CHACMA BABOON MOVEMENT AND BEHAVIOUR IN COMMERCIAL TIMBER PLANTATIONS IN SOUTH AFRICA AND THEIR ASSOCIATION WITH BARK-STRIPPING

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ABSTRACT

As human populations expand, natural habitats have been heavily transformed primarily for agricultural land use, disrupting ecosystems and reducing the abundance and diversity of native fauna. Commercial forestry plantations, often described as ‘green or ecological deserts’, are an example of an agricultural activity that has adversely impacted biodiversity. However, compared to commercial food crops, plantations offer relatively stable environments with longer rotations, and thus, may serve as a refuge for many wildlife species. In this thesis, I explore how native wildlife has responded to the widespread establishment of commercial tree plantations in the escarpment region of Mpumalanga Province, South Africa, and test the hypothesis that plantations are ‘green deserts’ with reduced biodiversity. Camera trap surveys revealed that many wildlife species persist even under heavily transformed commercial plantations, with natural corridors within the plantation matrix being important for species persistence and dispersal. I then explored how chacma baboons (*Papio ursinus*), which appear to thrive in and around plantations, utilise this modified landscape. Plantations have been described as marginal habitat for baboons, and hence, were predicted to show a preference for patches of natural habitat interspersed within plantations. Using GPS data collected from 17 free-ranging baboon troops over a three-year period, I showed that baboons prefer plantations to other land uses, including natural (riverine, grassland), particularly during the wet season. Factors such as tree age, compartment size, tree species and productivity emerged as significant influencers of baboon movement and habitat use within plantations. These insights challenge previously held assumptions about baboon avoidance of pine compartments, and reveal that plantations may well serve as a critical refuge for baboons and other wildlife, as natural land is converted for commercial crops and urban developments throughout the region. However, this conservation potential of plantations is challenged by baboons that engage in bark-stripping, which damages the quality and hence the value of the trees. Despite the economic importance of bark-stripping to the industry, little information is available on factors that influence baboon bark-stripping behaviour. This information gap is, in part, due to the difficulty in observing a heavily persecuted species that can easily evade human followers in rugged terrain. To circumvent this challenge, I deployed “smart collars” equipped with tri-axial acceleration and GPS devices on multiple individuals within a single baboon troop. Acceleration data were successfully used to identify and quantify bark-stripping behaviour with high precision (98.3%) and recall (95.9%). Plantation baboons allocated up to 9% of their daily activity to bark-stripping, far exceeding previous estimates, and spent less time foraging and more time resting compared to baboons in natural habitats. Bark-stripping increased with higher ambient temperatures and various plantation-level variables, such as compartment productivity, compartment size, slope and distance to local human settlements. Bark-stripping was performed by all collared individuals which, given the high occupancy of baboons in plantations, explains the extensive damage recorded by plantation managers throughout Mpumalanga. While these findings do not provide a solution to such damage, they represent a crucial first step in addressing and mitigating this conservation conflict by providing an understanding of how baboons use plantations and the drivers of baboon bark-stripping.

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ABBREVIATIONS

ALE	Accumulated Local Effects Profiles
BCI	Bayesian Credible Interval
cm	Centimetre
CU	Conservation Unit — delineated natural areas within plantation matrix
DBH	Diameter at Breast Height
DDMT	Daily Diary Multiple Trace software
dyn(X, Y, Z)	Dynamic acceleration of each axis
FFT	Fast Fourier Transformation
FN	False Negative, i.e., incorrectly classified negative behaviours
FP	False Positive, i.e., incorrectly classified positive behaviours
FSC	Forestry Stewardship Council
g	Gram
GAM	Generalised Additive Model
GLMM	Generalised Linear Mixed Models
GPS	Global Positioning System
ha	Hectare
Hz	Hertz
iCWild	Institute for Communities and Wildlife in Africa

iSSF	Integrated Step Selection Function
IVG	Inter-visit gap period
IQR	Interquartile range
kg	Kilogram
km	Kilometre
m	Metre
MCMC	Markov Chain Monte Carlo
MCP	Minimum Convex Polygon
MixRF	Mixed Effect randomForest model
MNLV	Mean number of locations per visit
NDVI	Normalised Difference Vegetation Index
NSV	Number of separate visits to a local hull
ODBA	Overall Dynamic Body Acceleration
OOB	Out-of-Bag
PDBA	Partial Dynamic Body Acceleration
PDP	Partial Dependent Plots
PSD	Power Spectrum Density
RMSE	Root-Mean-Square-Error
SD	Standard Deviation
SE	Standard Error
SI	Site Index
st(X, Y, Z)	Static acceleration of each axis
T-LoCoH	Time-Local-Convex-Hull
TN	True Negative, i.e., correctly classified negative behaviours
TP	True Positive, i.e., correctly classified positive behaviours
TRI	Terrain Ruggedness Index
UCT	University of Cape Town
UD	Utilisation Distribution
VeDBA	Vectorial Dynamic Body Acceleration

SYMBOLS

A	Summed area of all training hulls used in cross-validation-based parameter selection
α	Linear terms associated with species-specific detection model
aug	Number of augmented species added to the estimated number of species in the community (N)
β	Linear terms associated with species-specific occurrence model
°C	Degrees celsius
COV	Site–specific covariates
g	Number of training hulls that contained the test point location in cross-validation-based parameter selection
h	Unsmoothed heading values
I	Training/testing datasets used in cross-validation-based parameter selection of k and s values
i	Detected species
J	Test points used in cross-validation-based parameter selection of k and s values
j	Station defining the locations of the camera traps
K	Secondary sampling occasions over which sampling is replicated
k-value	Number of nearest neighbours used to create utilisation distribution
μ	Hyper-parameter defining the community-level mean, modelled using a half-Cauchy distribution

mtry	Optimum number of variables to be randomly selected at each node split used in a random forest model, selected using parameter tuning methods
N	Estimated number of species in the community
ntree	Optimum number of decision trees used in a random forest model, selected using parameter tuning methods
ω	Hyper-parameter defining the probability that species i is a member of the meta-community of size N
P	Value assigned to each combination of k and s values by summing across all of the test points in all of the training/testing datasets
p	Detection probability of a species
ψ	Probability of occurrence of a species
$\hat{R}$	Statistic where $\hat{R} < 1.1$ indicates convergence across all MCMC chains (Gelman, 2006)
ρ	Correlation between the occupancy model and the species-specific detection model
s-value	Time-scaled distance parameter used in nearest neighbour calculations
τ	Hyper-parameter defining the community-level precision, modelled using a half-Cauchy distribution
$\bar{\theta}$	Arithmetic mean after converting to degrees to Cartesian coordinates
w	Presence or absence of species i
Z	Geweke statistics (Geweke, 1992)

CHAPTER 1

Introduction

Human alteration of natural habitats has significantly impacted wildlife, leading to increased negative interactions between humans and animals, and conflicts amongst people on how best to mitigate these interactions (Redpath et al., 2015, 2013). As human populations expand, natural habitats are transformed into agricultural, industrial and urban systems, disrupting ecosystems and forcing many species to adapt or face extinction. In human-modified landscapes, new habitats and resources have emerged, which select wildlife have learnt to exploit for food, shelter and a refuge from natural predators (Filgueiras et al., 2021; Moore et al., 2023). However, this proximity between humans and wildlife has also intensified competition over resources, especially when animals exploit or damage commercial crops.

Wildlife damage to commercial crops is a pervasive and multifaceted challenge, with numerous studies documenting the economic and ecological consequences across diverse geographical regions and species (Redpath et al., 2015). In the United States, deer populations have been implicated in causing substantial crop losses, with, for example, white-tailed deer (*Odocoileus virginianus*) causing significant damage to crops like soybeans (*Glycine max*) and maize (*Zea mays*; Hewitt, 2011; Matthews, 2019). Similarly, across Europe, wild boars (*Sus scrofa*) have been a recurrent concern for farmers, impacting various crops, including maize and sunflower (*Helianthus annuus*), leading to substantial economic losses (Massei et al., 2011; Risch et al., 2021). Additionally, dingos (*Canis dingo*) in Australia exert a notable impact on livestock farming, particularly sheep (*Ovis* species (sp.); Allen et al., 2016, 2013; Fleming et al., 2001). In South Africa, black-backed jackals (*Canis mesomelas*) have been identified as significant contributors to small livestock depredation, particularly in semi-arid regions (Humphries et al., 2015; Nattrass et al., 2020).

Human approaches to mitigating negative interactions with wildlife have historically leaned towards lethal methods, including culling and hunting (Treves and Naughton-Treves, 2005). However, there is a growing global recognition of the need for more humane and non-lethal strategies to address these conflicts (Dubois et al., 2017). Studies have indicated that lethal control methods, such as culling, may have limited long-term effectiveness and can lead to unintended consequences, such as disruptions in ecosystem dynamics and the potential for increased reproductive rates among surviving individuals (Ripple et al., 2014; Treves and Naughton-Treves, 2005). The shift towards non-lethal methods is exemplified in various countries. In southern Africa, where conflicts with elephants (*Loxodonta* sp.) are common, innovative non-lethal approaches include the use of chilli-based deterrents to prevent elephants from raiding crops (Karidozo and Osborn, 2015; Le Bel, 2015). Similarly, the deployment of non-lethal tools like electric fencing and guardian animals (e.g., livestock guardian dogs) has gained traction in minimising predation on livestock by carnivores (Khorozyan and Waltert, 2019; Linnell et al., 2012). The global push for non-lethal methods is underpinned by ethical considerations, ecological awareness and a desire to foster coexistence between humans and wildlife, promoting sustainable solutions that benefit both parties (Dubois et al., 2017).

Conservation conflicts, a term coined by Redpath et al. (2015), refer to tensions arising from the intersection of human activities and conservation goals, with a significant portion of these conflicts manifesting as disagreements among people regarding how best to address the associated challenges. The crux of these conflicts lies in the divergence of human perspectives, competing interests and values, encompassing issues such as land use, resource allocation and wildlife management strategies. Cusack et al. (2021) emphasise that conservation conflicts rarely dissipate over time, and often escalate due to the complex interplay of ecological, social and economic factors. This escalation can be attributed to the persistence of underlying drivers, such as habitat loss, human-wildlife competition for resources and differing stakeholder values. The literature underscores that effective resolution of conservation conflicts requires acknowledging the multifaceted nature of these disputes and recognising the diverse perspectives and interests of all stakeholders involved (Redpath et al., 2015, 2013). Engaging communities, fostering dialogue and integrating local knowledge into conservation planning are essential for developing sustainable and context-specific solutions that address the root causes of these conflicts and contribute to long-term conservation success.

Primates, as a highly social and intelligent taxonomic order, exemplify the intricate dynamics of conservation conflicts on a global scale, highlighting the unique challenges and considerations associated with their coexistence with humans. Macaques (*Macaca* sp.) serve as a poignant example, facing negative interactions with farmers in South and Southeast Asia when they engage in crop raiding activities (Enari and Suzuki, 2010; Koirala et al., 2021). The financial implications for farmers are substantial as crop losses can result in decreased yields and income. Studies have shown that efforts to mitigate these conflicts, such as the use of deterrents or provision of alternative food sources, can have positive economic outcomes by reducing the impact of primate foraging on crops (Hill and Wallace, 2012; Lee and Priston, 2005). Chimpanzees (*Pan troglodytes*) face numerous conservation challenges, including poaching, disease transmission and habitat loss, but they too are persecuted for negatively impacting crops that are vital for local livelihoods (Hockings and McLennan, 2012).

Baboons (*Papio* sp.) are widely recognised as one of the most prevalent and serious "pest species" in Africa, causing significant damage to crops, livestock and infrastructure in both agricultural and urban areas (Butler, 2000; Drouilly et al., 2018b; Fehlmann et al., 2017c; Naughton-Treves, 1997; Tweheyo et al., 2005). Research conducted in various study areas, including South Africa, Saudi Arabia, Ethiopia, Zimbabwe, Nigeria and Kenya, consistently highlights the substantial economic impact of baboon-related issues. In South Africa, chacma baboons (*P. ursinus*) have been identified as formidable damage causing species, targeting crops like maize, beans, fruit orchards and vineyards, leading to substantial losses for local farmers (Fehlmann et al., 2017c; Findlay and Hill, 2020; Hill, 2017), prompting the implementation of diverse mitigation measures including rangers armed with paint-ball guns, electric fencing and noise aversion (van Doorn and O'Riain, 2020; Evers et al., 2022). In Zimbabwe, chacma baboons have been reported damaging crops such as maize, groundnuts (*Arachis hypogaea*) and tobacco (*Nicotiana tabacum*), posing challenges to subsistence farmers and exacerbating food security concerns (Musiwa and Mhlanga, 2020; Schweitzer et al., 2017). In Uganda, olive baboons (*P. anubis*) are reported to cause extensive damage to field crops such as maize and cassava (*Manihot esculenta*; Hill, 2000; Tweheyo et al., 2005), significantly impacting local agricultural communities. They are also known to take root and tuber crops ignored by other primates, and feed on a variety of crops, with a preference for maize and bananas (*Musa* sp.; Naughton-Treves, 1997). Urban areas are not immune to these challenges, with chacma baboons in places like Cape Town, South Africa, entering residential areas and causing damage to property and infrastructure (Fehlmann et al., 2021, 2017c, 2023; Hoffman and O'Riain, 2012a,b). The widespread nature of baboon-related conflicts in Africa underscores the urgency of adopting effective and sustainable management practices to mitigate economic losses and promote coexistence between humans and these highly adaptable primate species. The growing overlap between humans and baboons, coupled with the success of baboons in human-modified environments, further emphasise the need to understand their biology and behaviour.

