicted the number of times a sleep site was reused, a simple linear regression was used, analysed by collared individual. The fitted

linear regression predicted frequency of sleep site use by distance from the edge of the home range. To determine if there was a relationship between the distance from the last resource of the day and the first resource of the next morning to the chosen sleep site, a paired Wilcoxon Signed-Rank test was used. Data were examined to ensure they met the assumptions of the test, i.e., normally distributed differences between distance lengths, and then the distance from the sleep site to the first resource of the next morning was ranked against the distance from the last resource of the previous day.

4.4 Ethics Statement

This work was carried out with ethical clearance from Oxford University (APA/1/5/ACER/23Jan2018) and from the Ministry of Tourism and the Gorongosa Restoration Project in Mozambique (permit numbers PNG/DSCi/C114/2018, PNG/DSCi/C93/2018, PNG/DSCi/C147/2019 and PNG/DSCi/C142/2019). All handling of the study subjects was performed by professional staff, and following collar deployment all subsequent data collection was completed remotely and in the animals' natural habitat.

4.5 Results

4.5.1 GPS Data

GPS collars collected data from the moment of their placement until the day the battery died. All collars experienced some failure during data collection, and data were filtered to days where sleep sites were known and there were at least 8 hours of GPS points throughout the following day. Collars failed to acquire, or failed to download, preprogrammed fixes <1% of the time for all monkeys except Acacia (WT), whose collar failed to acquire fixes or acquired an impossible fix around 4% of the time. For all monkeys except Acacia, horizontal accuracy was measured as roughly 5m ± 5m; for Acacia, accuracy was measured at 10m ± 8m. Date of collar placement

was removed from the analysis. This yielded 296 days of data for Eve (FT), 287 for Abacaxi (FT), 313 for Kigalia (WT), and 264 for Acacia (WT).

4.5.2 Within-group Sleeping Patterns

To analyse sleeping patters, data for each group were filtered to only nights when sleep site data were available for both monkeys within that group (FT $n = 293$; WT $n = 276$), regardless of whether GPS data for the day existed. Over 293 nights, the FT monkeys were recorded to have slept on average 46 metres apart (SD = 45m; min = 2m; max = 248m). Over 276 nights, the WT monkeys slept an average of 163m apart (SD = 148m; min = 2m; max = 850m). These maximum distances are considered the lowest maximum possible group spread, given non-collared baboons may have slept further apart than the collared baboons. Because of the variation in distance between the two monkeys, each monkey was analysed individually for the remainder of the analysis.

In general, the baboons slept in more unique sleep sites in the wet season than the dry season, although some sleep sites used in the wet season were also used in the dry season (Figure 4.1).

Monkeys from FT showed a higher variation of sleep site use. Their most used sleep site alone accounted for 10% of their nights, while multiple identified sleep sites were only used once. Monkeys from WT had more evenly distributed use of sleep sites, but still had multiple sites that were only used once (Figure 4.1).

To understand how each troop moved in their environment, movement from each collared monkey was combined and the averages of both monkeys used. FT tended to move on average 400m more between consecutive nights in the dry season compared to the wet season, while WT moved on average 200m between consecutive nights across the whole year (Table 4.1).

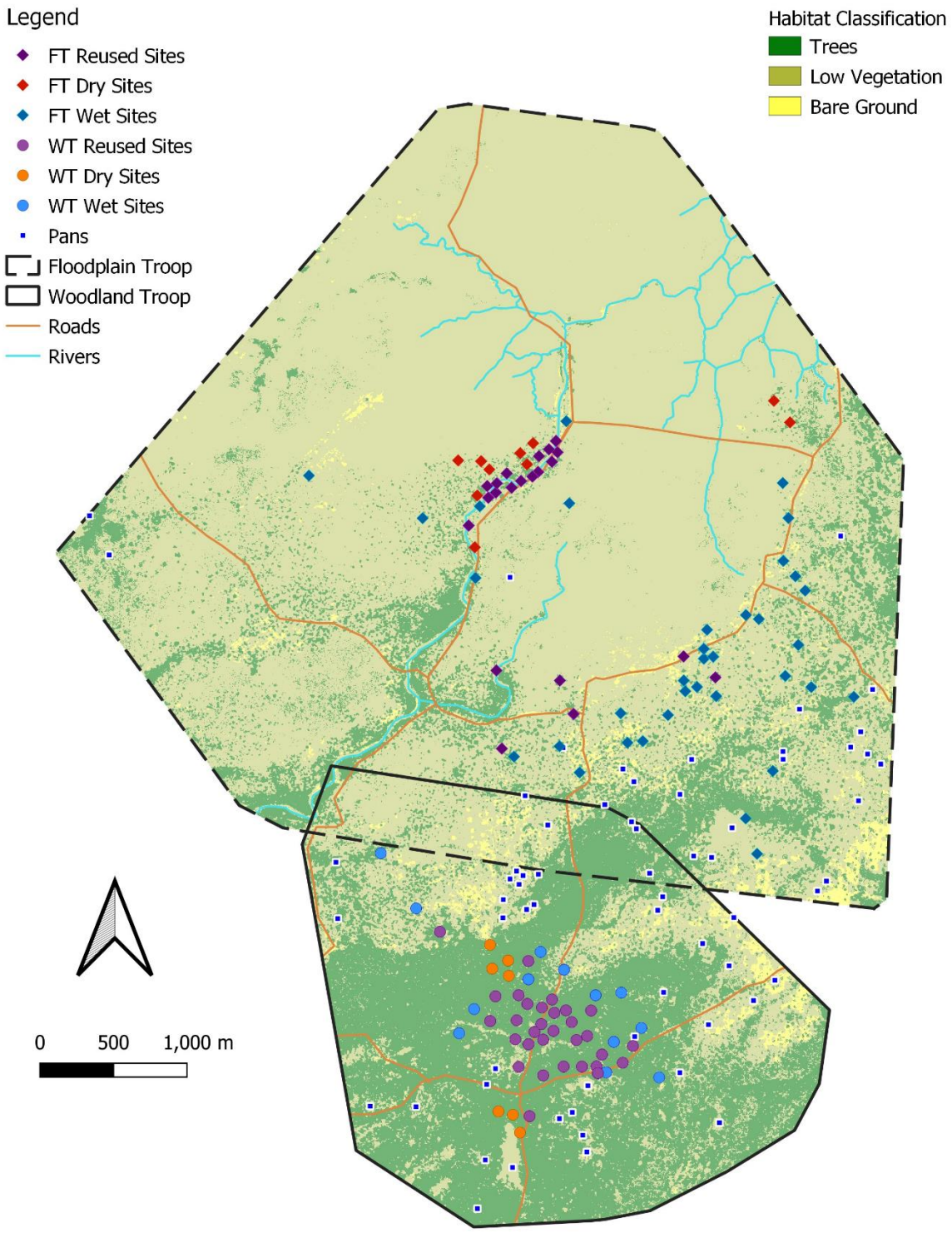

Figure 4.1. Annual sleep sites for study subjects. Colours indicate whether sleep site was used in dry, wet, or both seasons. Pans, roads, and rivers are also marked. Home range boundaries represent the minimum convex polygon of all GPS fixes. In total, FT slept in 10 sleep sites exclusively in the dry season, 35 in the wet season, and 21 in both seasons; WT slept exclusively in 7 dry season sites, 13 wet season sites, and 31 in both seasons.

4.5.3 Distance from Home Range Edge

We fit a linear model predicting the number of times a sleep site was used against that sleep site's distance from the home range edge for each monkey. For all monkeys, the effect of the distance from the home range edge was statistically significant and positive (Table 4.2), meaning that sleep sites further away from the home range edge were more likely to be used than those closer to it.

Table 4.1. Summary of sleep site use for each baboon. The "Total Nights" column indicates how many nights sleep site data were known for. The "Unique SS" columns indicate the total number of sleep sites used in each season. The "Avg Dist" columns show how the average distance between sleep sites on consecutive nights in each season.

	TOTAL NIGHTS	UNIQUE SS (WET)	UNIQUE SS (DRY)	AVG DIST (WET) (M ± SD)	AVG DIST (DRY) (M ± SD)
EVE (FT)	296	31	10	680 (±678)	207 (±526)
ABACAXI (FT)	287	31	11	653 (±692)	223 (±546)
ACACIA (WT)	264	17	14	248 (±359)	223 (±305)
KIGALIA (WT)	313	18	12	223 (±342)	217 (±297)

Table 4.2 Results of linear model lm(SleepSiteUse ~ DistanceFromEdge), used for each monkey.

	Abacaxi			Eve			Kigalia			Acacia		
Characteristic	**Beta**	**95% CI[1]**	**p-value**	**Beta**	**95% CI[1]**	**p-value**	**Beta**	**95% CI[1]**	**p-value**	**Beta**	**95% CI[1]**	**p-value**
HRdistance	0.01	0.00, 0.01	0.004	0.00	0.00, 0.01	0.004	0.01	0.01, 0.02	<0.001	0.01	0.00, 0.01	<0.001

[1] CI = Confidence Interval

4.5.4 Relationship between Sleep Sites and Resources

A Wilcoxon-Signed Rank Test comparing the distance to the first resource of the day to the distance from the last resource of the previous day was run for each monkey. For all monkeys, it was found that the distance from the sleep site to the first resource of the day was significantly

longer than the distance from the last resource of the previous day to the sleep site, with a moderate effect size (Table 4.3).

Table 4.3 Results of Wilcox Signed-Rank Tests comparing distance travelled from the sleep site to the first resource of the day to the distance travelled from the last resource of the previous day to the same sleep site.

	V	P	EFFECT SIZE	N
ABACAXI	27459	<0.01	0.33	282
EVE	29498	<0.01	0.33	292
KIGALIA	37105	<0.01	0.49	307
ACACIA	7088	<0.01	0.43	137

4.5.5 Return to Sleep Sites

When comparing sleep site use between the period before the wet season and after the dry season, each monkey returned to more than half the sleep sites previously used before the wet season (Eve 14/22; Abacaxi 14/20; Kigalia 20/27; Acacia 10/18). Additionally, each monkey returned to a previously used sleep site after an extended period of not using the sleep site; Abacaxi's longest absence from a sleep site was 171 days; Eve 275; Kigalia 277; Acacia 207. Sleep sites that were returned to tended to be in the troop's core home range, although occasionally sleep sites on the periphery of the home ranges were used in both seasons. However, in both seasons, several sleep sites were used less than five times per monkey, while some sites were reused over twenty times (Figure 4.2).