In the broader context of negative interactions between humans and baboons, the predominant focus has centred on crop damage. One of the most significant forms of crop damage is that of baboon bark-stripping within southern Africa's timber plantations (Katsvanga, 2011; Peerbhay et al., 2018). While 12 independent studies have explored bark-stripping by chacma baboons in South Africa and Zimbabwe, there remains a need for a more ecologically focussed understanding on the damage-causing behaviour exhibited by baboons in plantations. Previous research has predominantly focused on damage assessments, leaving a significant knowledge gap on the behavioural patterns surrounding bark-stripping events.

1.1. Bark-stripping behaviour

The act of bark-stripping, observed across various mammal species in both natural forests and commercial plantations, presents a significant challenge for managing these environments (Baxter and Hansson, 2001; Reimoser, 2003). Numerous species have been implicated in bark-stripping including various deer (Akashi and Nakashizuka, 1999; Gerhardt et al., 2013; Gill, 1992a; Weng et al., 2022) and antelope species (Katerere, 1982), elephants (Midgley et al., 2005; Tweheyo et al., 2013), bears (Giusti; Perry et al., 2016; Taylor et al., 2019), rodents (Baxter and Hansson, 2001; Eccles and Little, 1995; Gill, 1992b), lagomorphs (Gill, 1992b; Rooney and Hayden, 2002) and a number of primate species (Di Bitetti, 2019; Katsvanga, 2011; McCarthy et al., 2017; Mikich and Liebsch, 2014b).

Distinct motivations underlie bark-stripping behaviours among various species. For many, such as bears, the practice is primarily driven by nutritional necessity, serving as a fall-back food source in times of food scarcity (Kimball et al., 1998; Kobashikawa and Koike, 2016; Mori et al., 2020). The North American porcupine (*Erethizon dorsatum*) has also been documented engaging in bark-stripping behaviour as they can digest the inner bark of trees, providing them with a nutritional alternative when other food sources are limited (Snyder and Linhart, 1997). Conversely, deer appear to engage in bark-stripping for different reasons, influenced by the chemical compositions and physical properties of bark from specific tree species (red deer *Cervus elavus*, Hahn and Vospernik, 2022; sika deer *Cervus nippon*, Nagaike, 2020).

At least 13 primate species have been reported to engage in bark-stripping activities on commercially significant trees (Di Bitetti, 2019). Orangutans (*Pongo pygmaeus* and *P. abelii*), chimpanzees, gorillas (*Gorilla beringei beringei* and *G. gorilla gorilla*) and howler monkeys (*Alouatta caraya* and *A. pigra*) have been documented to strip bark on small-scale commercial plantations, predominantly targeting *Eucalyptus* species (Bonilla-Sánchez et al., 2012; Liebsch and Mikich, 2017; McCarthy et al., 2017). However, among large-scale industrial plantations, eight primate species, including chacma baboon, black capuchin monkey (*Sapajus nigritus*), samango monkey (*Cercopithecus albogularis*), Bornean orangutan (*Pongo pygmaeus*), yellow baboon (*Papio cynocephalus*), vervet monkey (*Chlorocebus aethiops*) and two colobus monkeys (*Piliocolobus tephrosceles* and *Colobus guereza*), have been responsible for most damage reports (Di Bitetti, 2019).

1.2. History and management of plantations in South Africa

Timber plantations in South Africa date back to the late 1800s (Brown, 2003), driven by government initiatives (Brown, 1887; Zahn and Neethling, 1929) and private investments (DWAF, 1997). Initially focusing on fast-growing exotic tree species in the Western Cape, especially from the *Pinus* genus (Brown, 1887), these plantations expanded nationwide incorporating many new, mostly exotic, species. Presently, South Africa boasts a thriving timber industry, encompassing approximately 1.2 million hectares (ha) of plantations

(Oberholzer, 2021) dominated by softwoods (48.6% pine) and hardwoods (44.2% *Eucalyptus* and 6.8% *Acacia*) due to their rapid growth rates and economic viability (Morris, 2022; Oberholzer, 2021). Large private corporations own a substantial portion of these plantations, primarily located in Mpumalanga and KwaZulu-Natal provinces, each with around 40% of total plantation area, where they benefit from favourable environmental conditions conducive to tree growth (Fergusson, 2005).

This industry plays a pivotal role in South Africa's economy, providing employment opportunities in rural areas and contributing significantly to gross domestic product (GDP) (2% total GDP; 10% agricultural GDP and 54.9% manufacturing GDP) with pulp and paper being the most significant contributors (FSA, 2019, 2020a). In 2018, South Africa was the leading exporter of wood pulp (948 000 tons) followed by the USA and then Brazil (GlobeNewsWire, 2020).

Plantation management involves diverse activities such as site preparation, planting, thinning and harvesting (du Toit et al., 2010). Plantations are managed using a combination of manual and mechanised techniques, depending on the size and terrain of the plantation. Site preparation involves clearing the land, removing natural vegetation and preparing the soil for planting (Little, 2012; Smith et al., 2000; du Toit et al., 2010). While most plantations in South Africa were established in indigenous grasslands, after the mid-1990s afforestation of virgin land has been minimal, with most areas being re-established after felling. Planting stock primarily consists of clonal cuttings sourced from nurseries. The cuttings are planted in rows and spaced out according to the species and the expected growth rate and tree size (Hechter et al., 2022). Thinning is done to remove the weaker or slower-growing trees, which helps to reduce competition for water and nutrients and reduce the risk of disease and pests (Little, 2012; Little et al., 2018), allowing the remaining trees to grow faster and produce higher-quality timber. In South Africa, harvesting is done exclusively by clear-felling when trees reach maturity, typically between 10 and 20 years, depending on the species and intended use of the timber (du Toit et al., 2010). Overall, forestry represents a low-input land use, providing vast areas that remain relatively undisturbed by human activity.

Timber plantations offer several positive impacts on the environment and economy. They contribute substantially to local and national economies by producing timber, pulp and paper, generating extensive employment opportunities (FSA, 2020a). Additionally, these plantations act as carbon sinks, sequestering carbon through photosynthesis and aiding in climate change mitigation (Böttcher and Lindner, 2010; Härtl et al., 2017). Being renewable resources, timber plantations support sustainable practices, ensuring a continuous supply of building materials and other products (Woodard and Milner, 2016). Importantly, they alleviate pressure on natural forests, reducing the need for intensive forest management and allowing natural forests to be preserved as ecological reserves (Bremer and Farley, 2010; Sedjo, 1999). Furthermore, well-designed plantations can serve as habitats and corridors for diverse wildlife (Norton, 1998; Pretorius et al., 2023), enhancing biodiversity conservation (Pryde et al., 2016), and generally outperforming other agricultural and industrial land uses (Moore and Allen, 1999). Moreover, they facilitate land rehabilitation by stabilising soil, reducing erosion and supporting certain ecological functions, making them beneficial for reforesting degraded or deforested areas (Bremer and Farley, 2010; Geldenhuys et al., 2017; Sedjo, 1999), although they may not fully restore the original environment and its ecological functions.

However, timber plantations also present significant challenges and adverse impacts on the environment. One of the major concerns is land use change, leading to biodiversity loss (Castaño-Villa et al., 2019), habitat fragmentation and displacement of indigenous faunal communities (Armstrong et al., 1998). Intensive plantation management can result in soil degradation, erosion and disruption of nutrient cycles (Amoo et al., 2021; Sandoval López et al., 2020; Shete et al., 2015). High water usage in plantations can lead to water depletion, siltation in rivers, aquatic ecosystem degradation and reduced in-stream flow (Kruger and Bennett, 2013; Shah et al., 2022). Chemical pollutants from pesticides, herbicides and fertilisers used in plantations can contaminate soil, water and air, impacting environmental and human health (McBroom et al., 2013; Michael, 2004). Additionally, densely stocked plantations with highly flammable tree species increase wildfire risks, posing threats to plantations, local flora and fauna, as well as neighbouring communities

(Lindenmayer et al., 2023). There are also uncertainties regarding long-term carbon storage due to factors like deforestation and soil degradation (Böttcher and Lindner, 2010). Furthermore, the production and transportation of wood products have diverse environmental implications, including greenhouse gas emissions and energy usage (Adhikari and Ozarska, 2018; Wootton, 2012).

Mitigating these negative impacts requires the implementation of sustainable forest management practices, such as agroforestry and reduced-impact logging, along with the preservation of high conservation value areas. These approaches promote biodiversity conservation, sustainable land use and soil and water conservation, ensuring a balance between the positive outcomes of timber forestry and the preservation of natural ecosystems. However, the economic sustainability of plantations is significantly jeopardised by damage-causing animals, especially those engaged in bark-stripping behaviour. Even if plantations aspire to provide refuge for biodiversity, their ability to do so hinges on their survival as viable businesses. The widespread issue of bark-stripping by various mammal species, and especially by baboons in southern Africa, intensifies these challenges.

1.3. Baboon bark-stripping in southern Africa

The exploration of bark-stripping behaviour has historically overlooked primates, particularly baboons, in tropical and subtropical forest plantation systems (Baxter and Hansson, 2001; Estrada et al., 2012; Gill, 1992a,b; Hill, 2018). Baboon-induced damage, though a relatively recent phenomenon in southern Africa, has rapidly emerged as a substantial threat to forestry production and profitability. Pioneering studies conducted by Bigalke and van Hensbergen (1990), Gwenzi et al. (2007), Katsvanga (2011) and Henzi et al. (2011) highlighted the destruction wrought by chacma baboons on pine trees. While some studies such as Fergusson (2005), McNamara (2005), Germishuizen et al. (2017) and Peerbhay et al. (2018) sought to quantify the damage, detailed insights into the behaviour of bark-stripping remains scarce.

Baboon-induced bark-stripping inflicts substantial economic losses on wood products. Direct tree damage reduces the available yield, affecting production models and hindering foresters' ability to predict and compensate for these losses. Baboon-induced damage, especially bark-stripping, results in resin infiltration, staining and rot due to fungal infections (Vacek et al., 2020). Fungal infections may compromise the entire compartments resistance to biotic and abiotic factors leading to widespread wood degradation (Cukor et al., 2019). This damage also distorts stem growth (Figure 1.1), increasing handling costs and reducing wood recovery efficiency (Vacek et al., 2020).

Additionally, damaged trees experience slowed growth due to resource diversion for repair, ultimately decreasing final wood volume. If the bark removal exceeds 75% of the trunk's circumference (Figure 1.2), the entire tree or its crown may perish, posing a significant threat to the forest resource production value chain (McNamara, 2005). In Zimbabwe, the economic ramifications of baboon bark-stripping are substantial and in 2004 were estimated at US$1.8 million, with subsequent years witnessing wood volume losses of around 50%, equating to revenue losses ranging from US$24 000 to US$32 000 per ha by 2011 (Katsvanga, 2011). In South Africa, in 2017 the Forestry Stewardship Council (FSC) estimated that the financial loss attributed to baboon damage, over a two-year period, amounted to R130 million (approximately US$12 million; FSC, 2017). These figures do not encapsulate additional losses, including reduced growth, re-establishment costs, thinning, clear-felling expenses, or processing costs at sawmills. The impact of baboon-induced damage is exacerbated by its cumulative nature over a plantation's lifespan, involving multiple baboon groups and consequently increasing the affected area. Baboon damage often targets the lower stem parts, leading to the loss or devaluation of the most valuable quality logs, further diminishing economic returns (Giesen, 1985; Katsvanga, 2011). Bark-stripping impacts the entire forestry process, influencing decisions related to thinning intensity and potentially necessitating adjustments in response to baboon damage. In extreme cases where understocking becomes economically unviable, premature clear-felling of entire compartments might be the only feasible option, even though it prevents the realisation of the full economic benefits from a complete rotation, where full rotations are associated with larger-sized trees, ensuring higher percentages of better timber grades and reduced logging costs (Moore et al., 2012).

Figure 1.1. Distorted stem growth after extensive baboon damage to the main trunk.

1.3.1. Understanding the extent of damage through standardised damage assessments

The first records of bark-stripping by chacma baboons were documented in the Dedza Mountain plantations of Malawi in the 1950s, though most damage was from baboons uprooting seedlings (Darwin, 1982). However, the escalation of bark-stripping was swift, with a 25% increase reported from 1981 to 1982 alone (Darwin, 1982). In South Africa, the first recorded bark-stripping event dates back to 1967 (Giesen, 1985). The extent of baboon damage increased over the years, affecting large areas by the 1980s. Approximately 2746 ha were impacted from 1977 to 1985 (Giesen, 1985). It was in 1985 that Giesen (1985) provided the first systematic description of baboon bark-stripping behaviour, marking a

Figure 1.2. Multi-nodal ring-barking without breaks at branch whorls.

crucial turning point in understanding baboon damage within plantations and estimating the potential extent of bark-stripping losses.