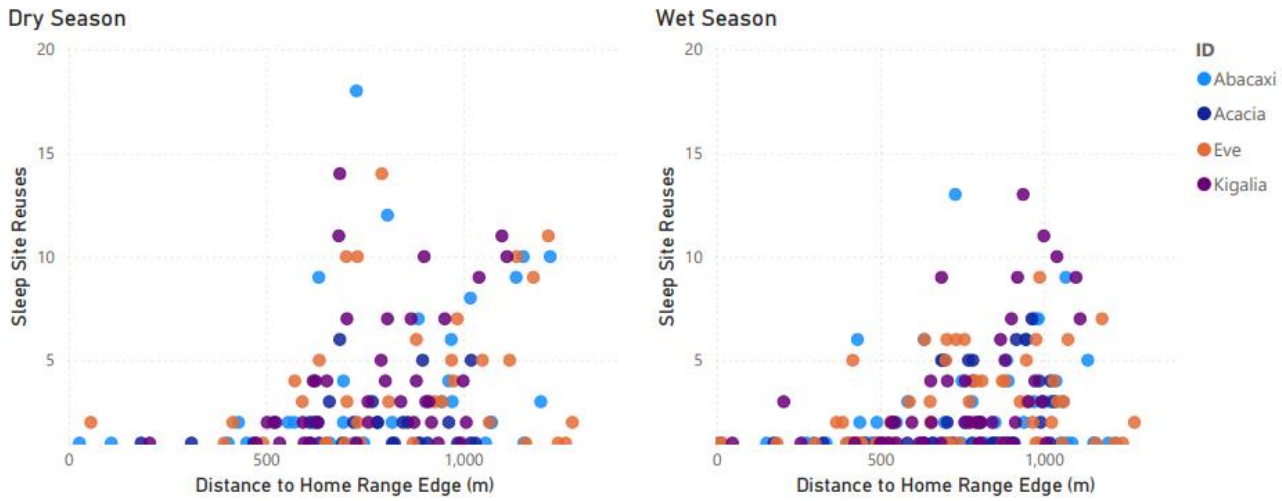

Figure 4.2. Scatter plots of reuses of sleep sites by season for all four monkeys. X-axis represents the distance from the home range edge, with 0 being on the home range edge and increasing distance in metres away from the nearest edge. Y-axis shows how many times a sleep site was reused relative to its distance from the home range edge.

4.6 Discussion

The sleeping patterns of primates have been long studied (J. R. Anderson, 1984); however, few sites present such drastic ecological conditions combined with a low density of predators and a high density of baboons. We found that, like in other baboon study sites, the baboons prefer to sleep in the more central part of their home range, and in the case of GNP this pattern holds regardless of seasonality. In addition, despite lower predator density than other parks, baboons moved sleep sites after just a few nights, as seen in other areas (Markham et al., 2016). We also found a large difference in the number of sleep sites used in the wet versus the dry season. This implies that the baboons changed sleep site more often in the wet season, and, for FT, moved further between sleep sites. During the wet season, all mammals and other non-aquatic life are forced to move away from the floodplain to higher ground. This means that the animals are more condensed in a smaller area, which may increase the risk of predation and inter-group encounters as seen in other study sites where seasonal flooding occurs, such as the Okavango Delta (Beardmore-Herd et al., in review; Cheney & Seyfarth, 2007). As most of the sleep site reuse

occurred in the dry season, it is possible that the baboons moved sleep site more often in the wet season due to higher predation risk and intergroup conflict. Additionally, a wetter environment combined with unpredictable flooding could prompt the baboons to move more often to avoid high parasite loads, low ground, or highly competitive areas. Because FT is forced to move into areas that are already the home ranges of established baboon troops due to the flooding, they may also be less familiar with where suitable sleep sites are or which are frequently used. Visual analysis of the data also shows that their sleep sites are generally on the road bordering the floodplain, indicating that they are remaining on the edge of the flood water and may be more limited in what areas they can access; however, further data on the extent of flooding is needed to support this theory.

Conversely, WT would be expected to have their normal home range encroached upon by the higher density of mammals in the area, forcing them to remain in their core home range. While they did not show such high preference for a single sleep site as FT, they also frequently moved sleep site, and had a number of sleep sites that were used less than three times over the study period. This be due to predation risk, or to remain temporally separate from other troops that overlap home ranges.

Our results also showed that the baboons of GNP preferred to sleep closer to their last resource of the day, regardless of how far they had to travel to their first resource of the next day. There could be several explanations for this. One might be that the baboons plan at least the last part of their day based on the sleep site they would prefer to end up at; in this case, the last resource of the day might be planned or opportunistic, but most relevantly on the way to their sleep site. A second explanation could be predation avoidance. Lions and crocodiles are known predators of baboons, and are the predators in highest abundance in GNP (Cheney et al., 2004; Cheney &

Seyfarth, 2007). Since lions are known to hunt at dusk, baboons may be avoiding extra time spent on the ground during twilight, instead completing their evening socializing in the safety of their sleep site (Makin et al., 2017). Additionally, since many sleep sites are near bodies of water, baboons may use the water as the last resource before moving to the safety of a sleep site while visibility is high to avoid crocodiles. A third explanation is opportunism. Given the large density of baboons in GNP, there should be some amount of competition for sleep sites. At the end of the day, it is likely many sleep sites have been claimed by troops already. Therefore, it is safer to find a suitable sleep site close to the final resource that may be suboptimal, but is available, rather than risk searching for a new sleep site that may have already been claimed and being left without one. Finally, it is possible that baboons are not planning sleep sites at all, but instead plan their last resource of the day, and sleep where it is convenient at nightfall; this theory could account for the number of sleep sites used only once. Further analysis should consider ways to test these hypotheses individually, by incorporating behavioural data and monitoring intergroup or predator encounters when approaching or using each sleep site.

Finally, our results indicate that, even after an extended hiatus, baboons find and reuse preferred sleep sites. Although the full period of displacement, where preferred sleep sites are completely inaccessible for FT, lasts only for about 30-40 days of the wet season, we now have evidence to show that baboons not only return to the same areas after this absence, but also the same sleep sites as the year before. This is in line with other studies' findings that baboons are able to remember resources over at least the medium-term (Noser & Byrne, 2007b, 2015). As severe weather events continue, and the length of the rainy season changes, future studies should monitor how readily baboons return to previously inaccessible areas, as well as find familiar areas to reside during the flooding.

Overall, our study shows that the baboons of Gorongosa National Park's sleep sites are predicted by distance from habitat edge, as well as proximity to the last resource used each day. This study forms a valuable baseline for baboon sleeping site decisions in GNP, which will undoubtedly change over time as more predators are introduced. Since the study, hyenas, leopards, and additional wild dogs have been released into GNP. As the predator numbers grow, so will the risk to baboons, changing their habitat choices. Further studies should look at reuse of sleep sites in relation to the predation avoidance hypothesis, as well as the types of sleep sites used by baboons. Although the baboons have been seen to sleep in trees, reports of park baboons sleeping on the ground were common at the time of the study, and baboons were frequently observed walking around at night. Indeed, even our GPS data shows some level of movement after dusk and before dawn (LLB, unpublished data). Future studies should look at the type of sleep sites selected, as well as utilize the accelerometer function of the collars of the troop. Additionally, other surrounding troops should be included in the data set to understand how competition for sleep sites plays into sleeping site decisions.

Although this study is limited in the detail it can give us about baboon sleeping site choice, it shows an important overall pattern of similarities and differences with other baboons' sleep sites. Repeated analysis of future collar data in the same troops, as well as on-the-ground information, will shed more light on what drives sleeping site choice as predation risk rises, and the baboon density subsequently drops.

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5

Chapter 5: Repeated Route Use in a Seasonal Environment

CONTENTS

5.1 Abstract

Route-based navigation is a common movement strategy for a variety of taxa, wherein animals repeatedly re-use familiar paths during travel. However, this type of navigation remains understudied in wild animals that experience regular displacement, raising questions about the robustness and longevity of such routes and route memories. The seasonal flooding of Gorongosa National Park (GNP), Mozambique, provides an opportunity to test multiple facets of route-based navigation in wild primates, due to its high seasonality and annual flooding. First, we establish that baboons living in two different troops affected by the flooding remain in or return to the same areas that they were ranging in before the floods. Then, we compare daily paths using nearest-neighbour analysis to show that the baboons have habitually used routes, and finally test whether those routes are maintained throughout the year, with a focus on areas that were vacated for more than two months. We find that the baboons vacate areas at the peripheries of their home ranges during the flooding period, but routes in these areas are either non-existent or are only reused within a season. This indicates that routes may not be maintained in long-term memory spanning several months, or that route reuse is in part dependent on seasonal resources or navigational aids.

5.2 Introduction

Animals moving through their environments are limited in where they can travel by a number of factors, including predation risk (Laundré et al., 2010), and access to food (Altmann, 1974; Amato & Garber, 2014; Caillaud et al., 2010; Di Fiore, 2003), shelter (Markham et al., 2016; Samson et al., 2018), and areas to rest and regulate temperature (Cain et al., 2008; Russell A. Hill, 2006; Pochron, 2000). When these variables change, through seasonality, migrations, or other major natural or anthropogenic events, animals may rely on information acquired during

previous analogous situations to navigate and make decisions (Crystal & Wilson, 2015; Griffiths et al., 1999; Janson, 2016). Beyond environmental variables, the animal's mode of locomotion, navigational strategies, and knowledge of its environment also impact the animal's daily travel (Nathan et al., 2008). Animals may make movement decisions based on previously acquired knowledge about the environment, move randomly through their environment, or combine both strategies in order to meet their basic daily needs (Boyer & Walsh, 2010). Although it is generally accepted that many animals move non-randomly (Alavi et al., 2022; Janson & Byrne, 2007), understanding how they make movement decisions, and the limits of their spatial memory, remains key questions.

One oft-studied navigational strategy in animals involves the use of routes, or repeatedly used pathways (Di Fiore & Suarez, 2007). These routes often emerge because they are more efficient than most alternatives; that is, they minimize travel distance or travel time, require less energy both to physically traverse and to navigate, maximise the gain-to-cost or resource-to-travel ratio, or some combination of these metrics (Janson, 2000). For instance, chimpanzees use landscape features to mitigate movement costs, preferring to use human-made trails to travel, as well as ridge tops, both of which may be energetically more effective to travel on than through dense forest (Green, Boruff, & Grueter, 2020). Route-based navigation is generally associated with a topographic mental map, or a mental representation of space based on how specific landmarks are connected. Other types of mental maps, such as Euclidean maps, may contain, but don't rely on, route networks, given that the individual can mentally represent their entire space and should be able to navigate between two points, using prior knowledge of an object's location in space, whether or not they have done so before (Mueller & Fagan, 2008; Poucet, 1993).

In understanding how and why animals use habitual routes, various experimental and observational approaches have been used. Some species lend themselves well to the study of route-based navigation. Over smaller spatial scales, navigating individuals, such as insects, can be directly observed traversing over a fine-scale route repeatedly in experimental or natural conditions, either through following pheromones or using memorised landmarks (M. Collett, 2010; T. S. Collett et al., 2006; Sasaki et al., 2020). Larger animals that make annual migrations have also been shown to reuse habitual routes, with some ungulates (mule deer, *Odocoileus hemionus*) following the same route annually; within individuals, the routes they use strongly predict their survival rate, although the factors responsible for this trend are unknown (Sawyer, LeBeau, et al., 2019; Sawyer, Merkle, et al., 2019). Until relatively recently, fine-scale data collection of moderate-scale movements, e.g., an animal moving daily through its home range over an extended period, was difficult to collect, particularly in wild animals, due to constraints on biologger size, battery life, and memory capacity (Joo et al., 2022). However, as biologgers become a more accessible research tool for studies of wild animals, fine-scale longitudinal data sets have become increasingly common, allowing for more in-depth analysis of movement than through observation alone (Nathan et al., 2022).