However, challenges persisted, including a lack of standardised damage assessments, hindering comparisons across regions and time. Zimbabwe made strides to address this gap by commissioning a study in 2002 to establish a reliable damage assessment method (Ngorima et al., 2002; Valintine, 2002). This study highlighted the complexities in estimating actual timber volume losses, leading to an acknowledgement of historical underestimations. Despite mitigation efforts, baboon-induced losses in Zimbabwe remained substantial, posing a severe threat to the pine saw timber industry (Katsvanga, 2011). At this time, in the Mpumalanga province of South Africa, baboon damage was estimated to have affected approximately 7641 ha, resulting in an estimated loss of R20 802 622 (McNamara, 2005). This estimate, though considered at the time to be alarming, did not include estimates of incremental growth losses, re-establishment costs, revenue losses due to timber wastage during thinning and clear-felling, or downstream processing losses in sawmills.

More recent efforts to assess damage levels across South African plantations have used damage assessment plots and harnessed modern technology, specifically remote sensing

(Ferreira et al., 2020; Germishuizen et al., 2017; Peerbhay et al., 2018). Germishuizen et al. (2017) used random forests models on data collected from long term damage assessment plots to achieve high predictive success in assessing damage occurrence in pine plantations. Key predictors, such as tree age, species, site index and altitude, related to pine-stand characteristics, played pivotal roles in the model's accuracy. Surprisingly, variables associated with the environment surrounding the damage plots had limited impact on the model's performance. Building on this, Peerbhay et al. (2018) employed Landsat-8 sensor data to create a regional baboon-damage map, enhancing the capabilities of spatial damage quantification with an overall accuracy of 82.45%. This map not only aided in understanding economic constraints and quantifying forest resource production but also identified damage hotspots, enabling future targeted interventions. Further advancements included the use of Sentinel-2 imageries and the XGboost algorithm for sub-compartment scale detection and mapping of baboon damage (Ferreira et al., 2020). Tracking damage severity over three years revealed escalating impacts, prompting salvage operations in some compartments. Collectively, these studies have contributed to a spatial and temporal understanding of baboon damage, providing valuable tools for forest managers to develop risk-management strategies and implement targeted interventions.

In the face of mounting losses, a paradigm shift occurred in the management of baboons in commercial timber plantations. Previously, baboons were often viewed akin to introduced invasive species, but this perspective evolved. Policies, like those implemented by the FSC, emphasised a more balanced approach (FSC, 2017). Under these new guidelines, baboon management practices necessitate a rigorous assessment of damage impact (Fergusson, 2005), with ethical and non-lethal control methods preferred. Non-lethal controls take precedence where available, aligning industry practices with a more ecologically conscious approach to managing baboon-related challenges in commercial timber plantations.

While assessing the extent of baboon-induced damage is crucial for quantifying losses to the forestry industry, the trajectory of these losses is likely to persistently rise without a comprehensive ecological understanding of bark-stripping behaviour. Several studies have attempted to address this gap, investigating diverse approaches, ranging from non-lethal to lethal methods (Katsvanga, 2011; Nadel et al., 2012), and monitoring troop behaviour within commercial plantations (Henzi et al., 2011; Ndagurwa, 2013; de Wet, 2012), with the aim of mitigating baboon-induced damage.

1.3.2. Exploring the potential causes of bark-stripping

The fall-back food hypothesis

The fall-back food hypothesis is the most popular theory for explaining bark-stripping behaviour among primate species, having been cited as a cause in 27 independent studies (Di Bitetti, 2019). This hypothesis is often paired with the theory that plantation landscapes are ecologically impoverished due to years of habitat transformation and degradation (Bremer and Farley, 2010). Consequently, plantations do not adequately meet the nutritional needs of primate species which are then forced to fall back on less preferred, but readily available resources, such as bark or cambium. Fall-back foods can be defined as "foods whose use is negatively correlated with the availability of preferred foods" (Marshall and Wrangham, 2007) and represent a variety of forms depending on the primate taxon and environment. Examples of fall-back foods commonly utilised by primates include herbs, seeds (Davenport et al., 2010; Ma et al., 2017), lichens (Grueter et al., 2009; Miller et al., 2020), exudates (Porter et al., 2009), invertebrates (Mosdossy et al., 2015), crops (Chancellor et al., 2012), underground storage organs, e.g., forbs or tubers (Fashing, 2001; Marlowe and Berbesque, 2009) and bark (Basabose, 2002; Knott, 2005; Pruetz, 2006). Fall-back foods may be less preferred as they are (1) less nutritious and/or harder to digest (Stanford and Nkurunungi, 2003), (2) require specialised dental or digestive systems (Lambert, 2007), or (3) are high quality but mechanically challenging and/or time consuming to extract or manipulate (Mosdossy et al., 2015; Sauther and Cuozzo, 2009). Therefore, based on the evolutionary and ecological implications of their consumption, two different classifications of fall-back foods have been suggested: "staple" and "filler" (Marshall and Wrangham, 2007). Staple fall-back foods are food resources that can be accessed throughout the year, especially during seasonal shortages of other foods. Staple foods may therefore comprise the majority of a primate species' diet. In contrast, filler fall-back foods can be either seasonally or annually available, but never comprise the majority of a primate's diet (Marshall and Wrangham, 2007). For example, frugivorous primates eat sweet succulent fruit whenever it is available, but when it is not, they consume less easily digestible alternatives such as leaves or bark (Stanford and Nkurunungi, 2003).

Lambert et al. (2004) found that in an extreme El Niño induced drought in Uganda, grey-cheeked mangabeys (*Lophocebus albigena*) switched from a diet of predominantly fruit to bark. A number of bark-stripping primate species also conform to this fall-back food theory, namely capuchin monkeys (Liebsch et al., 2015; Liebsch and Mikich, 2015, 2017; Mikich and Liebsch, 2014a,b), golden snub-nosed monkeys (*Rhinopithecus roxellana*, Li et al., 2010; Yiming et al., 2002), Kashmir gray langurs (*Semnopithecus ajax*, Mir et al., 2015), rhesus macaques (*Macaca mulatta*, Zhang et al., 2022) and gorillas (Fuh et al., 2022), all of which use bark to survive harsh winters when other preferred food resources are scarce. This idea of "diet-switching" has also been observed in baboon species across varying habitats, where they adapt to reduced food availability by incorporating scarce but high-return foods into their diet or by increasing their intake of abundant, low-quality food (van Doorn et al., 2010; Foley, 1987), however, little research has attempted, with none succeeding, in linking baboon bark-stripping with fall-back food.

Despite the lack of empirical evidence supporting the fall-back food hypothesis, various mitigation strategies, including the provisioning of supplementary feeding, have been implemented to prevent baboons diet switching to bark (Bigalke and van Hensbergen, 1990). However, these feeding schemes have been largely unsuccessful, with damage often increasing in the immediate area around the feeding station. Henzi et al. (2011) found that capture sites that were pre-baited (i.e., provisioned with supplementary food) were damage hotspots. Other studies have also found that bark-stripping is more pronounced within the vicinity of important food resources, e.g., in plantations that border food crops, human settlements or water points (Katsvanga et al., 2009b). Further contesting this fall-back hypothesis in baboons is the weak correlation between food shortages and bark-stripping. Although baboon damage intensity has been found to increase during winter in the southern

Cape of South Africa (Erasmus, 1993), when food is thought to be less abundant, this pattern is not consistent across baboon populations within plantations. Bark-stripping occurs mostly during the rainy and post-rainy seasons in Zimbabwe when alternative food items were relatively abundant in the environment (Katsvanga et al., 2009b).

Another theory that is closely linked with the fall-back hypothesis, is the habitat transformation hypothesis, which predicts that greater crop-herbivory damage will occur when management practices negatively affect forage availability (Beguin et al., 2016). Beeson (1987) suggested there may be a threshold of habitat transformation beyond which bark-stripping behaviour is initiated. Multiple studies suggest that baboons within commercial plantations are reliant on small pockets of natural vegetation that are interspersed among pine compartments (Brown et al., 2005; Fergusson, 2005; Henzi et al., 2011). These natural areas provide vital resources such as food through endemic fruiting trees, thermally protected microhabitats, access to water and appropriate sleeping sites (Henzi et al., 2011). However, with increasing habitat modification, these natural areas become progressively more exploited and resource depauperate (Marais, 2009), greatly restricting resource availability within and adjacent to plantations and exacerbating damage in these areas. As such, Henzi et al. (2011) found that bark-stripping occurred mostly along the edges of pine compartments adjacent to natural areas, and baboons only entered pine compartments when travelling between natural areas .

Habitat degradation, through livestock grazing on under story was thought to have been the trigger for bark-stripping behaviour in Barbary macaques (*Macaca sylvanus*) in the Middle Atlas Forest. However, the quality of undergrowth and the density of livestock were not significant predictors of damage (Ciani et al., 2001). Other studies suggest that despite being a highly modified landscape, plantations provide an abundance of nutritious food such as invertebrates, pine seeds, mushrooms and grasses (Katsvanga et al., 2009b). Hoffman and O'Riain (2011) found that despite having access to abundant natural habitat, baboons showed a strong preference for plantations for both foraging and sleeping. The theory that bark-stripping occurs as baboons move through the compartment towards natural areas (Henzi et al., 2011) was also contradicted by Germishuizen et al. (2017). They modelled the susceptibility of pine compartments to bark-stripping and showed that damage was associated with the utilisation of the compartment itself, thus supporting Katsvanga et al. (2009a), who stated that damage was not related to proximity to natural areas. However, the dataset made available for their study did not specify which trees within a pine compartment were damaged and could not establish whether trees along compartment boundaries were more frequently subjected to bark-stripping, as observed by Bigalke and van Hensbergen (1990) and Henzi et al. (2011). Additionally, their study did not take into consideration the seasonal incidence of damage and the circumstances when bark-stripping was performed.

Profitable resource

The consumption of bark has been shown to form a significant portion of the winter diet of a number of primate species occurring in natural forests, especially under extreme weather conditions (Di Bitetti, 2019). These species include Japanese macaques (Enari and Sakamaki, 2010), Kashmir gray langurs (Mir et al., 2015) and Sichuan snub-nosed monkeys (Li et al., 2010). In particular, the bark of *Eucalyptus* trees, despite their high concentrations of secondary metabolites (Brezáni and Šmejkal, 2013), are consumed by various primate species, including red colobus monkeys (*Piliocolobus tephrosceles*; Rode et al., 2003), black-fronted titi monkeys (*Callicebus nigrifrons*; Estrada et al., 2012), two sub-species of black howler monkeys (*Alouatta caraya*; Agostini et al., 2010; *Alouatta pigra*; Bonilla-Sánchez et al., 2012) and chimpanzees (McCarthy et al., 2017). Secondary metabolites can bind with plant proteins or digestive enzymes to form insoluble complexes which have toxic effects on an animal's physiology and influence their digestion and nutrient uptake (Wasserman et al., 2012a, 2013, 2012b). Specifically, in mammalian herbivores, these tannins can cause a sharp, astringent sensation in the mouth as they bind with salivary proteins. Despite this, *Eucalyptus* bark is thought to form a critical component of some primate species diets, such as black-and-white colobus monkey (*Colobus guereza*), where groups make regular (i.e., monthly) forays into *Eucalyptus* plantations despite the core of their home ranges being located far from the plantations (Harris and Chapman, 2007).

In baboons, however, the bark of both pine and *Eucalyptus* species is not itself consumed (Bigalke and van Hensbergen, 1990; Erasmus, 1993), but rather the inner tissue or cambium. The xylem, cambium and phloem (often referred to as "cambium" for convenience) of pines contain high concentrations of sugars, particularly sucrose and carbohydrates (McNamara, 2005), therefore making it a potentially nutritious food source for some animals. In fact, the concentration of sugars in the phloem of pines is in similar concentrations to that of fruit (Almeida, 2013) and while it may provide a valuable source of energy it is unknown whether it forms a significant proportion of baboon diet. The hypothesis that pine is a valuable resource has been tested in other mammals, e.g., squirrels (Gill, 1992b) and deer (Gill, 1992a), however, little research has addressed its importance in primate diet (Di Bitetti, 2019).

Exotic (*Pinus*) and native tree species (*Vachellia*; previously *Acacia*) are important foraging sources for baboons with the seeds and flowers of both species being readily consumed (Hoffman and O'Riain, 2012b; Hoffman and O'Riain, 2011; Pebsworth et al., 2012). Nutrient translocation prior to needle fall in pines can significantly alter the nutrient concentration of the inner bark layer, as does moisture stress and increased demand for nutrients prior to the growing season. Baboon damage has been reported to increase before the growing season, therefore baboons may be taking advantage of these changes in the inner bark tissue concentration (McNamara, 2005). Significant differences in phosphorus concentration and moisture content have been found between baboon damaged and undamaged trees (McNamara, 2005), however, it is not clear if this is due to baboons selecting trees with higher nutrient concentrations, or if there is just a change in resource allocation towards the wounded area of the tree.

The water availability hypothesis

This theory suggests that primates may consume bark to gain access to moisture located in the sap, especially in drought-prone areas. Again, this appears to be case-specific, even within the same species. For example, Ciani et al. (2001) showed that Barbary macaques increased bark-stripping in areas without enough suitable water, whereas Ménard and Qarro (1999) found bark-stripping occurred despite an abundance of free water and high moisture levels in natural vegetation. They also found that the consumption of bark had no effect on relative water intake by macaques (Ménard and Qarro, 1999).

Baboon damage has been shown to increase during the spring and summer months in the Western Cape (Erasmus, 1993). As summer is the dry season in this area, baboons may use the cambium tissues as an additional moisture source. Contrary to this, baboon damage has been found to increase during the wet season in Malawi, which was attributed to the sap rising in the trees prior to the rainy season growth flush (Darwin, 1982). Additionally, in some Zimbabwean study areas, such as the Erin forest (Ndagurwa, 2007), rainfall occurs throughout the year and bark-stripping is observed continuously across all seasons.

Pharmacological hypothesis

Bark may also provide primates with medicinal benefits (McCarthy et al., 2017; Ndagurwa, 2007, 2013). Humans have long used the bark of now commercially important trees for medicinal purposes (Di Bitetti, 2019), including *Eucalyptus* leaves and bark to treat colds, influenza, toothaches, snakebites, fevers, diarrhoea and other complaints (Brezáni and Šmejkal, 2013; Gottesfeld, 1992). Extracts from pine bark have long been used to cure open wounds, skin damage and to prevent scurvy (Ohkita et al., 2011) as well as treat cardiovascular and neural disorders, diabetes, anti-inflammatory and immunomodulatory diseases (Mármol et al., 2019). Pine bark extracts have also been used as antioxidants in the meat industry, and over the last few years, increased focus has been placed on *Pinus* species in various forms of cancer treatment (Mármol et al., 2019).

Huffman and Seifu (1989) noted that animals, such as primates, use plant parts with secondary compounds to improve their health. Various primates species (e.g., woolly spider monkeys *Brachyteles arachnoides*: Petroni et al., 2017; Sifaka *Propithecus verreauxi verreauxi*: Carrai et al., 2003; gorilla: Cousins and Huffman, 2002; chimpanzee: Huffman and Wrangham, 1996; Japanese macaque: MacIntosh and Huffman, 2010) reportedly consume plants containing secondary metabolites, suggesting there may be both a nutritional and medicinal value. The consumption of some plant secondary metabolites (such as condensed tannins) also can have positive side effects, including protection against intestinal parasites (Min and Hart, 2003) and reduction of the negative physiological effects associated with the consumption of other toxic secondary metabolites (Cork and Foley, 1991).

The only study investigating the potential medicinal benefits of baboons ingesting bark and cambium was conducted by Ndagurwa (2013) in the Zimbabwean Highlands. In this region, bark-stripping of pines (*Pinus patula*) occurs mainly in winter and thus may be used as a prophylactic by baboons, however, no significant relationship was found between respiratory ailments in baboons and the consumption of bark and cambium. Another way in which the consumption of bark may be beneficial for primates is by improving gut motility due to its high fibre content (Di Bitetti, 2019). However, most reports indicate that baboons discard the outer bark, the fibrous component, and only ingest the soft inner cambium tissue (Bigalke and van Hensbergen, 1990; Erasmus, 1993). Additionally, faecal assessments of baboons living in plantations found no evidence of bark fibre (Erasmus, 1993; Ndagurwa, 2013).

Density-dependent hypothesis

It has been suggested that “overcrowding” may trigger bark-stripping behaviour. For example, Ligot et al. (2013) showed red deer density was the most important factor in explaining bark-stripping rates by deer in Belgium. Increased competition due to greater primate densities in plantations may cause certain groups to switch their diet to a less preferred resource, such as cambium (Mutiso et al., 2008). While some studies have shown that reducing the population size and density of damage-causing animals can reduce bark-stripping (Chollet et al., 2016; Hothorn and Müller, 2010; Wright et al., 2012), this has largely not been the case for baboons. Katsvanga et al. (2006) assessed the impact of population reduction (treating baited maize with *Papiol* (brodifacoum), a rodenticide) on bark-stripping in plantations. Using poison in the population exhibited a sharp decline (mean troop size reduced from 72 to 20) with bark-stripping being significantly reduced in the two months following the poisoning event. However, after this period, damage increased to pre-poisoning levels with increased baboon immigration from surrounding areas. Therefore, the lethal removal of more than 60% of the baboon population did not stop bark-stripping behaviour in the medium to long term (Katsvanga et al., 2006).

1.3.3. Understanding baboon behaviour in plantations and unravelling the impact of time, space and individual factors on damage

Season

Seasonal variations in baboon damage to trees have been observed across southern Africa, shedding light on the complex factors influencing this behaviour. In Zimbabwe, baboon damage has been observed to intensify during winter (dry season), a pattern attributed to increased time spent within plantations due to proximity to sleeping sites and natural vegetation, potentially driven by food scarcity (Erasmus, 1993; Valintine, 2002). In the southern Cape of South Africa, increased winter damage has been linked to food shortages (Erasmus, 1993), compelling baboons to seek additional food sources. Conversely, Katsvanga (2011) found that bark-stripping occurred more intensely during the rainy season when foraging requires less energy and more time is available for engaging in other activities, including bark-stripping. Similarly, McNamara (2005) suggested that bark-stripping occurs seasonally with relation to "ease" of stripping. In Malawi, damage appears to peak during the wet season (summer), possibly linked to rising sap levels in trees before the rainy season's growth flush or the availability of fewer fruits in native trees (Darwin, 1982).

In the Western Cape, damage appears to escalate during spring and summer months. Spring damage could be due to thermoregulation needs, while in the summer dry season, baboons might strip bark to access moisture in the "cambium" tissues (Erasmus, 1993). Studies have explored nutrient concentrations in baboon-damaged trees, revealing significant differences across seasons and between damaged and undamaged trees (McNamara, 2005). These findings suggest that bark-stripping behaviour may be influenced by seasonal variation in moisture, nutrient availability and the ease of bark removal.

Age

Previous baboon bark-stripping research appears to exhibit distinct patterns influenced by tree age and morphological features. Common findings suggest that bark-stripping incidents are often initiated after the first pruning stage and intensify through to the clear-felling phase (Katsvanga, 2011). Morphological traits such as bark thickness, roughness, stem "branchiness" and ease of removal are pivotal factors in determining damage (Papageorgiou and Neophytou, 1981).

Bigalke and van Hensbergen (1990) found that baboon damage became significant after trees reached the age of four years, with notable reductions observed in the Western Cape when trees attained twenty years, attributed to the protective thickness of their bark. This was further observed by Germishuizen et al. (2017), where damage increased in older (up to 20 years) and larger (diameter at breast height and total height) trees within plots. Bark thickening as trees age, resulting in a rougher structure, is a common trend observed in various tree species (Gill, 1992a; Kuiters et al., 2006). Similar to deer damage dynamics (Gill, 1992a), baboon damage initiation aligns with variations stem's rigidity. However, unlike deer, which cease bark-stripping when bark thickens, baboons can exploit the upper and thinner portions of the trunk, where bark is still forming and remains more vulnerable to damage. Older trees, previously damaged, may be revisited, exploiting prior wounds as access points through the resilient, thick bark.

Tree species

Pinus taeda has historically been severely damaged by baboons in Malawi where surveys in the mid-1980s revealed approximately 3500 *P. taeda* trees damaged, compared to 160 *P. patula* trees and 70 *P. elliotti* trees (Giesen, 1985). This study provided the first evidence that baboons might exhibit preferences for specific tree species, a hypothesis supported by subsequent research, for example in Zimbabwe (Katsvanga, 2011), where there is seasonal variation in which species are favoured. In 1997, the South African forestry industry reported that approximately 18.1% of all pine trees were damaged by bark-stripping with *P. taeda* having the highest rate of damage (20.8%), followed by *P. patula* (17.5%) and *P. elliottii*

(13.6%) (Viljoen and Pienaar, 1997). However, Bigalke and van Hensbergen (1990) argue that all commercial species are susceptible to bark-stripping and that high levels of damage to particular species may simply reflect their higher relative abundance in a region.

Over the years, baboon damage in South Africa has intensified, particularly in *P. taeda* trees (McNamara, 2005; Table 1.1 and 1.2), thought to be associated with their higher concentrations of sugar and protein. Germishuizen et al. (2017) identified species and hybrids like *P. patula*, *P. taeda* and *P. patula* × *P. tecunumanii* as highly susceptible to baboon damage, especially in high productivity sites, highlighting the economic repercussions of baboon damage on highly productive forestry sites.

Although damage in South Africa predominantly occurs within *Pinus* compartments, damage to *Acacia* and *Eucalyptus* species compartments have also been reported (Figure 1.3; Bigalke and van Hensbergen, 1990). Notably, damage to *Eucalyptus* trees by chacma baboons is less severe in both frequency and extent when compared to pine damage, a phenomenon potentially attributed to *Eucalyptus* trees having higher concentrations of phytoestrogens, leading to behavioural changes and fertility suppression in primates (Wasserman et al., 2012a,b).

Figure 1.3. Baboon damage to *Eucalyptus*.

Table 1.1. Percentage of damage to different *Pinus* species in South Africa during the 2002 and 2004 assessments (taken from McNamara, 2005).

Species	**2002**	**2004**	**Average**
Pinus taeda	22.5%	29.9%	26.2%
Pinus elliottii	15.8%	23.2%	19.5%
Pinus patula	13.3%	17.8%	15.6%
Average	**17.2%**	**23.6%**	**20.4%**

Table 1.2. Estimated volume and value lost due to baboon damage for three *Pinus* species in South Africa during the 2002 and 2004 assessments (taken from McNamara, 2005).

Species	**Volume lost** (m^3/ha)		**Value lost** (Rand/ha)	
	2002	**2004**	**2002**	**2004**
Pinus patula	2	3	240	379
Pinus elliottii	3	3	372	355
Pinus taeda	7	9	831	1450
Average	**4**	**5**	**481**	**728**

Spatial variation

Previous studies have observed localised patterns in baboon damage within plantations. Some research suggests increased damage at compartment edges (e.g., roads and fire breaks; Bigalke and van Hensbergen, 1990; Henzi et al., 2011), which provide vantage points with an open area ahead and may be useful for baboons to monitor their surroundings (Katsvanga, 2011). Damage to compartment edges has also been noted in other bark-stripping primates in the Central African rainforest, who severely strip tree bark within a few metres from roads (Beeson, 1985). Areas adjacent to compartment edges, including open grassland or fire breaks, could serve as feeding zones, particularly during periods of food scarcity as baboons consume various grass species (Norton, 1998), thereby further attracting baboons to these areas. Additionally, damage has been noted to be higher near sleeping sites and areas that are used to pre-bait before capturing baboons (Bigalke and van Hensbergen, 1990; Henzi et al., 2011), suggesting a link between damage and amount of time baboons are in a particular area. Support for this theory is limited with both Fergusson (2005) and Katsvanga et al.

(2009b) stating that the extent of damage does not consistently align with the time spent in an area. Finally, baboon damage has been found to be higher in valley bottoms and on the upper slopes, however, the reasons for this are unclear (Germishuizen et al., 2017).

Position on tree

Baboon bark-stripping behaviour exhibits specific patterns in relation to tree morphology and timber value. Bark removal can occur on any section of a tree, from the base to the crown (i.e., the uppermost part of a tree consisting of branches, leaves and reproductive structures, collectively forming the tree's canopy), but tends to be concentrated where the bark thickness is around 5 mm, approximately one-third to one-half of the tree's height (Giesen, 1985). Bark-stripping height varies between pine species; for instance, in *P. pinaster*, where the bark is thicker, stripping occurs higher up the tree compared to *P. radiata* which has thinner bark. The ease of bark detachment also affects the damage pattern, with *P. radiata* experiencing long strips of bark removal as the bark detaches more readily (Bigalke and van Hensbergen, 1990).

The position of bark lesions on the tree trunk is important because it impacts the timber's value, with the lower bole being the most valuable part used for veneer and plywood. Therefore, lesions within the 1st quarter of the tree can lead to loss of the most valuable timber (Katsvanga, 2011). The onset of bark stripping is believed to be linked to the timing of the first pruning treatment (Ndagurwa, 2007). Although the exact reasons are not fully understood, one factor may be that removing lower branches makes certain compartments and areas of a tree more accessible to baboons (Ndagurwa, 2007). Furthermore, Bigalke and van Hensbergen (1990) suggested that the strong scent of resin from freshly pruned trees could attract baboons and trigger bark-stripping behaviour. As a result, bark-stripping is often concentrated around the pruning level. Over time, pruning can also shift the damage location; by removing lateral branches, perching opportunities at lower heights are eliminated, prompting baboons to strip bark higher up where they can sit comfortably. Studies indicate that once a tree is damaged, it is more likely to be stripped again (Katsvanga, 2011; Nagaike, 2020; Welch and Scott, 2017). This repeated damage further reduces the value of the affected trees making an argument for the thinning of trees that have already sustained damage.