In wild, group living animals, route-based navigation has been studied with a combination of observation and GPS devices. Both group-living animals such as elephants (*Loxodonta africana*) and solitary animals such as the lynx (*Lynx canadensis*) have been found to use routes to navigate within their territories (Presotto et al., 2019; Squires et al., 2013). However, few studies have looked at route fidelity, or the habitual reuse of routes over long periods, in populations where routes are not used continuously over time. In experimental studies in a natural environment, homing pigeons (*Columba livia*) were found to remain loyal to their own

navigation routes when released from the same site to navigate home multiple times, to return to these routes even when released off-route, and to partially remember their previous routes after a hiatus of 3-4 years (Biro et al., 2004; Collet et al., 2021). However, different pigeons released from the same site do not follow the same routes, suggesting that multiple alternative routes exist rather than there being one globally optimal one (Biro et al., 2004). These findings indicate that even animals with limited terrain constraints reuse routes, in these cases based on visual landmarks. Often in terrestrial or arboreal animals, routes are associated with stopping points in the form of a feeding patch, rest area or sleep site (Di Fiore, 2003; Hopkins, 2011; Porter & Garber, 2013). However, even without stopping to utilize a resource patch, pigeons may follow previously used paths because they are "tried and tested", i.e. known to lead safely to the correct end point, because of the high cognitive cost of computing a new path, or a combination of both, and this reasoning may be transferred to other animals that are more topographically constrained.

How routes are identified, to what extent a route network is mapped, and how reuse is defined varies between studies. A recent study of four arboreal animals in Barro-Colorado Island, Panama, proposed a route detection framework using machine learning to analyse path directedness, density, and directionality to identify routes. While the researchers detected routes in all four species studied, modelling showed that this analysis might not be suitable for coarser-resolution data, i.e., GPS fixes more than every 10 minutes (Alavi et al., 2022). However, other studies have similarly found routes with lower resolution data and by visual analysis (Bebko, 2021; De Guinea et al., 2019; de Raad, 2012; Di Fiore, 2003). Many such studies used manual recording or handheld GPS devices to track their subjects, and all visually identified routes by plotting each track and categorizing routes as paths with similar directionality that fall within a certain buffer, usually 10-50 metres.

Another more recently developed method of identifying route networks is line density analysis. This method allows researchers to effectively measure grid cells superimposed on the landscape, counting how often a grid cell is passed through, generally with the aid of spatial analyst software; however, it does not account for the direction in which the paths cross the cell (Alavi et al., 2022; Green, Boruff, & Grueter, 2020; Gregory et al., 2014).

Wild primates are exceptionally well suited for studies of movement, given their often-large daily ranges and ability to wear GPS collars. Among primates, multiple instances of route-based navigation have been found (Janson & Byrne, 2007). Arboreal primates in particular are frequently found to use routes, as their movement is limited by treetop "highways". Bearded saki (*Chiropotes sagulatus*) used ridge tops and slopes as travel routes, either to avoid canyon-preferring predators, to monitor fruit trees, or a combination of both (Gregory et al., 2014). Orangutans (*Pongo pygmaeus morio*) were found to use routes, with multiple individuals using the same route corridors near resources (Bebko, 2021). Similarly, spider monkeys (*Ateles belzebuth*) and woolly monkeys (*Lagothrix poeppigii*) not only used the same routes, but entered into a cycle where the routes they used became better arboreal travel routes as they dispersed seeds along them, allowing the routes to continue to be used in subsequent years (Di Fiore & Suarez, 2007). In a comparison of terrestrial chimpanzees (*Pan troglodytes verus*) and arboreal saddleback tamarins (*Leontocebus weddelli*), two primates that rely on fruit for a large portion of their diet, tamarins were found to use routes, but reuse only 14% of their total identified routes between study years, while chimpanzees' reuse of routes varied from 0-59% (Porter, 2021). Chimpanzees further used terrain features to their advantage, using higher ground to travel when approaching another group's area but not leaving it, allowing them to have a safer approach (Lemoine et al., 2023).

Amongst primates, considerable work has been done on the movement drivers of baboons (genus *Papio,* Coleman & Hill, 2014; Russel A. Hill et al., 2004; Marshall et al., 2013; Stelzner, 1988; Strandburg-Peshkin et al., 2015a), but less on their navigation strategies. In chacma baboons, *Papio ursinus*, evidence for out-of-sight memory was shown, as well as evidence of route-based navigation, based on observational data and GPS analysis of movement patterns (Noser & Byrne, 2007b, 2007a). A study of a different population also found evidence of a dense route network in chacma baboons, with enough routes to mimic Euclidean mental maps but lacking approaches to resources from all directions, implying topological mental mapping. Interestingly, this study also found similar travel patterns and equally dense route networks in both the core and periphery of the study troop's home range (de Raad & Hill, 2019).

Widely studied across sub-Saharan Africa, baboons are group-living generalist omnivores, able to occupy a wide range of habitats and ecological conditions (Altmann, 1974; Fuchs et al., 2018; Stone et al., 2013). While their range encompasses many areas of high seasonality, marked by periods of intense rain juxtaposed with drought throughout the year, baboons have shown a remarkable ability to adapt to water shortages, floods, and wide temperature ranges (Cheney & Seyfarth, 2007; Stone et al., 2013). However, there have been no studies on navigation in areas where these seasonal events disrupt their ranging patterns in such a way that they are forced to vacate an area for an extended period of time.

Here we present the first study of route preferences and route reuse in the baboons (*Papio ursinus griseipes*) of Gorongosa National Park, Mozambique (GNP). This unique study site presents an opportunity to study how seasonality affects ranging patterns, and whether or not baboons are able to remember and reuse routes in areas that are inaccessible or simply not used by them for part of the year. A mosaic habitat, GNP exhibits a defined rainy season and dry

season annually (Herrero et al., 2020; Stalmans & Beilfuss, 2008; Tinley, 1977). During the rainy season, GNP's central Lake Urema floods, inundating the floodplain, including a large portion of the road network. During the dry season, the lake and its rivers recede, turning from deep rivers to oxbow lakes to pans to dry riverbeds over the course of months. This causes a major shift in wildlife as animals are forced to move to higher ground, although they return to their normal areas as flooding recedes (Beardmore-Herd et al., in review; Walker et al., 2023). At the time of the study, GNP also had an unusually high density of baboon troops, but a low density of predators, following the effects of the Mozambique Civil War, which led to extensive poaching of all fauna in GNP, but especially carnivores (Bouley et al., 2018; Correia et al., 2017; Gaynor et al., 2020; Stalmans et al., 2018).

Two baboon troops ranging in the southern portion of GNP have been studied since 2017 and 2018, the first in this unique environment. The two troops, while having overlapping home ranges, exist in dramatically different environments. The Woodland Troop (WT) lives primarily in a woodland in the central part GNP's road network, navigating through dense vegetation, frequently resting on termite mounds and relying primarily on transient pans for water. The Floodplain Troop (FT) occupies the southern portion of GNP's alluvial floodplain for a portion of the year, sleeping most often in fever trees (*Vachellia xanthophloea*) and navigating on flat, open grassland with fewer roads but two major, seasonal rivers in their home range. For the other part of the year, seasonal flooding forces them into the southern half of their home range, where they occupy fever trees and *Vachellia robusta* woodland until they return annually to their floodplain range.

Using similar methods to previous studies of pigeon navigation to identify habitually used routes (e.g., Collet et al., 2021), and analysing data to quantify the extent to which seasonal changes

affect baboons ranging areas, we are able to evaluate the effects of a natural phenomenon to help understand whether baboon navigation strategies in a highly seasonal environment match those of other study sites, and whether baboons are able to retain memory of these habitual routes when they are unable to use them for more than two months at a time.

5.3 Methods

5.3.1 Study Site and Subjects

Data were collected in Gorongosa National Park, a 4,000km^2 park located in central Mozambique. GNP is home to a number of vertebrate and invertebrate taxa, including an exceptional density of baboons (Stalmans et al., 2018). The two troops in this study, FT and WT, ranged in the southern portion of GNP within the main road network.

This study utilized GPS collar data from four chacma baboons (*Papio ursinus griseipes*) from two study troops: Eve (FT), Abacaxi (FT), Acacia (WT) and Kigalia (WT).

At the time of study, FT had approximately 30 individuals, including all age classes. Their full home range was approximately 15 km^2, and their diet consisted mainly of underground corms from *Cyperaceae* sedges, grasses, and *Vachellia xanthophloea* and *Chrozophora plicata* seeds. They were also frequently observed hunting snails, river mussels, birds, infant warthogs and infant ungulates. The troop travelled approximately 3500m (± 1200m) daily (Chapter 2). FT ranged directly north of WT, with the southern portion of their home range overlapping the northernmost section of the WT home range. Their home range surrounded a large loop formed by two roads across the floodplain, and was bisected by the Mussicadzi River in the west and the Tsungue River in the east. Both rivers are seasonal, overflowing in the wet season and drying to puddles or dirt in the peak of the dry season. FT's habitats consisted of open flood plain made up

of grasses and sedges, dense elephant grass patches, riparian woodland along the Mussicadzi, and low-vegetation fever tree woodland. There was sparse *Vachellia* woodland in the southern portion of their home range.

WT consisted of over 90 individuals at the time of the study, of all ages. Their full home range was approximately 7 km^2, comprising moderate to dense *Vachellia-Combretum* savannah woodland, including areas of dense *Vachellia robusta*, numerous termite mounds, and two large, seasonal pans, as well as a small section of the Mussicadzi River utilized only during the dry period. They foraged on *Vachellia* seed pods, and engaged in bark stripping of *Vachellia robusta*, as well as eating numerous plant species in the woodland and occasionally hunting small vertebrates. This troop travelled approximately 2700m (± 700m) daily (Hammond et al., 2022).

At the time of the study, lions (*Panthera leo*) and painted wolves (*Lycaon pictus*) ranged within both troops' home ranges, but were not known to predate on baboons in GNP (Atkins et al., 2019; Bouley et al., 2018). One of the main predators of baboons, leopards, was not known to routinely inhabit GNP, but one was occasionally sighted by camera trap (Gaynor et al., 2020).

5.3.2 Collar Data

Individual baboons were captured either using a baited cage with a manual door release (n = 1), or through free darting from a vehicle (n = 3). Once sedated by a licensed veterinarian, the baboons were then fitted with collars (model 1D, e-obs Digital Telemetry, Grünwald, Germany) equipped with GPS and tri-axial accelerometers, placed in a shaded recovery cage, and observed until they had recovered enough to be released.

Collaring took place between 28 July 2019 and 16 August 2019, and spatial data were collected from 30 July, 2019 to 24 June, 2020. The days of active data collection varied across monkeys due to the timing of collar placement and the end of the collar's battery life (min = 232, max = 311, mean = 282). Collars were designed with a fabric strap connecting the ends of the collar, which would wear down over a period of at least two years and ideally after no more than four to five years, and were not intended to be retrieved.