Individual baboon variation in bark-stripping

In 17 of the 18 studies documenting bark-stripping, not all study groups or populations were observed engaging in this behaviour (Di Bitetti, 2019), which implies that bark-stripping is a learned behaviour. Research on chacma baboons (Bigalke and van Hensbergen, 1990) and samango monkeys (von dem Bussche and van der Zee, 1985) supports the idea that bark-stripping entails a learning process. Therefore, it is possible for the behaviour to spread through a population with the immigration of adult males that have already acquired the behaviour. Katsvanga (2011) suggests that damage to pines is primarily caused by a few individuals in a group. Katsvanga (2011) also noted that bark-stripping receives minimal time allocation within baboon troops, indicating that it is opportunistically performed for a short duration. However, this observation might be influenced by a 'visibility bias', where larger or less fearful individuals, such as adult males, are more frequently observed engaging in the behaviour (Katsvanga, 2011). Consequently, previous observational studies may have mistakenly concluded that bark-stripping is exclusive to these individuals, potentially misrepresenting the broader spectrum of participants in such behaviour.

1.4. Aims and Objectives

Baboon-induced damage to pine plantations poses a significant threat to the long-term viability of this economically important industry, amplifying existing challenges such as fire, insect damage and diseases. The global demand for timber is expected to lead to a doubling of land converted to plantations by the century's end (Kok et al., 2018). As market expectations rise, efficient processes become imperative to maximise tree value and profit. However, baboon-induced damage adversely effects both goals, exposing trees to infections and subsequent rot, leading to lower-quality timber (Cukor et al., 2019; Vacek et al., 2020). This degradation often relegates timber to lower-grade categories, reducing overall recovery rates and economic potential.

Given the threat posed by baboons to forestry in southern Africa it is surprising that we know so little about the factors that might influence baboon use of plantations and the rate and extent of bark-stripping. Direct observations of bark-stripping by forestry personnel are exceptionally rare with baboons typically fleeing the approach of people on foot or in vehicles, presumably because of historical persecution. Only a few studies have sought to directly observe and quantify baboon behaviour in and around plantations (Henzi et al., 2011; Katsvanga, 2011; Ndagurwa, 2007) with difficulties in habituation limiting close observations in many plantations (Thys De Wet, *pers comm*). Consequently, the potential drivers of bark-stripping behaviour remain poorly understood, and hence, efforts to prevent or mitigate its frequency and extent are poorly developed.

This lack of knowledge has also promoted conflict amongst stakeholders on how best to manage damage-causing baboons in plantations. An enormous number of interventions have been trialled ranging from using people and dogs to drive baboons out of plantations (Nadel et al., 2012) to lethal removal of multiple troops in a single area (de Wet, 2012). However, none of these methods were tested systematically with appropriate before and after data on damage levels to trees, or the frequency with which bark-stripping behaviour was performed and by which individuals. The absence of robust data on either damage levels or damage mitigation interventions coupled with the popular perception that plantations are ‘green deserts’, opened up Forestry South Africa to public criticism for their impacts on biodiversity in general and baboons specifically.

In response to mounting public pressure and the stipulations of the FSC that the cultivation and harvesting of timber must adhere to sustainable and environmentally responsible practices (FSC, 2017), the industry convened a workshop on understanding baboons and baboon-related damage in commercial plantations in South Africa. This collaborative initiative, involving all relevant stakeholders, was held in 2012 (Nadel et al., 2012). The primary objective of this workshop was to delineate key research objectives crucial for empirically framing the conservation conflict at hand and an improved understanding of the impacts of plantations on local mammal populations and the impact of baboons on timber plantations. These objectives included: (1) conducting a landscape-level assessment of biodiversity across plantation-modified lands, (2) evaluating damage to plantations at both landscape and plantation levels, and (3) undertaking detailed contextual behavioural observations of baboons engaged in tree damage. Remote sensing models have been deployed to address the second objective (Ferreira et al., 2020; Germishuizen et al., 2017; Peerbhay et al., 2018). Therefore, the focus of my thesis will be directed towards addressing the remaining two objectives, namely (1) and (3).

In **Chapter 2**, I use data collected from camera trap surveys to investigate how plantations have affected mammalian biodiversity, and whether plantations can be fairly described as ‘ecological deserts’. In addition, I explore whether there are wildlife winners and losers in plantations by running multi-species hierarchical occupancy models for two equal sized areas that differ in the level of transformation of natural land for plantation. By assessing their potential role in conservation planning, this research seeks to contribute to a nuanced understanding of afforestation impact on local fauna.

In **Chapter 3**, my focus shifts to the chacma baboon, a species of commercial significance, that was revealed in Chapter 2 to have very high probability of habitat use and as such is a wildlife winner in plantations. Given plantations are nested within a matrix of diverse land uses, I test the hypothesis that baboons only use plantations to commute to the remaining patches of natural vegetation (Henzi et al., 2011). I used an existing database of GPS collar data from 17 free-ranging troops, living on and adjacent to plantation land owned and managed by the forestry company Sappi. I use Integrated Step-Selection, T-LoCoH home range analyses and mixed-effects random forest models to explore variation in home range size within the diverse land use matrix, and to analyse troop revisitation rates to explore movement patterns and habitat selection.

I had initially hoped to explore bark-stripping behaviour through direct observations of a habituated troop living in an area with confirmed bark-stripping damage. However, despite six months of following a troop on foot, I was not able to habituate them to close (< 20 m) observations, essential for detecting bark-stripping behaviour in dense foliage. Further attempts at habituation were limited due to the Covid-19 lockdown restricting field access. Additionally, the rugged terrain greatly impeded continuous tracking of the troop across their extensive home range. Consequently, I deployed “smart collars” (Bracken et al., 2022; Christensen et al., 2023; Fehlmann et al., 2017a,b,c) equipped with accelerometers and GPS technology to remotely capture the spatial (GPS points) and vectorial (tri-axial accelerometry and magnetometry) movements of individual baboons within a plantation setting. I used these data in **Chapter 4** to identify all instances of bark-stripping using supervised machine learning methods. I then derived an activity budget for the troop and explored when and where bark-stripping behaviour occurred, and how it was influenced by various environmental/extrinsic covariates, include tree species, tree age, proximity to human settlements and slope, as well as intrinsic factors such as the age class and sex of the baboons.

This thesis aims to provide nuanced insights into the relationship between afforestation, mammalian biodiversity and baboon behavioural ecology. These findings hold the potential to improve our understanding of the impacts that commercial plantations have on wildlife and how baboons use plantations and when, where and why they engage in the damaging behaviour of bark-stripping. It is only through an improved understanding of how this agricultural activity influences wildlife, and how wildlife in turn use this novel resource, that improvements can be made to both how the crop is farmed and how to manage baboon damage to trees in a sustainable and humane manner.

CHAPTER 2

Mammal species richness and occurrence under transformation from commercial plantations[*]

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Abstract

The global loss of biodiversity paired with the shortcomings of protected areas highlights the need to improve the conservation potential of human-modified lands. Although often referred to as “ecological deserts”, large spatial scales and long rotation periods make tree plantations a relatively stable and permeable environment that could provide an important link between fragmented natural habitats. Different intensities of afforestation within the same geographic grassland region provide an opportunity to test how transformation by commercial plantations affects local biodiversity. In this chapter, I conducted camera trap surveys at two sites characterised by different degrees of afforestation. I demonstrate a higher mammalian diversity and a higher probability of habitat use in less transformed areas, suggesting that preserving large tracts of native vegetation is vital when offsetting biodiversity loss from timber plantations, especially regarding grassland-specialist species. Community-level habitat use increased in more rugged areas, while in the highly transformed site, habitat use increased closer to indigenous patches and roads. For chacma baboons, although the less transformed site was preferred, habitat utilisation in the heavily transformed area was still high, relative to other mammalian species, with increased habitat usage in more rugged and productive areas. This chapter highlights the importance of maintaining comprehensive networks of protected units as part of a broader landscape management approach and identifies a major challenge for the forestry industry moving forward, with plantation compartments being dominated by species that threaten the long-term sustainability of the crop itself.

2.1. Introduction

Satisfying the growing global demand for agricultural and commercial forestry products invariably increases the rate of global biodiversity loss (Díaz et al., 2019; IPBES, 2019). Protected areas, while having been acknowledged as important for conserving biodiversity (Brooks et al., 2006), are both too few and cover too small an area to stem the current rates of biodiversity loss (Williams et al., 2022). Consequently, it is essential to evaluate species diversity within human-altered landscapes to better understand the impacts that land transformation can have on various aspects of biodiversity (Kshettry et al., 2020), and improve proactive management to enhance their conservation potential and increase connectivity between remaining unmodified areas (Resasco, 2019).

At present, approximately 132 million ha of global land are covered by timber plantations, composed of several native or exotic tree species, of the same age and planted with regular spacing (FAO and UNEP, 2020). Management efficiency is improved by this simplification and homogenisation of compartment structure, and production is maximised through intensive, high-input management practices aimed at increasing tree growth (Betts et al., 2021). Although these methods have been successful at boosting yields, this has come at the cost of global and local biodiversity (Armstrong et al., 1998; Barlow et al., 2007). The scale of this cost is still hotly debated, from the belief that tree plantations are "green deserts" without valuable habitat for species (Barlow et al., 2007; Makino et al., 2007; Matthews et al., 2002) to the idea that under certain conditions plantations still support valuable components of natural ecosystems (Brockerhoff et al., 2005, 2001, 2008; Carnus et al., 2006), but it is generally agreed that plantations negatively affect the structure and occurrence of local species compared to native habitats.

Nonetheless, when compared to other commercial monocultures (e.g., food crops), timber plantations show a great potential for supporting biodiversity (Brockerhoff et al., 2005, 2001, 2008; Carnus et al., 2006; Cusack and Montagnini, 2004). For example, plantations can provide an important refuge for many species, as long rotation periods create relatively stable environments with low levels of human disturbance (Betts et al., 2021; Brockerhoff et al., 2008; Moore and Allen, 1999). Furthermore, plantation land units are typically on a much larger spatial scale than other agricultural systems, and therefore, can provide an important link between fragmented indigenous habitats (Werema and Howell, 2015), a process that can be facilitated by improved design and management (Pryke and Samways, 2012). Previous studies exploring this relationship between forestry and biodiversity focus almost exclusively on afforestation within previously forested areas, with few studies exploring biodiversity under complete vegetation shifts. A considerable divergence from the original habitat type can influence the number of species retained in the new community (Betts et al., 2021) and potentially limit the conservation value of plantations in these regions.

In South Africa, over the last 150 years, approximately 1.1 million ha of land ($\sim$ 0.98% of the total land area of South Africa) have been converted to commercial tree plantations of exotic genera such as *Pinus*, *Eucalyptus* and *Acacia* (FSA, 2020a). This extensive afforestation was necessary because local indigenous forests and woodlands could not meet the country's need for structural timber and fibre to manufacture pulp and paper (Bennett and Kruger, 2013). Most of this afforestation occurred within the grassland biome, as its relatively high rainfall combined with steep slopes and thin soils were particularly suited to the growth of exotic tree species (Armstrong and van Hensbergen, 1999). Although the original conversion to timber plantations was substantial, no new land has been converted since mid-1990, with afforested areas decreasing by 6.3% since 2009 (FSA, 2020a). Unfortunately, the grassland biome also supports the highest densities of human population and the highest levels of agricultural transformation in the subcontinent (O'Connor and Kuyler, 2009), with grassland conversion primarily through agricultural intensification (especially row-cropping and pastures), urban expansion and mining activities. As a result, the grassland biome is one of the most at-risk South African biomes, with 40–60% irreversibly modified and less than 2% formally protected (Carbutt and Kirkman, 2022; Lipsey and Hockey, 2010).

In an attempt to reduce the environmental impacts of plantations, South African forestry landholdings delineate all permanent and seasonal water sources with a protected buffer of at least 20 m. This was first based on a memorandum with the South African

Department of Water and Sanitation to preserve water flow through plantations, and was later adopted as a formal procedure within certification schemes such as FSC (FSC, 2017). This management practice is similar to hedgerows in food cropland which have been shown to provide “valuable secondary habitats” and promote biodiversity in highly fragmented landscapes (Vanneste et al., 2020). These green corridors can provide a natural refuge for species within the modified plantation landscape and link patches of natural habitat to facilitate movement and dispersal. Furthermore, 500 000 ha of forestry-owned land are permanently unplanted (SANBI, 2013) and are set aside as protected reserves. These areas consist of a biodiverse mosaic of moist grasslands, wetlands, riparian and natural forests, many of which fall into priority biodiversity areas. Therefore, the intensity of afforestation can vary significantly within the same geographic region and provides an opportunity to study how afforestation in previously grassland-dominated regions can affect native grassland fauna.

Previous plantation land management studies in South Africa have tended to focus on forestry-specific impacts such as fragmentation (Armstrong and van Hensbergen, 1996; Malan et al., 2007), harvesting practises such as clear-felling, or impacts of afforestation at the compartment level (Armstrong et al., 1998; Armstrong and van Hensbergen, 1996). Therefore, there is a general lack of understanding on how landscape-level afforestation can affect species diversity and community-level habitat use under complete vegetation structural changes. I focus on medium- to large-bodied mammalian species since previous biodiversity-forestry studies in South Africa have almost exclusively focused on birds and invertebrates (Kotze and Samways, 1999 *but see* Ehlers Smith et al., 2018 and Sosibo et al., 2022). I predicted that areas that have been heavily transformed by plantations would have reduced mammalian species richness and habitat use when compared to areas that retained native grassland (Cravino and Brazeiro, 2021; Ng et al., 2021), and that the afforested mammal community would be characterised by predominantly “generalist species” (able to thrive under a wide range of environmental conditions) as they are more capable of using transformed habitats (Cravino and Brazeiro, 2021; Iezzi et al., 2020). Finally, I predicted that habitat use would increase closer to indigenous corridors, which are generally associated with riverine passages and rugged areas where planting and harvesting are difficult, whilst distance to urban areas and roads would have a negative effect on habitat use due to increased rates of disturbance and poaching potential. This information can help in our continued effort to understand how human activities and land transformation affect mammal communities outside of protected areas, and how management efforts can reduce the negative impacts of these activities (Andrade-Núñez and Aide, 2010; Brodie et al., 2015) and promote biodiversity conservation across tree plantations.

Land management is not the only factor that can influence productivity output. The presence of species that routinely damages the crop can lead to dramatic reductions in production and profitability. In the main forestry region of Mpumalanga, where the study was located, chacma baboons have been found to damage commercially planted trees through the behaviour of bark-stripping (Germishuizen et al., 2017; McNamara, 2005; Peerbhay et al., 2018), which impairs growth and kills trees, both reducing the commercial value of the timber and the overall production rates (Nadel et al., 2012). Bark-stripping of *Pinus* plantations, in particular, is reportedly increasing and resulting in unsustainable levels of damage to trees and ultimately timber products (Peerbhay et al., 2018). There are numerous theories as to why baboons strip bark from plantation trees (Chapter 1; Di Bitetti, 2019; Katsvanga et al., 2009b; Ndagurwa, 2013) but only a limited understanding of baboon habitat use within plantations and how different land management practices may influence this use. Understanding how baboons utilise plantations and how this influences their relative abundance is important to efforts that seek to manage bark-stripping damage and curb production losses. Given their reputation for routinely damaging planted trees, my second research aim was to explore how afforestation intensity may affect baboon habitat use specifically, and which factors drive this use within the plantation landscape. I predicted that baboons would prefer areas of natural grasslands, i.e., moderately transformed areas, but that habitat use would be more similar between the different degrees of transformation than compared to other species in the area, given baboons' adaptability to varying environments. I also predicted that within the plantation-dominated landscape, i.e., heavily transformed site, baboon habitat use would increase closer to indigenous vegetation pockets as these habitats provide essential foraging and sleeping opportunities.

2.2. Methods

2.2.1. Study site

The study was conducted in the Sabie region of Mpumalanga province, South Africa (Figure 2.1). Land in this region has largely been converted to commercial tree plantations of exotic genera such as *Pinus* and *Eucalyptus* (FSA, 2020a; Shai, 2021). Plantations in the area span broad altitudinal and climatic ranges (altitude: 400–2100 m above sea level; mean annual precipitation: 630–1600 mm; mean annual temperature: 13–21 °C). Compartment size ranges from under 1 ha to ∼100 ha and managed primarily for the production of structural/building timber and pulp (Bennett and Kruger, 2013). Within a commercial plantation, ∼70% of the land is planted, with the remaining 30% of land being allocated to roads, infrastructure, firebreaks, rugged land and delineated riparian vegetation (FSA, 2021).

The first study area (Site 1) was selected to represent highly transformed grasslands, as it comprised continuous exotic *Pinus* plantation compartments in which over 70% of the land was planted. Site 2 was selected to represent moderately transformed grasslands, largely comprised of a protected grassland reserve, dominated by mesic highveld grassland species, predominately C4 species (Figure 2.1: B2 and C2; Mucinia and Rutherford, 2006). Approximately 33% of Site 2 was allocated to plantation compartments planted at the same spacing as trees in Site 1. The area of both study sites was originally planted around mid- to late-1960 and had undergone 2–5 rotations with an average length of 30 years. Variation in the rotation period was due to production output (saw timber or pulp; Bettinger et al., 2016) or as a result of compartments being cleared due to extensive damage (frost, insects/fungi or wildlife damage). Tree spacing depended on the stems per ha: 3–3.5 × 1.7–2 m for *Pinus patula* species and 3.0–3.5 × 2.1–2.5 m for all other pine and pine hybrids. Wetlands and riparian areas within the plantation matrix were delineated ($\geq$ 20 m) as per Forestry South Africa (FSA) guidelines (FSA, 2021) and comprised a mixture of indigenous forest, woodland and thicket. Additional unplanted natural areas comprised firebreaks, cliffs, and rocky outcrops.

2.2.2. Camera trap survey design

The first survey (Site 1) was carried out in July–September 2013 (70 days), with 60 camera stations (75%) located within plantation compartments and 20 stations (25%) located in indigenous corridors, mainly composed of riverine vegetation. The second study area (Site 2) was surveyed in the same season (August–September) in 2014 (74 days), with most sites (n = 60, 75%) located in a protected grassland reserve and n = 20 (25%) within *Pinus* plantation compartments (Figure 2.1: B2 and C2). With only 80 camera traps, the surveys had to be conducted over two years, controlling for season. Consequently, this introduces 'year' as an uncontrolled variable that is confounded with 'site'. Both plantations and protected grasslands are considered stable environments over the short term (Betts et al., 2021; Kirkman et al., 2014), and as no fires nor extreme weather were reported for either area during the study period, I did not expect drastic changes across the medium/large mammalian community (Drouilly et al., 2018a).

To allow for direct comparisons between study areas, I used a systematic camera trap sampling design (camera stations placed on a 2 km grid), with a randomised starting point (Figure 2.1C). This survey design ensures that key habitat characteristics are sampled in proportion to their occurrence in the landscape and prevents bias in the detection of particular species (Hofmeester et al., 2019). Acorn cameras (Ltl-6210 MC) were deployed within 100 m of the centroid of each grid cell, placed at the height of approximately 30 cm at the base of a tree or on a wooden stake. The microplacement of each camera was selected to maximise species detection, that is, in areas with a good field of vision and along movement corridors or areas with signs of animals, e.g., scat and spoor (Colyn et al., 2018). It is important to note that this approach may introduce bias, as cameras placed along movement corridors or areas with visible signs of animals may skew the results toward species that frequent those locations, potentially under-representing species that are less visible or prefer more secluded habitats. To minimise the chance of theft, cameras were offset from roads by approximately 5 m. Three images were captured per trigger with a one-minute delay between each image. To avoid bias and unreliable estimates related to small sample size, I limited my analyses to native mammal species with $\gg$10 detections (MacKenzie et al., 2002), and as such I removed detections of human activities, domestic animals, stocked wild animals and unidentifiable species (Table A.2). I also excluded detections of birds and small mammals (including bats) due to camera height (30 cm) biasing against these species. Despite the survey design being ground-based and thus biasing against arboreal species, I chose to keep vervet and samango monkeys in my analyses for two reasons: (1) in grassland habitats both species have been found to utilise ground and subterranean sources of food, therefore, their occurrence at the ground-level cannot be discounted (Nowak et al., 2017) and (2) both species have been linked with plantation damage (Di Bitetti, 2019), though to a lesser degree than baboons, and thus I felt it was important to include them for management implications. Finally, fast-moving mongooses captured in black-and-white night photos are difficult to identify to the species level, and thus I pooled all captures into a broad family group. Mongoose species with ranges extending into the study sites included: marsh mongoose (*Atilax paludinosus*), slender mongoose (*Galerella sanguinea*), white-tailed mongoose (*Ichneumia albicauda*), banded mongoose (*Mungos mungo*), and Meller's mongoose (*Rhynchogale melleri*). It is important to note that different species of mongoose have diverse habitat specialisations and, therefore, the estimates of habitat use and detection could vary greatly between species.

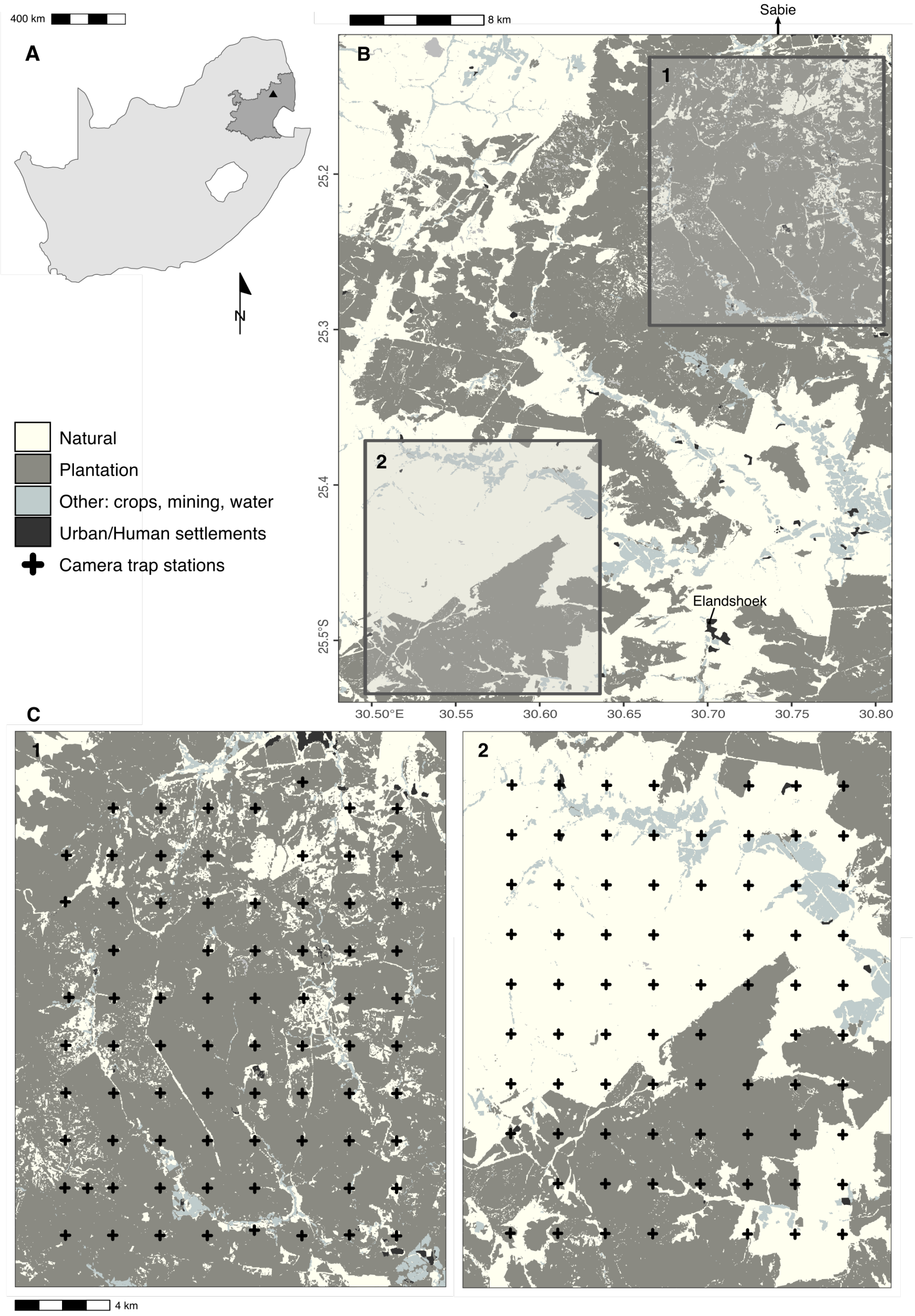

Figure 2.1. Sampling stations in study areas: (**A**) Mpumalanga province of South Africa highlighted in dark grey, with the triangle demarcating the general location of the two study sites. (**B**) Location of the two study areas: Site 1 (heavily transformed) and Site 2 (moderately transformed). (**C**) Land uses considered in the studied landscapes: natural vegetation, tree plantation compartments, urban areas and other land use types, such as crops and mines. The sampling stations of camera traps are shown by crosses, with plot numbers coinciding with the individual sites stated in (B).