5.3.3 GPS Data Cleaning

Data were cleaned and processed in R version 1.3.159 and QGIS 3.14.10-Pi (QGIS Development Team, 2020; R Core Team, 2020)

All four GPS units were programmed to sample baboon location once a second for five seconds every 15 minutes (i.e., a burst of up to 10 fixes at 1Hz at 15-minute intervals). GPS data were downloaded from the collars monthly from August 2019-November 2019, then again in February 2020, May 2020, and June 2020, using the e-obs BaseStation II connected to a Yagiantenna (868 MHz 10E), at a distance of between 10-50m. Downloaded data were then processed using e-obs decoder_v10s1.

During analysis to identify oft-used paths in the environment, only the final fix out of each 10-second burst was used from each collar. First, points were filtered to only days with a 95% or above fix success rate; that is, of 96 scheduled fixes in a day, at least 90 must have been successful. These points were then filtered to remove any points within 50m of the sleep site used at the start or end of the day, in order to minimize bias from being close to the site as well as the monkeys staying in the same place for extended periods.

5.3.4 Daily Route Use Over Extended Periods

To compare route similarity on a daily level across the study period, each day-long trajectory, from departing the morning sleep site to entering the evening sleep site, was isolated. We created a "dissimilarity score" between pairs of days, which represented the average nearest neighbour distance between two daily trajectories. A higher dissimilarity score indicates the daily routes were on average further apart.

The analysis compared pairs of days, with one daily trajectory assigned as the reference day, and the other as the comparison day. The distance between each GPS point in the reference day was measured to each point in the comparison day to create a list of distances. The smallest of these distances, or the nearest neighbour distance, was taken for each point in the reference day. The average of the nearest neighbour distances was taken twice for each pair, with each daily trajectory respectively being the comparison and reference day. The average of these two averages was taken as the dissimilarity distance for that pair of days.

5.3.5 Identification of High-Use Paths

To identify routes that were reused by the baboons, points were compared using a rolling-window approach.

After data cleaning, each of the remaining points were grouped into rolling groups of four sequential points ("tracklets"), with the first point of the group (r_1) being the reference point and the next three points being the rest of the reference track (r_2, r_3, r_4). The tracklet was evaluated to ensure that (a) the fixes occurred consecutively at 15-minute intervals, i.e., no fixes were missed, and (b) each point was at least 50m distance from the previous point, to ensure the baboons were moving at the time of the fix as opposed to stationary.

If the tracklet met the criteria of both (a) and (b), then it was considered a valid *reference tracklet*. This was repeated for all possible consecutive sets of four points, resulting in a set of multiple temporally overlapping tracklets. Once all valid reference tracks were identified, they were also considered to be valid *comparison tracklets*.

Each reference tracklet was converted from a set of four points to a line feature, assuming straight line travel between each consecutive point. The distance between this line and the first point of each comparison tracklet (c_1) was then measured. If c_1 was greater than 50m away from the reference tracklet, then no further comparison was made between the two features. If c_1 was within 50m of the reference tracklet, then the same comparison was made for all points in the comparison tracklet. In order for the comparison tracklet (*c)* to count as a reuse of the reference tracklet (*r*), it had to meet a number of conditions: (1) all points in *c* must fall within 50m of the *r*; (2) *r* must not be made up of points from *c*, i.e., be the same tracklet; (3) *r* and *c* must have been travelled at least 30 minutes apart, or with a difference of two GPS fixes; (4) *c* must not have been travelled within 30 minutes of another comparison tracklet that already reused *r* (Figure 5.1).

If a comparison tracklet met all four conditions, it was considered a reuse of the reference tracklet. To account for differences in speed of travel, each comparison tracklet was also analysed as a reference tracklet, although reuse was only counted once for each pair. Despite the conditions imposed, preliminary analysis showed a high margin of error in identifying tracks that were only reused two times, as in other studies (de Raad, 2012; Di Fiore, 2003), due to the fact that this analysis does not explicitly account for the linearity and directionality of each tracklet. To mitigate this, only routes in the top quartile of all reuses were considered reused routes for

this analysis, given that the more times a route was reused the less likely it was to be a false match, based on visual analysis.

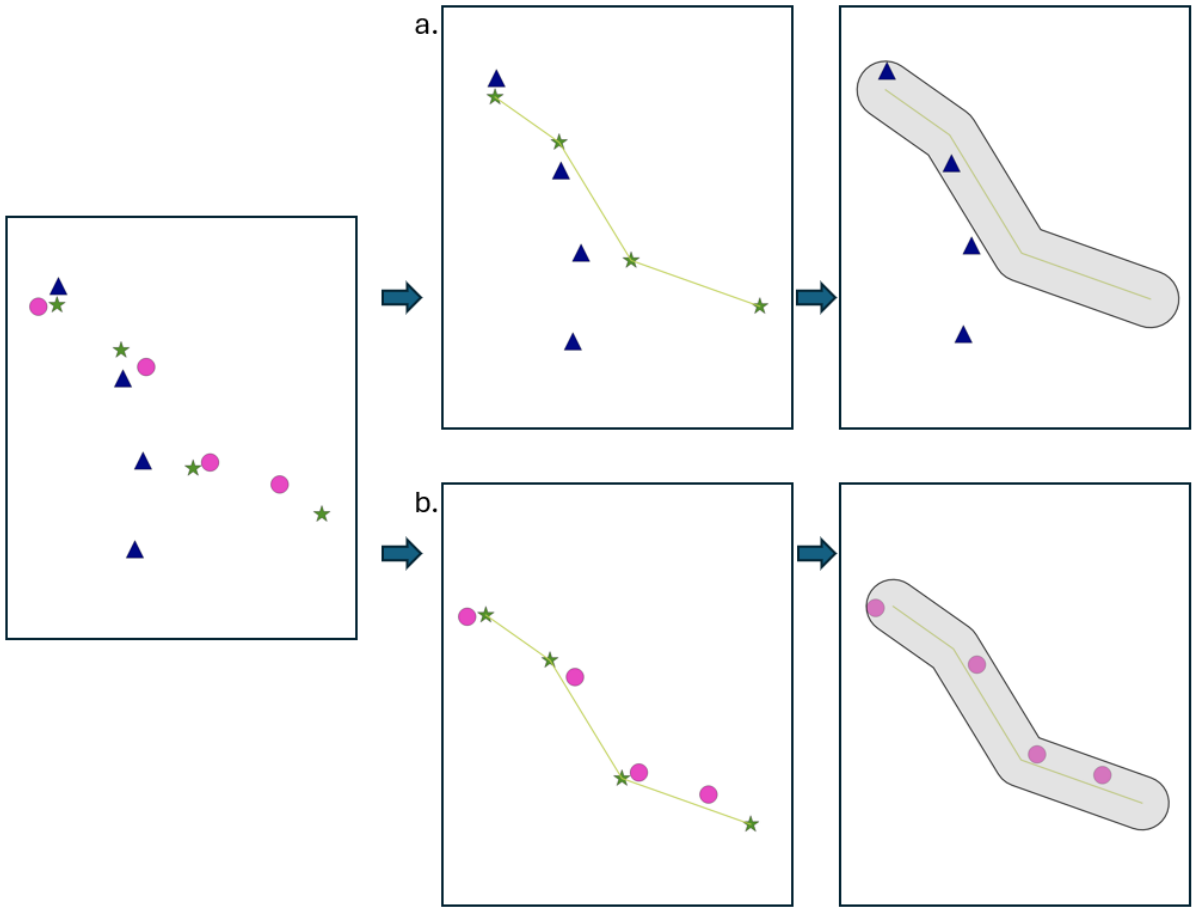

Figure 5.1 Method of identifying reused routes. Each route started by identifying tracklets, shown in the first panel. (a) identifies a reference tracklet, converts it into a line, and adds a buffer; because all points of the comparison tracklet (triangles) do not fall within the buffer, this is not a valid reuse. (b) follows the same methods, but shows an example of a valid "reuse".

5.3.6 Route Re-use Following Displacement

In order to identify periods and areas of displacement, full GPS data for each monkey was plotted and visually examined both weekly and monthly. Areas that were identified as being vacated for more than two months (vacation period), and subsequently reoccupied, were considered vacated areas (Figure 5.2).

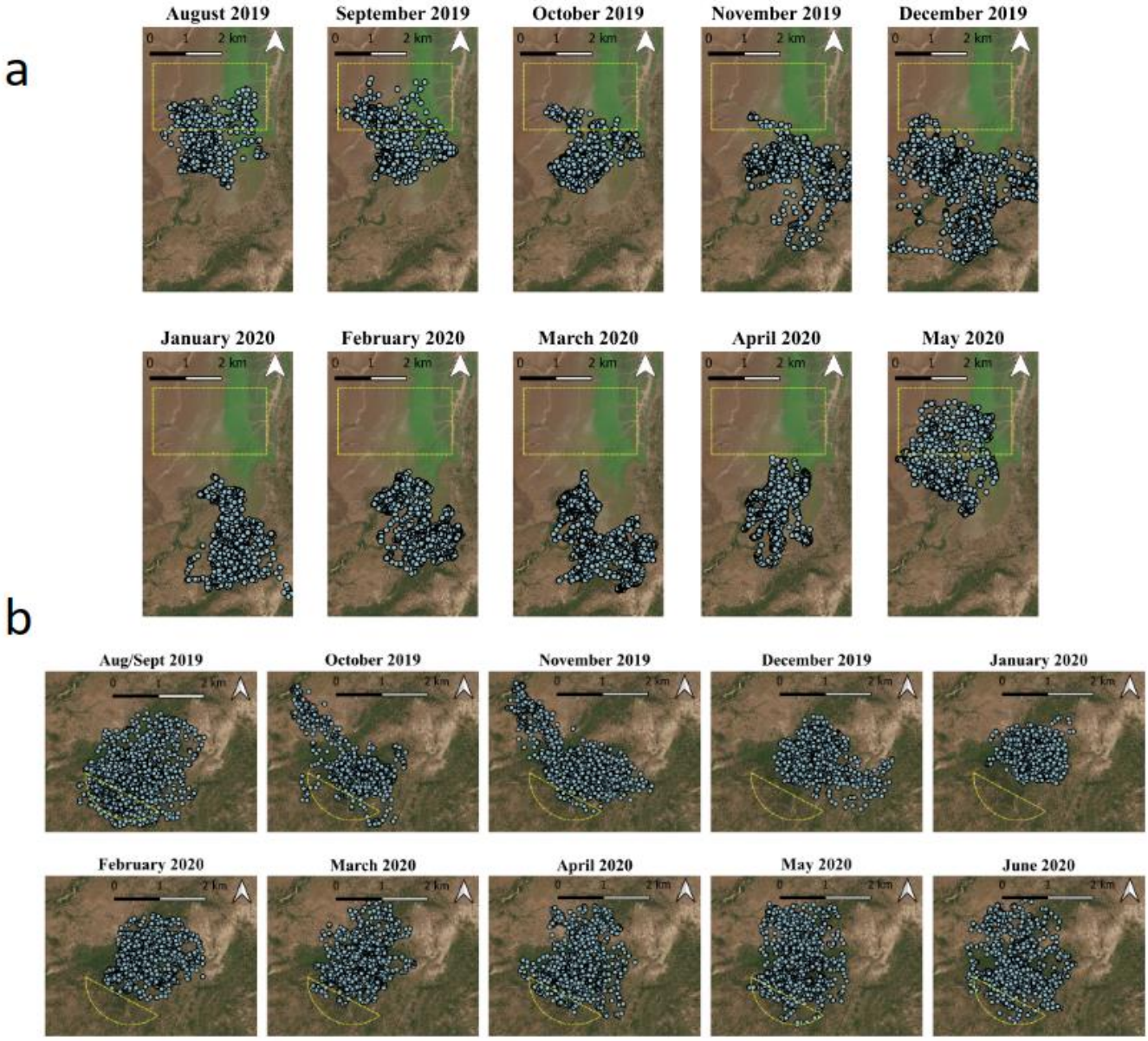

Figure 5.2 Monthly mapping of daily ranging data for FT (a) and WT (b). Identified vacated areas are shown in yellow. For analysis, these were transformed to match the edge of the home range.

To analyse whether routes were reused in vacated areas, all identified routes that were majority inside the vacated areas (3/4 fixes) were isolated in QGIS (QGIS Development Team, 2020). The isolated routes and all records of their reuse were then compared to see if they were used both before and after the area was vacated.

5.4 Ethics Statement

This work was carried out with ethical clearance from Oxford University (APA/1/5/ACER/23Jan2018) and from the Ministry of Tourism and the Gorongosa Restoration Project in Mozambique (permit numbers PNG/DSCi/C114/2018, PNG/DSCi/C93/2018, PNG/DSCi/C147/2019 and PNG/DSCi/C142/2019). All handling of the study subjects was performed by professional staff, and following collar deployment all subsequent data collection was completed remotely and in the animals' natural habitat.

5.5 Results

5.5.1 Similarity of Daily Routes

When comparing route dissimilarity over time, we found that the two troops showed different patterns consistent with the known patterns of flooding in GNP. WT remained almost consistently dissimilar throughout the study period, particularly for days that were more than two weeks apart; that is, there was little variation in how different their daily paths were, despite visual differences in their ranging patterns, implying that the majority of their movement occurred in the core of their home range (in this case defined as the central 50% of the total area around the centroid) throughout the year, and that changes to the periphery of their home range seasonally (Figure 5.2) did not strongly affect route dissimilarity.

However, FT was cyclically dissimilar. In pairs of days that were temporally close together (<50 days), or very far apart (>250 days), their daily paths were more similar. In other pairs, pairs became more and more dissimilar until about 125 days apart, when they began gradually becoming more similar. This follows the pattern of displacement throughout the year, with periods before and after displacement due to flooding being more similar than the periods during

and not during the flooding, indicating that the baboons had smaller ranging areas at the periphery of their home ranges that they used seasonally, rather than a central core as in WT (Figure 5.3).

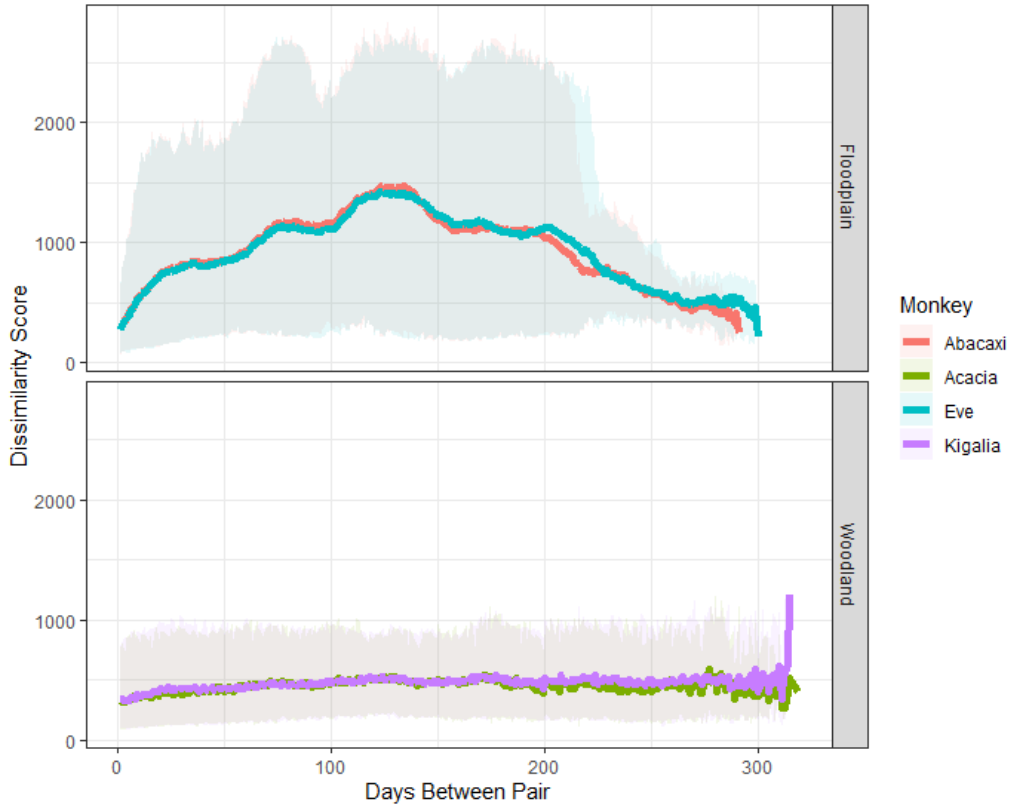

Figure 5.3 Dissimilarity scores, indicative of average metres between compared daily routes, between baboon daily tracks across the year. The y-axis indicates how dissimilar each pair of days was, while the x-axis indicates how many days occurred between each pair. The more dissimilar the scores are, the further apart two days' daily tracks were.

5.5.2 Occurrence of Route Reuse

For each collar, between 378-1137 tracklets were identified. From these, between 69-179 tracklets were found to have been reused more than the upper quartile, which ranged from 4-8 reuses. Tracklets that were reused more than the upper quartile are hereafter simply referred to as "routes."

The most any route was reused was 30 times, with the average length of the route ranging from 631-836 metres. Further information can be found in Table 5.1 and the route networks are visualised in Figure 5.4

Table 5.1 Summary of analysable tracklets, or sequence of four points meeting defined criteria, and routes, or tracklets used more times than the upper quartile for that individual.

	Eve	***Abacaxi***	***Acacia***	***Kigalia***
Tracklets	919	967	378	1137
Routes	81	90	69	179
Average length of route (metres)	836	818	631	672
Max Reuses	22	30	11	14
Min Reuses	8	7	4	5
Max days between reuse	289	270	280	277

5.5.3 Route Reuse in Vacated Areas

Vacated areas were identified on the periphery of each group's home range. WT occupied the same core home range for the entirety of the year, while only the peripheries were vacated for extended periods. FT displayed similar patterns; however, one area near the centre of their home range was vacated for a four-week period at the peak of flooding. Because it was vacated for less than the two-month displacement chosen to test memory and route robustness, route reuse in this area was not directly examined.

In WT, only one route occurred partially inside the vacated area, despite multiple tracklets. This route began close to the core home range, and was only used over a period from the end of September to early January when there was no vacation of the area, and so was not included in any further analysis.

In FT, several routes occurred within the vacated area. However, these routes were only used for a portion of the year from October to November, despite the troop ranging in the vacated area outside of these months. Only one route from after the displacement period occurred partially within the vacated area, and as the majority occurred outside of the area, we were unable to analyse route reuse in FT's vacated area (Figure 5.4).

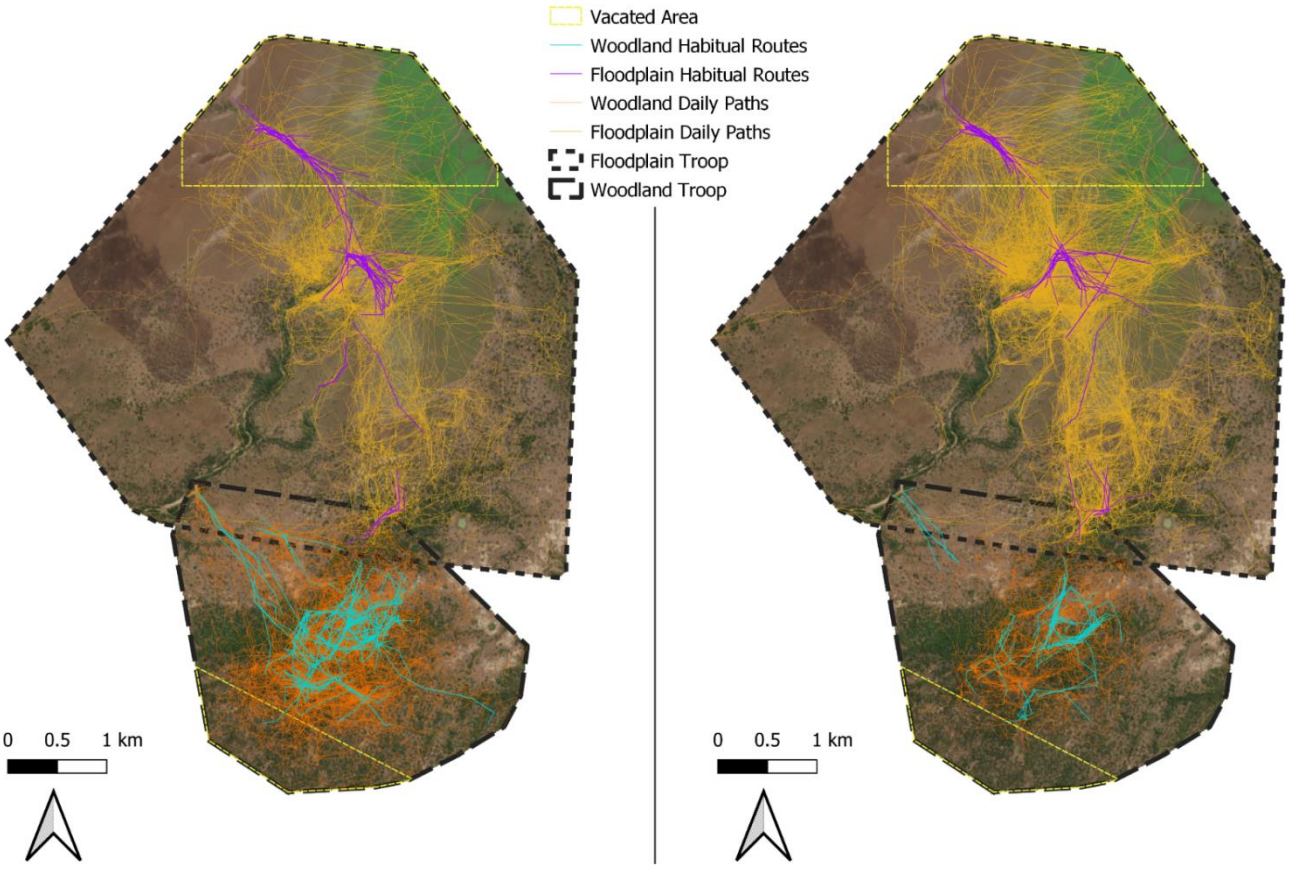

Figure 5.4 Baboon home ranges with full daily paths (yellow for FT and orange for WT) as well as identified routes (purple and blue, respectively).The map on the left shows the routes of Eve (FT) and Kigalia (WT) while the map on the right shows the routes of Abacaxi (FT) and Acacia (WT).