2.2.3. Habitat covariates

To quantify terrain heterogeneity, I calculated the average Terrain Ruggedness Index (TRI) at each station from 30 m resolution Shuttle Radar Topography Mission (SRTM) elevation data (USGS, 2014). Each pixel was rescaled to 500 m and calculated as the square root of the summed squared difference between a pixel and its eight neighbours (Wilson et al., 2007). The TRI at each station was then calculated as the average TRI within a 500 m buffer area around each station. Vegetation productivity was estimated using the Normalized Difference Vegetation Index (NDVI), estimated per camera station (mean per grid cell) using Moderate-resolution Imaging Spectroradiometer (MODIS) data at 250 m spatial and 16 days temporal resolutions (Didan, 2015). NDVI is a widely utilised vegetation index, with values ranging from -1 to $+1$; higher NDVI values indicate increased vegetation density and overall plant health (Pettorelli et al., 2005). This index is especially useful for monitoring extensive agricultural landscapes and forest canopies, as it is highly sensitive to chlorophyll content (Huete et al., 2002). Thick vegetation could hinder the detection of certain species; therefore, NDVI was also included as a detection parameter. Euclidean distances to urban, roads, rivers and indigenous vegetation were calculated from the Mpumalanga Biodiversity Sector Plan (MPTA, 2014) and were extracted using `ArcGIS` (Version 10.1; ESRI, 2011). Distances were measured from the sampling location at the center of the cell to the nearest feature of interest (e.g., river, water source, road). If the sampling location was within the feature of interest (e.g., within indigenous vegetation), a distance of zero was assigned. Detection of domestic animals (incl. humans, cars, cows, dogs) was greater in Site 2 (N = 214) than in Site 1 (N = 107). While the presence of humans and domestic animals has been found to affect mammalian communities (Hughes and Macdonald, 2013; Zapata-Rios and Branch, 2018), I did not include this as a possible covariate for two reasons: (1) I purposefully avoided setting the cameras on roads to reduce theft, therefore the effect of car or human-foot traffic that is mostly confined to roads would be significantly under-represented in the sampling; (2) almost all detections of domestic animals were located around urban areas; therefore, I feel that the ‘distance to urban’ covariate would have been an adequate proxy for this potential disturbance. I tested the collinearity between covariates using Pearson's correlation with a threshold of $|r|$ = 0.7 (Dormann et al., 2013). No covariates were highly correlated with each other. Finally, all continuous data were standardised to a mean of zero and a standard deviation of one.

2.2.4. Occurrence modelling

I used multi-species hierarchical occurrence modelling (Dorazio and Royle, 2005) to estimate the probability that species used the area sampled by a camera station during the survey period, whilst accounting for incomplete detection (MacKenzie et al., 2002). Community modelling methods assume behavioural and functional similarities between species within a community, resulting in species-specific random effects that are drawn from the same distribution (Kéry and Royle, 2016). However, as I am comparing across different intensities of transformation, the relationship between species richness/occurrence and predictor variables may differ between the two sites (Drouilly et al., 2018a). Hence, to avoid the random effects being incorrectly shrunk towards a shared mean, I ran independent habitat use (occupancy) models for the two study sites to allow for differences due to transformation to emerge.

I adopted occupancy nomenclature, in which "Site" refers to the specific land management in which the surveys occurred. "Survey" defines a continuous primary sampling period within the site. The survey period is subdivided into several secondary sampling "occasions" over which sampling is replicated, and finally, "station" defines the locations of the camera traps.

I defined each occasion (hereafter denoted by k) as a pooled 7–day period. For each target species i the observed data consisted of a station by occasion matrix (Devarajan et al., 2020; MacKenzie et al., 2002). I defined the observed occurrence state of species i at station j by the binary variable z_{ij}, where z_{ij} = 1 if species i occurs at station j, or zero otherwise (Zipkin et al., 2010). z_{ij} is assumed to be the outcome of a Bernoulli random variable, such that:

$$z_{ij} \sim Bern(\psi_{ij}) \tag{2.1}$$

where ψ_{ij} is the probability of habitat use of species i at station j (Devarajan et al., 2020). To account for imperfect detection, repeated sampling ($K > 1$) was incorporated into the detection model to distinguish between ‘true’ absence and non–detection (MacKenzie et al., 2002; Zipkin et al., 2010) and defined as:

$$x_{ijK} \sim Bern(p_{ijK} \times z_{ij}) \tag{2.2}$$

where p_{ijK} is the detection probability of species i at station j on occasion K, conditional on its presence (z_{ij} = 1; Dorazio and Royle, 2005). Site–specific covariates hypothesised to influence species habitat use and detection (COV: TRI, NDVI, Distance to indigenous, urban, river and road), were incorporated into the model with associated linear terms (β and α). Therefore, the occurrence model for species i at station j was specified as:

$$logit(\psi_{ij}) = \beta_{0i} + \sum_{x}^{6} \beta_{xi} \times COV_j \tag{2.3}$$

where x is the index of the chosen covariates. Similarly, species–specific detection probabilities were calculated as:

$$logit(p_{ij}) = \alpha_{0i} + \alpha_{1i} \times NDVI_j \tag{2.4}$$

For each of the management models (n = 2 representing the two study sites), I linked species-specific responses to increased precision in estimates of species-specific habitat use, particularly for rare and elusive species (Zipkin et al., 2010). I used weakly informative priors for each habitat use (Equation 2.3) and detection (Equation 2.4) model; covariate coefficients were modelled as $\beta_{xi} \sim norm(\mu\beta, \tau\beta)$, where $\mu\beta$ is the community-level mean and $\tau\beta$ is the precision (Chandler and Royle, 2013). I modelled μ using a normal distribution and τ using a half-Cauchy distribution (Clark and Altwegg, 2019). Thus, covariate coefficients were functions of both the community-level hyperparameter and the species-specific effect for the respective covariate.

In many cases, the abundance of a species is related to both the overall habitat use probability and the average site-specific detection probability, resulting in positive correlations between habitat use and detection among species (Royle and Nichols, 2003) Therefore, I accounted for this correlation (ρ) between the occupancy model and the species-specific detection model (Equation 2.3 and 2.4) by specifying the two parameters (β and α) to be jointly distributed (Dorazio and Royle, 2005).

I augmented the models by adding a number of zero detection histories (N_{aug}), allowing me to estimate the number of species that were unobserved during the sampling process (Devarajan et al., 2020; Zipkin et al., 2010), and giving me an estimation of the number of species in the community N. The occurrence process was thus modified, such that:

$$z_{ij} \sim Bern(\psi_{ij} \times w_i) \tag{2.5}$$

where w_i is a binary variable indicating whether species i is present or absent, and is governed by the hyper–parameter ω:

$$w_i \sim Bern(\omega) \tag{2.6}$$

ω is defined as the probability that species i is a member of the meta-community of size N.

Augmentation

Although the majority of target species were detected in both sites, two species were undetected in the heavily transformed site (Site 1), namely klipspringer (*Oreotragus oreotragus*) and grey rhebuck (*Pelea capreolus*), despite their predicted ranges extending across both study sites. Additionally, rarefaction curves indicated that I likely recorded most species at the surveyed sites as both curves reached an asymptote (Figure A.1). To allow for comparisons between models, I used different augmentation values (N_{aug}) for the two sites. This resulted in N_{aug} = 6 all-zero records added to Site 2 and N_{aug} = 8 (i.e., 6 + 2) all-zero records added to Site 1, to account for the two missing species. I also ran two alternative test models: N_{aug} = 0 and N_{aug} = 30. In both cases, I obtained similar model estimates (ANOVA factor analysis: F(1, 30) = [0.003], p-value = 0.95) to the values obtained in the adopted model (N_{aug} = 6 and 8), and therefore concluded that data augmentation did not inflate the estimates. Finally, I excluded the first four capture days from the Site 2 survey, allowing the same survey lengths between sites, and pooled occasions into 7-day periods, resulting in 10 sampling occasions per station.

Habitat use modelling was carried out in `R` (Version 4.0.2; R Core Team, 2021), using the package `NIMBLE` (de Valpine et al., 2022, 2017). I used the multivariate adaptive random-walk Metropolis-Hastings sampler (or block sampler) for species random effects and sampled the remaining parameters using `NIMBLE`'s default samplers (Turek et al., 2017; de Valpine et al., 2017). I made inferences from 30 000 samples of the posterior distribution obtained from three chains of 120 000 Markov Chain Monte Carlo after a burn-in of 90 000 and a thinning rate of 10. Model convergence was assessed through a combination of Geweke statistics (Z; where $-1.96 < Z < 1.96$ indicates adequate convergence within single chains; Geweke, 1992), $\hat{R}$ statistics (where $\hat{R} < 1.1$ indicates convergence across all chains; Gelman, 2006) and visual examination of the chains through trace and autocorrelation graphs. All inferences are based on posterior means and Bayesian Credible Intervals (BCI). Finally, two separate generalised additive models (GAMs; one for each study site) were applied to model the relationship between baboon-specific habitat use and predictor covariates used in the habitat use models above. All GAMs were run using thin plate regression splines using `mgcv` (Version 1.8-38; Wood, 2011) and visualised using `visreg` (Version 2.7.0; Breheny and Burchett, 2017).

2.3. Results

Due to camera failure/theft, data were extracted from 76 (95%) of the 80 cameras at the heavily transformed site (Site 1) and 77 (96%) at the moderately transformed site (Site 2). Camera traps were active for a total of 3986 (heavily transformed; Site 1) and 2411 (moderately transformed; Site 2) trap days. Some cameras stopped recording before the survey ended due to battery failures from false triggers (e.g., moving grass), flash malfunctions (n=2, Site 1), and a camera falling off its stake (n=1, Site 1). A total of 28 species were recorded for the study, all of which were detected within the moderately transformed site (Site 2), including rare or secretive species, such as oribi (*Ourebia ourebi*), leopard (*Panthera pardus*), hippo (*Hippopotamus amphibious*) and aardwolf (*Proteles cristata*). Fewer species were detected at the highly transformed site (N = 18; Site 1; Table A.1). Species-specific detections varied greatly between sites (Table A.2) with all species having a greater number of detections within the moderately transformed site (Site 2).

Model assessments indicated that the two models had sufficient convergence, $\hat{R}$ scores were less than 1, and Gweke score values for all chains fell within the acceptable range ($-1.96 < Z < 1.96$). Overall species richness was not significantly different between the two sites, with the moderately transformed site (Site 2) having a mean of 23.09 (median = 23.35; 95% BCI = [21.37, 23.95]) and 21.67 (median = 21.92; 95% BCI = [18.89, 23.6]) in the heavily transformed site (Site 1). However, station-level species richness was significantly different (p-value $\ll$ 0.05; Figure 2.2) between the two sites, with the moderately transformed site having greater species richness.

Species-specific habitat use varied between the two sites (Figure 2.3A), with common duiker (*Sylvicapra grimmia*) and chacma baboon having greater probabilities of habitat use than all other species across both sites. The most widespread species were common duiker in the highly transformed site (0.79, 95% BCI = [0.69, 0.88]) and the chacma baboon in the moderately transformed site (0.77, 95% BCI = [0.66, 0.87]). Only two species had the highest estimated habitat use within the heavily transformed site (Site 1), namely common duiker and vervet monkey (0.25, 90% BCI = [0.15, 0.37]), with the lowest estimated habitat use for samango monkey (0.08, 95% BCI = [0.03, 0.14]). For the moderately transformed site (Site 2), the highest habitat use estimates were recorded for chacma baboons and the lowest for grey rhebuck (0.14, 95% BCI = [0.07, 0.24]).

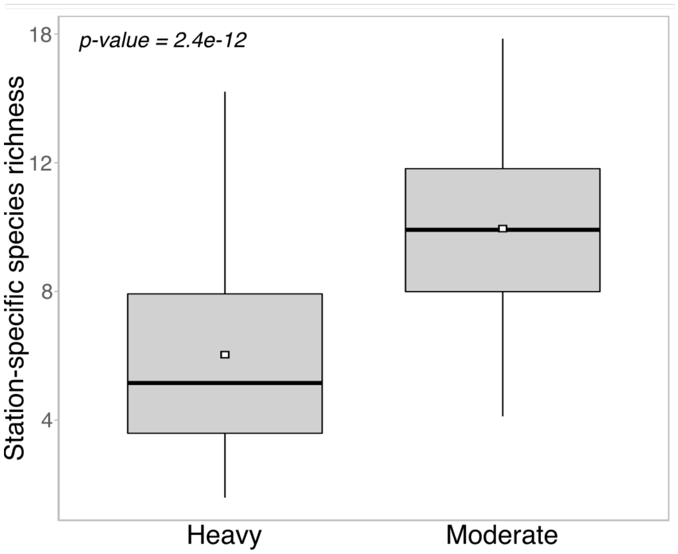

Figure 2.2. Estimated station-level species richness across the two study sites: heavily (Site 1) and moderately (Site 2) transformed (*see* Figure 2.1). Lower and upper box boundaries represent 25% and 75% Bayesian Credible Interval respectively, whilst the bold line represents the median. Significant differences between means (white squares) were estimated using an unpaired two-samples Wilcoxon test, where p-value < 0.05 was deemed to be significantly different.