5.6 Discussion

Besides the Okavango Delta, where baboons have adapted to cope with the annual flooding by wading and swimming between islands (Cheney & Seyfarth, 2007), GNP is the only baboon

study site that faces extensive annual flooding. Unlike the Okavango, baboons in GNP are rarely seen to enter the water, and as a result must take considerable measures in order to cross rivers and streams, such as jumping from treetop to treetop or crossing on sandbanks by sunning crocodiles. In this study, we examined to what extent this seasonal disruption affects baboons' daily ranging areas, whether or not they have habitually used routes despite these disruptions, and whether or not those routes are robust to disruptions, i.e. whether baboons return to previously established routes after areas of their home range are vacated seasonally.

We found that the two troops showed different levels of annual variation, or dissimilarity, in their daily movement routes. High dissimilarity could indicate a complete displacement where the baboons (and hence their routes) are in two physically different locations, or it could indicate high variability where baboons move through the same environment but follow very different paths. Previous analysis showed that WT experienced a general shrinking of their home range during the wet season, while FT shifted south; however, both troops maintained a core home range for most of the year (Chapter 2), although this area was simply the area where FT's wet season and dry season home range overlapped, was entirely inaccessible for FT for four weeks of the year at the height of flooding.

Given this, it is unsurprising that WT maintained a stable dissimilarity score across the year, as they maintained the same core home range and variation on the peripheries occurred only for relatively short time periods. However, despite continuously occupying a core home range, FT's dissimilarity showed variation across the year, with days in opposite seasons being more dissimilar than days close together or in the same season almost a year apart. In addition, even days close together showed more dissimilarity than the same pairs of days in WT. This indicates that they may have used the periphery of their home range more than WT, and at different parts

of the year.

This difference between troops could be related to a number of factors. First, FT relies seasonally on various food sources that each exhibit a different growth cycle, often spending entire days utilizing a single resource patch, and travelling further than WT on days where they utilize multiple resource patches (Chapter 3), implying more scarce or transient resource patches that require longer travel distances to exploit. FT also utilizes more spread-out, low-density food types than WT, and are one of the smallest troops in their area (LLB, unpublished data). These long travel distances between seasonal patches, and a high potential for displacement from patches due to intergroup encounters, could cause more route dissimilarity even between days close together in time.

In addition, habitat type could alter route similarity. We found that Kigalia (WT) exhibited a higher number of reused routes, but a lower number of reuses per route compared to FT. Acacia (WT) also had a low habitual-route-number-to-reuse ratio; however, Acacia's collar often failed to record GPS fixes, giving less overall analysable movement data than any other monkey. Nevertheless, this indicates that WT has a larger, dense route network, with each route being used less often, while the FT baboons exhibit a smaller route network that is used more frequently. This is supported by visual examination of the data (Figure 5.4). In an earlier study, baboons in a mosaic habitat that primarily foraged in woodland areas in Limpopo, South Africa, displayed a similarly dense route network to WT, extending to the edges of their home range and remaining dense even in the periphery (de Raad & Hill, 2019). The similarity in habitat type may indicate that baboons are topographically constrained in woodland areas, where tree and undergrowth density create significant energetic barriers, and repeated routes could carve paths that are easier to travel, as shown in arboreal primates (Di Fiore, 2003). Observational data

collected on these troops in 2018 indicated this pattern was similar to the paths of WT, and FT in denser areas, but not in open floodplain areas. Other inhabitants of the woodland of GNP, such as elephants and antelope, may similarly contribute to a more easily traversable route network. In addition, baboons in densely treed areas may be exhibiting patch to patch travel networks, utilizing discrete food items as in a trapline, but using the dense route network to travel between food patches in different orders as depletion and seasonality vary (Noser & Byrne, 2009, 2015). One of the denser parts of the route network in WT's peripheral home range led to the Mussicadzi river; similar tracks were also recorded by handheld GPS in 2018, when baboons had to travel daily to the one remaining water source in their home range, indicating that this resource also led to the formation of a habitual route.

On the other hand, baboons ranging in open areas may not need to utilize routes so frequently. The main topographic barriers in FT are the Mussicadzi River to the east, the Tsungue river to the west and north, and a large, dense patch of elephant grass in the core of the home range, in which lions, buffalo, and elephants are frequently sighted. Interestingly, the most central part of FT's route reuse network occurs in the area that traverses the edge of the elephant grass through a patch of palm trees where the baboons often rest. Travel through this area mimics travel through the woodland in terms of low visibility and difficult terrain. The second densest part of their habitual route network extends to the northeast, following the Mussicadzi river seasonally when large swaths of *Chrozophora plicata*, a preferred food source for FT baboons, grows in the drying riverbed. These observations indicate that topographic barriers may promote route reuse rather than routes being a preferred form of navigation, and that baboons may not use routes when they are able to easily visually orient themselves, or that these routes are more general orientations based on landmarks rather than distinct movements along a 50-metre-wide path.

These observations were furthered by on-the-ground troop follows of FT, where baboons could predictably disappear into dense grasses at the same location daily, and be expected to appear on the other side at a known location after crossing. A single attempt to cross the dense grass showed that there was in fact a narrow path leading from the entrance to the exit, crossing a patch of palm trees where the baboons foraged, and that buffalo also used this path. Further studies should incorporate both linearity of routes and vector angles from one point to another, rather than relying on fixed width, to better identify more spread-out routes in open habitats.

Despite finding route reuse in line with other study sites, this study failed to identify route reuse in vacated areas, primarily due to the lack of routes in these areas. This is may not be reflective of a true lack of routes, however. The baboons used the peripheries of their home ranges less often, and the edges of their home ranges changed seasonally, meaning there were less overall tracklets in these areas. Further, because the data did not cover a full year, seasonal resources that might have led to the formation of routes in these areas may not have been available at both ends of the study period. This, combined with the relatively high number of reuses we used as the criterion for classifying routes as "habitually" used, may indicate that it is a lack of data limiting the identification of routes reused after vacation, rather than a lack of those routes themselves. What effect varying this strict threshold has on the nature and density of baboon route networks identified should be revisited in future studies.

Nonetheless, this study did find that baboons returned to vacated areas, and FT did have some routes in those areas. Because of battery failure, the GPS points from this study do not cover an entire year. Future work should look at routes over a full calendar year or multiple years as a better indication of the role memory plays in repetition of routes. In addition, factors besides flooding that cause vacations from areas should be considered in future studies. Temperatures on

the Floodplain consistently reach above 40C, which might influence the baboons' ability to travel to the vacated area in their home range (Chapter 2); in 2020, temperatures reached 50C on the floodplain (SC, unpublished data). However, observational data from 2018 showed baboons repeatedly crossing the floodplain in high temperatures due to the need for water that was only available in the northwestern section of their home range (Lewis-Bevan, Biro, et al., 2019), showing that a balance between shade, food and water availability might drive route use. Replications of this study over multiple years would help to further identify factors causing route reuse.

Another limitation of this study is the resolution of the GPS points taken. Our positional fixes were taken at 15-min intervals, and we interpolated the routes connecting these locations as straight lines - this represents an overall route estimate that is almost certainly shorter and less tortuous than the actual paths taken by the baboons. In the future, more frequent GPS fixes would allow for higher-resolution reconstructions of routes, and hence for a more robust nearest neighbour analysis both at the daily-route level and at the tracklet-level. While this would come at the expense of battery life, we expect that technological advances in biologging will soon enable researchers to collect the necessary long-term datasets at sufficient resolution to explore our questions with added precision.

Despite its drawbacks, this study presents a tractable analysis of route reuse that is both faster and more replicable than visual examination, but does not necessarily require high-resolution data. Further improvements on this method should involve accounting for the angle of travel in each point in the tracklet, similar to change-point analysis (Byrne et al., 2009), and a measure of the parallelism of both the reference and corresponding tracks. This study provides methodology to help understand how baboons navigate in a changing environment, and will hopefully be

followed up by further studies monitoring baboon movement, environmental knowledge and memory in a rapidly changing world.

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6

Chapter 6: Discussion

CONTENTS

6.1 Introduction

The goal of this thesis was to contribute to our understanding of some of the key questions that Nathan et al. (2008) proposed in their attempt to unify movement studies: how, when, where and why animals move. Although these questions have been asked in baboon studies before, this thesis combines new or updated methods with a novel study site and population. This thesis presents the first work on baboons in a low-predator, high-seasonality environment, and creates a baseline knowledge of Gorongosa's baboon population that can be built on in the years to come. In this conclusion, I synthesise the findings of each of my empirical chapters, outline some of the limitations of the research, and discuss opportunities for future work.

6.2 Situating the Results in the Wider Literature

In Chapter 2, I introduced the Gorongosa National Park (GNP) ecosystem and established that baboon troops living in different habitats of GNP have different predictors of movement. The monkeys' seasonal home range sizes varied, with the FT having a larger dry season home range than wet season range, and with the WT having the opposite effect. Both troops overlapped home ranges with multiple other troops, and with each other for parts of the year. This overlap increased in the wet season home range and decreased in the dry season, demonstrating the pressure placed on space for baboons in GNP during flooding. Monkeys within the same troop could be side by side or almost two kilometres apart, demonstrating the large group spread that may have implications for decision making in these groups (Farine et al., 2016), and the difference in troop size (~30 vs >90 individuals) showcased the large variation in baboon troop size within GNP.

The results of this chapter showed that predictors of movement in baboon troops can vary not only amongst troops, but also amongst individuals of the same troop. Although the sample size was relatively limited with only four subjects, the results between monkeys were significantly different, with some individuals preferring open or low vegetation while others preferred more covered habitats. It has been shown that baboons democratically decide where to travel (Strandburg-Peshkin et al., 2017a), but that nearby monkeys, presumably social affiliates, as well as position in the group help decide the individual path taken (Farine et al., 2016, 2017). While the much lower-resolution GPS data used in this thesis did not allow for a similar analysis, direct observation of both troops showed that individuals formed subgroups, which often split apart and reunited at a later destination, consistent with the results of both my Chapter 2 and the studies of olive baboons in Mpala Research Centre, Kenya, and previous studies, supporting the notion that these movement mechanisms are generalizable to the *Papio* clade.

The reasons why the baboons may choose to take different routes to arrive at the same location vary. Baboons are very socially stratified and have a stable dominance hierarchy (J. Altmann, 1980; Cheney & Seyfarth, 2007), and so lower ranking individuals may have to take routes that increase their calorie intake through opportunistic foraging or avoid competition with more dominant individuals (Lihoreau et al., 2011; Marshall et al., 2013). Some individuals may have preferences for certain resources, causing them to go out of their way to use those resources, as shown in other wild and captive primates (Bonnie et al., 2019; Huskisson et al., 2021; Masi et al., 2009).

While it is to be expected that baboons of the Woodland Troop spend more time under tree cover, given their home range has very little open space, the Floodplain Troop's preference for tree cover is indicative of other drivers. Preference for more cover could stem from the need for

shade (R. Hill & Dunbar, 2002; Russell A. Hill, 2006; but see Stelzner, 1988), access to the water that is generally found by the trees (Mitchell et al., 2009; Paietta et al., 2022), access to preferred food resources such as *Vachellia xanthophloea* (fever trees), or to be able to better access refuge from predators (R. Hill & Weingrell, 2007; Russel A Hill & Cowlishaw, 2009). Gorongosa, during the time of this study, provided a unique opportunity to study step selection in the context of high seasonality, high conspecific density, and relatively low predation risk. Previous step selection or habitat selection studies in baboons have occurred over a much smaller time scale (Strandburg-Peshkin et al., 2017a), in human-modified environments (Hoffman & O'Riain, 2011; Taylor et al., 2016) or in areas of relatively high predation risk (Cowlishaw, 1997). While Cowlishaw (1997) found that baboons' movement was more predicted by risk than by availability in the environment and foraging opportunity, the similarities in Gorongosa, with a preference for trees and more covered areas despite low availability in the environment, indicate that perceived predation risk may also play a part in movement even without an acute predation risk.

Further, sleep sites have previously been found as a predictor of baboon movement (Barton et al., 1992; Strandburg-Peshkin et al., 2017a), as has distance to water (Barton et al., 1992). These similarities help confirm overarching drivers of baboon movement, regardless of habitat type and predation risk. However, while Barton et al. (1992) found no correlation between "greenness" -- in my study measured by NDVI -- and baboon habitat selection. This contrasts with my results, which show that a higher NDVI is associated with more frequent use for WT in both seasons, and FT only in the wet season. Barton et al. (1992) studied baboons in dry woodland and wooded grassland, along with rocky outcrops; in Gorongosa, the WT ranged in dense woodland while FT was primarily in open grass or fever trees, with no rocky areas and little bare ground. The

differences in the overall habitat structure between sites may contribute to the different results, given that the predictors are relative to the total available variation in the environment. Thus, this thesis further establishes the role of water and sleep site availability in the overall ranging patterns of baboons in various habitat types, but showed that further insight into the correlation between NDVI, habitat type, and food availability is needed.

Alongside predictors of movement, this research shows that how these baboons travel and where they end up is affected at the individual as well as group level. Despite largely overlapping predictors of movement shown within troops in Chapter 2, Chapter 3 showed that baboons take different paths, and even stop at different resources within the same day than their troop mates. These results emphasize the democracy of democratic decision making, wherein each individual in a group has the ability to influence the overall decision of the troop (A. J. King & Sueur, 2011). Given the large group spread in Chapter 2, it is unsurprising that the baboons may occasionally fission, taking different routes and stopping at different resources before reuniting at or near the sleep site.

Within their individual routes, the baboons took shorter paths between resources compared to the nearest neighbour heuristic, and on occasion took the most optimal route between resources. While visibility on the floodplain is often more than a kilometre for humans, making an average distance of 90m spread (Chapter 2) potentially negligible in terms of group cohesion for baboons, visibility in the dense woodland is much more restricted, making it harder to follow troop mates, especially when the average distance between the two collared monkeys was around 220m. Conversely, the high visibility on the floodplain increases the risk of predation, which may lead to compromise on the part of troop members to reap the benefit of dilution in a group (Stueckle & Zinner, 2008). Although group-living often comes with the benefit of collective

memory, where animals should be able to find the correct or optimal path from the combined knowledge of troop members, there are also consensus costs, wherein the most optimal route may not be the route that most benefits those with the highest influence (Couzin et al., 2002; King et al., 2008). Further study is therefore needed to disentangle the relationship between habitat and route efficiency, in particular through incorporating the role of social influences on movement.

Despite the further spread and potential difficulty in following group mates, likely leading to dilution of collective memory, WT had a slightly higher proportion of optimal routes used than FT. This may reflect the habitat structure, where certain routes become ingrained by being used over and over due to physical constraints, e.g., dense undergrowth, creating a route network, it may also reflect the lower variation in seasonal home range in WT (Chapter 5). While the use of topological maps in baboons is well-studied (de Raad & Hill, 2019; Noser & Byrne, 2007a), it is also shown that some route networks are dense enough to mimic Euclidean maps (de Raad, 2012). Chapter 5 shows that WT have more widespread repeatedly used routes, which may increase optimal movement between resources.

In addition to demonstrating differences in route efficiency between troops, this study shows that the routes used by baboons are not simply based on what resource happens to be closest at any given time, but that baboons show some level of planning in order to travel more efficient routes. Although the use of hierarchical clustering has previously been applied in primate studies to identify resources or "hotspots" (de Raad, 2012), this thesis demonstrates a way to study route optimization in an observational context using such resource patches. Previous studies of the Travelling Salesman Problem in primates either occurred in a captive setting or using high-value provisioned food in "arenas" set up in wild primate ranging areas (Cramer & Gallistel, 1997;

Menzel, 1973; Teichroeb, 2015). By combining hotspot analysis with this problem, I show that optimization studies can be done without provisioning and in a natural setting.

Part of each route evaluated in Chapter 3 was the sleep site for the beginning and end of the day. Given that sleep sites impact overnight thermoregulation, predation risk, and potentially access to resources, they should play a relatively large role in movement planning (José-Domínguez et al., 2015; Svensson et al., 2018; Teichroeb et al., 2012). In Chapter 4, I showed that GNP baboons preferred to sleep closer to the centre of the home range, and travelled significantly less distance from their last resource of the day to the sleep site compared to the first resource of the next day, showing much less sleep site reuse than is seen in Mpala but in line with the baboons of Amboseli (Loftus, 2022; Markham et al., 2016). The short distance travelled at the end of the day implies some level of planning of their end-of-day route and is in line with the results of Chapter 2, which showed that baboons are more likely to travel towards their sleep site than away from it. However, multiple sleep sites in both troops were only used 1-2 times across the entire study period. Sleep sites were clustered fairly close together, and without ground truthing I was unable to determine the exact extent of a single sleep site. From personal observation, sleep sites were rarely a distinct cluster of trees, and further observation is needed to fully define where one sleep site ends, and another begins. Nevertheless, it is possible that the close proximity of sleep sites meant that baboons could aim for an area with a high density of sleep sites, rather than a specific site.

This proximity was further shown in comparison to the baboons of Amboseli; in Gorongosa, movement between sleep sites was relatively low compared to the findings of (Markham et al., 2016). That study showed movement of 500 metres during the majority of the time between consecutive sleep sites across five troops, while the average of the two Gorongosa troops was

300 metres, with high variability (Table 4.1) This variability may indicate that sleep site selection is not tied to a specific seasonal resource, but rather day to day factors such as intergroup competition or predation risk.

Further, the baboons in both troops reused sleep sites that were restricted to them during the wet season, when their home ranges either shrank or changed altogether. This could be indicative of a number of factors. First, it shows that baboons remember sleep sites over long periods, or are able to reidentify them; the longest absence from a sleep site for each monkey ranged from 171 days to 277 days, showing that even less preferred sleep sites are reused after and over long periods. This might also indicate a low availability of preferred sleep sites in the environment, particularly in the dry season, when the total number of unique sleep sites was lower for both groups, causing overall higher rates of reuse.

The reuse of sleep sites also likely contributed to the results of Chapter 5, where I showed that the study subjects had habitually used routes through their environment, consistent with the baboons at other field sites, despite the seasonal displacement they undergo (de Raad, 2012; de Raad & Hill, 2019; Noser & Byrne, 2007b). This study is the first in baboons to utilize the nearest neighbour technique of analysing route reuse over full days of travel. While this gave similar results to a line density analysis conducted on the same data (unpublished analysis), it was able to identify more routes and was less prone to identifying routes that were in fact high-traffic resources, or a criss-cross of paths. The use of routes is in line with other studies on baboons (Byrne et al., 2009; de Raad & Hill, 2019; Noser & Byrne, 2007a); however, due to the parameters placed on defining a route, a full route network was not identified, limiting my ability to draw comparisons with de Raad & Hill (2019), who found a dense route network in the periphery of the home range. Ground truthing, alongside remote sensing analysis similar to

Chapter 2, should be used in future work to identify if any features predict the use of routes in these baboons, and whether a full route network with wider parameters would show evidence of route reuse in vacated areas.

6.3 Context and Limitations

This thesis showed that the baboons of GNP use repeated routes, and that their daily paths are more efficient than random movement or the simple nearest neighbour heuristic. As in other study sites, they prefer to move towards their sleep site and in more covered areas. Thus, based on the results of this thesis, the question of where baboons move can be predicted by a combination of habitat type, their known route network between resources, and the location of their sleep sites. However, I was unable to collect or analyse many potentially influential variables that might further this research, due to logistical constraints.

The initial aim of my research was to examine dominance, hormones, and leadership in a group of previously unhabituated baboons. The 2018 field season was intended to habituate two baboon troops, collect behavioural and dominance data, and preliminary movement data before collars were placed (Hammond et al., 2022). However, at the end of the 2018 season, early onset of the annual floods meant a shorter than expected field season. Lack of accessibility from Cyclone Idai and increasing political instability, leading to multiple attacks around GNP, cut short the 2019 field season at both ends and prevented the export or on-site analysis of faecal samples. Due to the COVID-19 pandemic, I was unable to return to the field in 2020; therefore, I was unable to collect sufficient behavioural data on FT, while WT was largely unobserved outside of collaring in 2019. While the collars used were equipped with accelerometers, insufficient data collection due to failures meant that there was not enough longitudinal data to compare behaviours between the four monkeys across the study period through accelerometer data, as proposed and used in

other studies (Soltis et al., 2016). All these factors meant that I was unable to answer the questions I had originally set out to address, and that I lacked sufficient comparative behavioural and observational data for a full analysis of how movement and behaviour are linked. However, there are comparisons that can be made from the 2018 field season to the data presented.

As in 2019, the 2018 field season showed water sources played a significant role in baboon movement in both troops. Unlike 2019, the dry season of 2018 was significantly drier, with the pans in WT and the southern part of the Mussicadzi drying around October, while the Mussicadzi did not dry during the 2019 season, and the pans in WT's home range remained drinkable until November due to the effects of Cyclone Idai. This led to both troops walking significant distances to access water daily. Additionally, the seed pods on the *Vachellia* trees were not as abundant on the floodplain, and so the FT spend much more time in the open floodplain, not only crossing to access water from the Tsungue but also eating the underground sedges and corms, often in the heat of the day (Lewis-Bevan, Biro, et al., 2019). Handheld GPS data from FT shows them ranging further north and east in 2018 compared to 2019, spending more time near the Tsungue and less time in the fever tree woodland (Figure 6.1).

Also during this study, the lion population of GNP grew, and painted wolves were released (Atkins et al., 2019; Bouley et al., 2018). Although no predation attempts were recorded during the study period, and painted wolves are not considered predators of baboons (but see Dyer, 2018), the baboons showed marked vigilance towards them, including barking, "wahooing", posturing, and climbing trees. When predators were encountered on the open floodplain, however (usually as a lone lioness), they moved away, and remained on the floodplain and away from trees as long as the predators were a sufficient distance, showing a less marked response to lions than observed in other field sites (Cheney & Seyfarth, 2007).

These comparisons indicate that water and food may be the main drivers of movement of baboons in a low-predator environment. However, as predator populations continue to increase in GNP, and the baboons have more encounters with predators, vigilance and reaction to predators should increase in response to the changing landscape of fear, which in turn should affect movement decisions. The impacts of this are inevitable, with leopards and hyenas since having been released into GNP (in 2021 and 2023 respectively). While there are GPS trackers placed on a number of predators within GNP, the majority of encounters with lions while following the baboons were with uncollared lions, while wild dogs rarely ventured into the study troops' home ranges, limiting my ability to account for predator density.

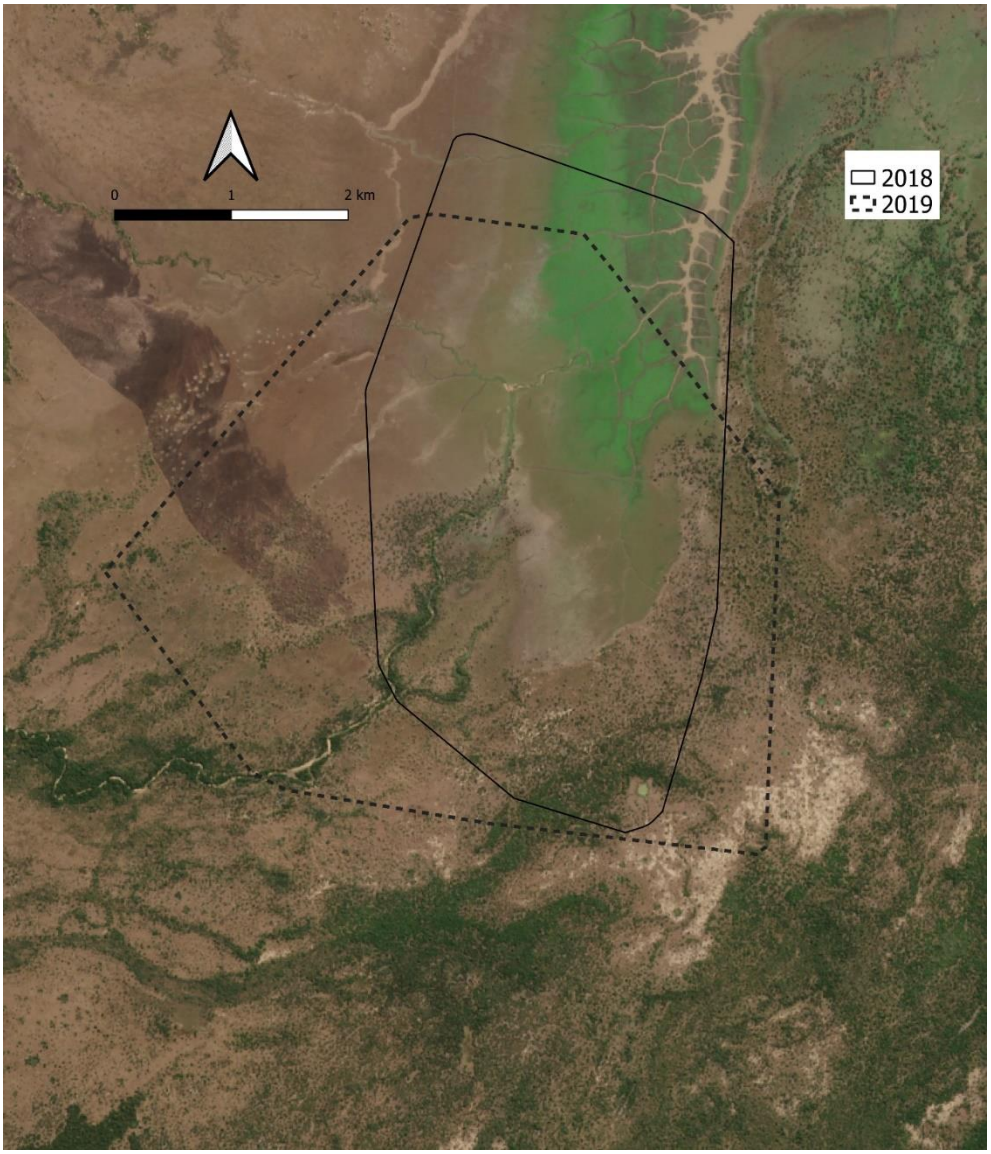

Figure 6.1. Comparison of minimum convex polygon of all GPS tracks from the Floodplain Troop across two years. 2018 data were collected from May-November using a handheld Garmin GPS device. 2019 data were collected from August 2019-May 2020 using GPS collars.

An additional shortcoming of this thesis was the number of collars and duration of the collar battery life. With only four collars, all results presented must be taken in the context of two monkeys in two troops, rather than multiple troops inhabiting similar areas or an entire troop. The data collection of these collars also created limitations. Although originally programmed so that they would last an estimated 12 months, all four collars failed between 2-3 months short of a full year, meaning that a portion of the dry season is missing from analysis. However, data show

that the baboons were well within their dry season home range by the time the collars failed. The original programming also meant that data were lower resolution than would be ideal for this type of study, as the baboons were shown to be able to move quite long distances in the fifteen-minute intervals between fixes (Chapter 5).

Further, the design of collar placement could have been changed to give different results. Financially, we were limited to four collars, but had multiple potential distributions of those collars. In choosing to place collars on two monkeys per troop, we were able to show differences in group spread, movement drivers, and route and resource use. However, by placing four collars in a single troop, social factors could have been analysed (Strandburg-Peshkin et al., 2017a), although this likely would have required higher-resolution data that would, in turn, deplete battery life; by placing one collar per troop in four different troops, the role of intergroup interactions, as well as more examples of habitat type, could have been studied (Markham et al., 2013), although with a high risk of losing data for an entire troop if one collar failed. For the purposes of the studies relying on this data, the methods chosen have served well with some limitations, but future work should strongly consider a different distribution pattern of available biologgers.

A final shortcoming is the lack of temperature data in this thesis. While temperature monitors were placed in the baboon home ranges in 2019, due to the COVID-19 pandemic, I was not able to periodically download them and change their batteries, leading to large chunks of missing data (Figure 1.2). Data from temperature loggers in 2018 show significant variation between each home range and the research area in Chitengo, and comparative initial analysis showed that temperature monitors in nearby Chimoio are not always a valid proxy for temperature in GNP. This variation meant that different thermoregulatory factors would be influencing the two troops

differently at the same time, and robust analysis could not be sufficiently done by using temperature data recorded elsewhere; therefore, temperature is excluded from analysis in all chapters.

6.4 Future Directions

This thesis sets important groundwork for future studies of the baboons of Gorongosa National Park. Using GPS and remote sensing data, I demonstrate methods for analysing movement patterns -- and potentially even revealing their underlying cognition -- outside of direct observation. These methods are easily replicable both on future data from GNP, as well as using any medium-to-high resolution GPS data from other field sites with or without behavioural covariates. This allows for further use of historic GPS data collected for other purposes, or for use when fieldwork is a limited option, due to time, funding, mental health, politics, or global pandemics. While I focus exclusively on GPS collar data, these methods could also be used with hand-held GPS devices, with careful data cleaning and combined with observational data.

Future studies would benefit, however, from the addition of ground truthing, as well as accelerometer data. By identifying resources such as in Chapter 3, on-the-ground checks could determine what is being identified, how it is being used and how better to define the parameters that define a waypoint.

This method of defining waypoints through hierarchical clustering could also be used to test other questions surrounding decision making and spatial cognition. While more than half of the available days were excluded due to them not fitting one of the key rules of the Travelling Salesperson Problem (each site must only be visited once), identifying which waypoints are returned to multiple times, or bypassed early in the day and reused later, could help to identify

how baboons prioritize movement decisions, and which resources are considered high-value. Similarly, a route reuse analysis as in Chapter 5 applied to the paths identified in the Chapter 3 could help further solve the question of what baboons use as navigational aids, as they may use the resources as "change-points" (Byrne et al., 2009).

This study also assumed that water bodies in GNP are static. While this was generally true for the study period, given that the effects of Cyclone Idai continued until the next rainy season, and resulted in a data set where water was not an obvious constraint, observations from the 2018 field season indicate that many of the water sources in GNP dry up throughout the dry season, including the Mussicadzi river and the pans that WT rely on for water. To fully understand the effects of water availability and season changes to vegetation on the ranging patters of baboons, each chapter could be replicated during a "normal" year in Gorongosa. Flood monitoring, water-detection using satellite imagery, and ground truthing would allow for understanding how access to water, for not just the focal troops but all animals in GNP, affects ranging behaviour.

In addition, one of the major hurdles faced in studying movement is the role of conspecifics, as well as other inhabitants of the area. With a rise in GPS collaring projects, more and more species of animals are being tracked around the world (Joo et al., 2022). Increasingly, antelopes, lions, and predators are being collared in GNP, creating a web of GPS monitored animals that affect each other's behaviour by acting as predators, prey, or competition (see Atkins et al., 2019; Pansu et al., 2019; Walker et al., 2023). Placing collars in multiple baboon troops, as well as ongoing collaboration with other scientists in GNP, would add depth to future analysis and allow for an understanding of how a densely inhabited park affects movement decisions compared to other areas.

Finally, these studies could be repeated as GNP continues to grow and recover from the effects of the Mozambique Civil War (Daskin et al., 2016). Already, huge progress has been made since the war, with the 2022 aerial census showing the highest count of wildlife within GNP (Stalmans et al., 2022). Although this thesis began when Gorongosa was a relatively low-predator environment, the efforts of the Gorongosa Restoration Project make this the ideal environment to map changes in baboon movement strategies as the landscape of fear is brought into sharper focus.

6.5 Concluding Remarks

Through this study, I have established that the baboons of Gorongosa National Park show similar movement patterns to baboons in other areas in some ways, and are unique in others. I have demonstrated that they show similar habitat preferences to other study sites, despite differences in predator and troop density, but that they reuse sleep sites more often and for longer periods. They are also able to navigate more efficiently than by either random movement or by using a simple nearest neighbour heuristic, and they use and remember habitual routes across the year, despite long periods of disruption. Not only do these works give insight to how baboon movement may change as the world changes, leading to new issues for large ecosystems like GNP, but it also may shed light on how human ancestors historically moved through their changing environment (DeVore & Washburn, 1963; Swedell & Plummer, 2012). Finally, no species is immune to the effects of global climate change and anthropogenic issues, and ongoing monitoring of large populations of generalist species are often overlooked. I hope that the work presented here shows ways to compare current movement ecology with historic data, as well as help create methods for fully remote data collection when fieldwork is unattainable.

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