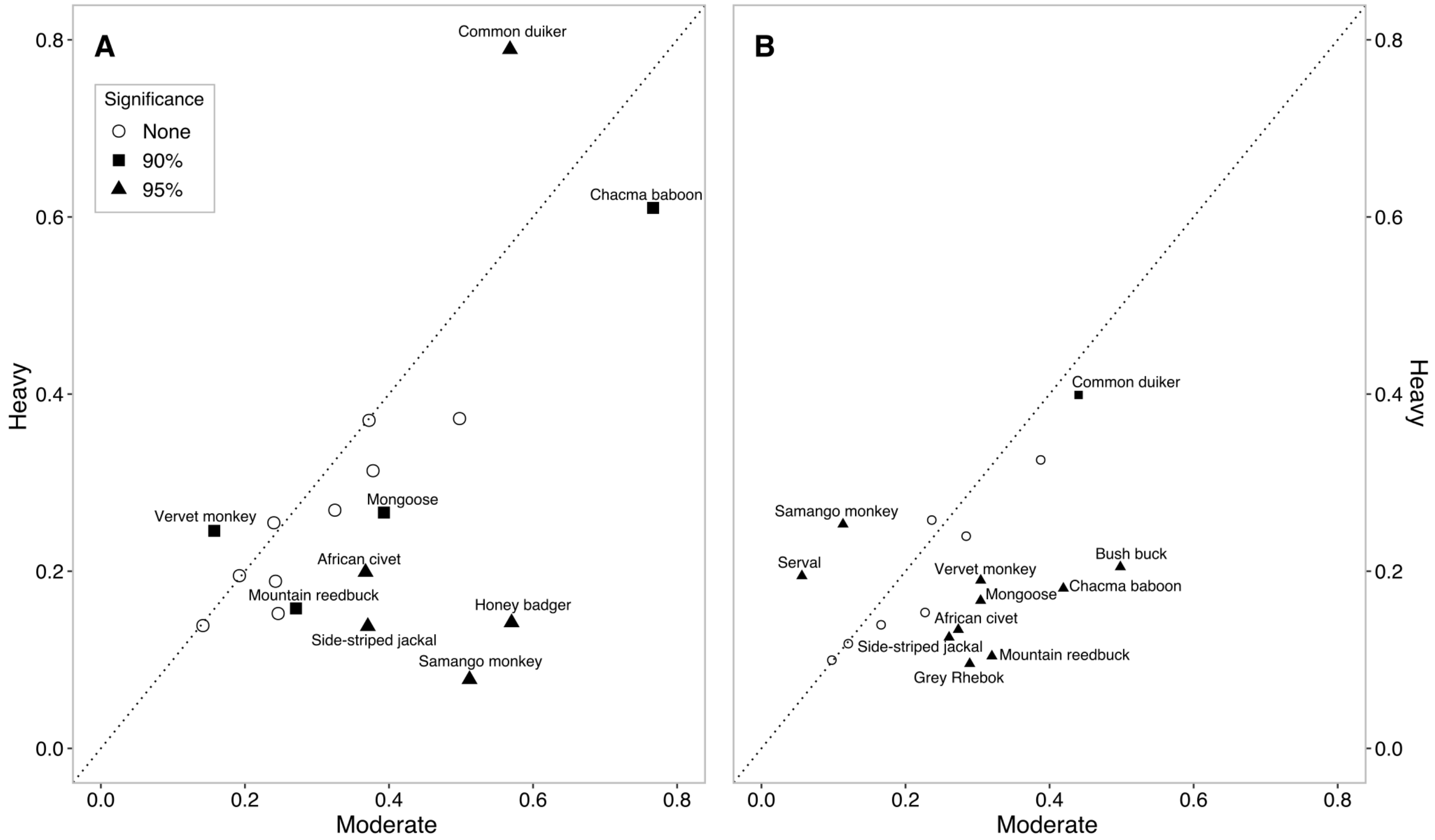

Figure 2.3. Species–specific mean (**A**) habitat use and (**B**) detection probabilities between the two study sites: heavily (Site 1) and moderately (Site 2) transformed (*see* Figure 2.1). Habitat use was defined as the proportion of camera trap stations used by a species and detection probability as the probability of recording a species if present in the study area. The dotted black line illustrates the 1:1 line and points symbols represent deviations from this line. Clear circles represent species where the 90% Bayesian Credible Intervals (BCI) for that species cross the 1:1 line, and therefore, no significant deviations were observed. Black squares represent species that significantly deviate from the 1:1 line at 90% BCI and black triangles at the 95% BCI. For clarity, I only labelled points that significantly deviated from the line.

Detection probabilities for most species in both sites were low, with mean detection probabilities of less than 0.5 per sampling occasion (Figure 2.3B). Species-specific mean detection varied markedly between the two sites, and half of the detected species had significantly higher detection probabilities at the moderately transformed site (Figure 2.3B). Only two species had higher detection probabilities in the heavily transformed site (Site 1), namely samango monkey (0.25, 95% BCI = [0.34, 0.40]) and serval (*Leptailurus serval*; 0.19, 95% BCI = [0.11, 0.30]).

The factors affecting mammalian community-level habitat use differed between sites (Figure 2.4). As expected, the probability of habitat use was significantly higher (95% BCI) in more rugged terrain (greater TRI), and in the highly transformed site, habitat use increased closer to indigenous patches (90% BCI). However, contrary to my predictions, habitat use increased further from indigenous areas in the moderately transformed site (90% BCI; Site 2), and in the highly transformed site, habitat use increased closer to roads (95% BCI; Figure 2.4).

There were no obvious spatial patterns in baboon habitat use across the heavily transformed site (Figure 2.5 *top right*). However, under moderate transformation, habitat use was notably higher outside of the plantation area (Figure 2.5 *bottom left*), the highest occurring along the edges of the plantation matrix before it transitioned into the tract of natural vegetation. The response of baboon habitat use to the different covariates varied between sites (Figure 2.6). For both sites, baboon habitat use was significantly higher at extreme TRI levels (Figure 2.6A), while intermediate TRI was associated with lower baboon habitat use. Distance to urban land did not strongly affect baboon habitat use in the heavily transformed site (Figure 2.6B), but significantly influenced habitat use under moderate land transformation, with increased habitat use further from urban areas. Finally, NDVI showed a weak (i.e., non-significant) negative relationship with baboon habitat use under moderate transformation (Figure 2.6F) but was significantly greater for higher NDVI within the heavily transformed site. Although distance to indigenous, distance to rivers and distance to roads did not have a significant effect on baboon habitat use (Figure 2.6C–E), some interesting relationships did emerge. Within the heavily transformed site, habitat use increased closer to natural indigenous vegetation. Though showing inverse relationships between the two sites, distance to rivers (or riverine areas) didn’t appear to greatly influence baboon habitat usage under either afforestation intensity. Finally, distance to roads showed similar relationships at both sites, with baboon habitat usage higher closer to roads.

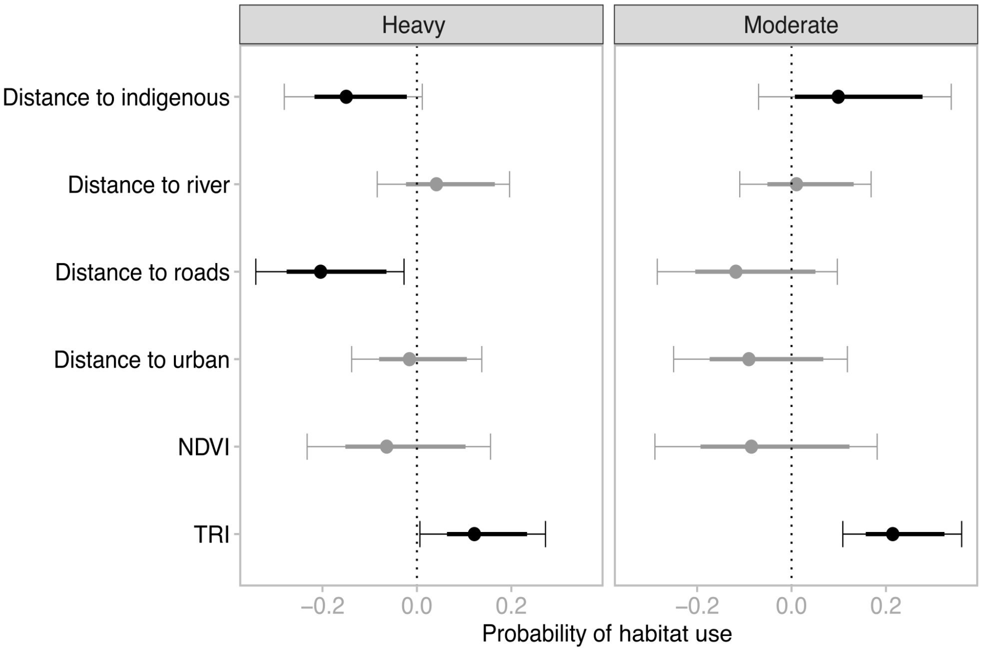

Figure 2.4. Caterpillar plot delineating effects of covariates on community-level habitat use across the two sites: heavily (Site 1) and moderately (Site 2) transformed (*see* Figure 2.1). Mean posterior summaries are denoted with points, the point range represents the 90% Bayesian Credible Interval (BCI) and the error bars are the 95% BCI. Significant relationships are in black (where either 90% or 95% BCI do not overlap zero). Distance covariates are Euclidean distances measured in metres, TRI: Terrain Ruggedness Index and NDVI: Normalised Difference Vegetation Index.

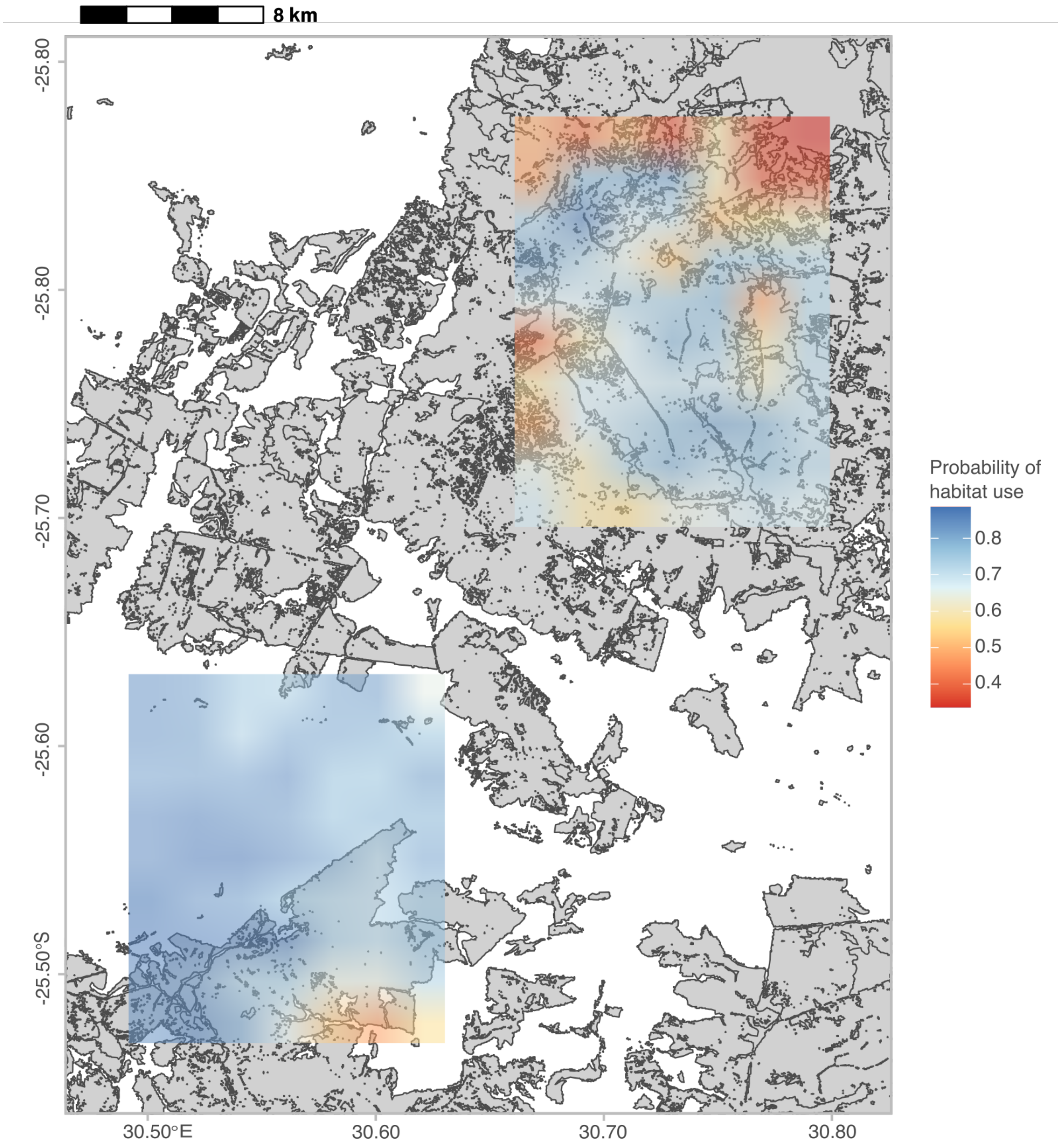

Figure 2.5. Probability of chacma baboon habitat use across the two sites: heavily (Site 1; *top right*) and moderately (Site 2; *bottom left*) transformed (*see* Figure 2.1). Grey areas represent plantation compartments. Other land cover types shown in Figure 2.1 were excluded for visualisation clarity.

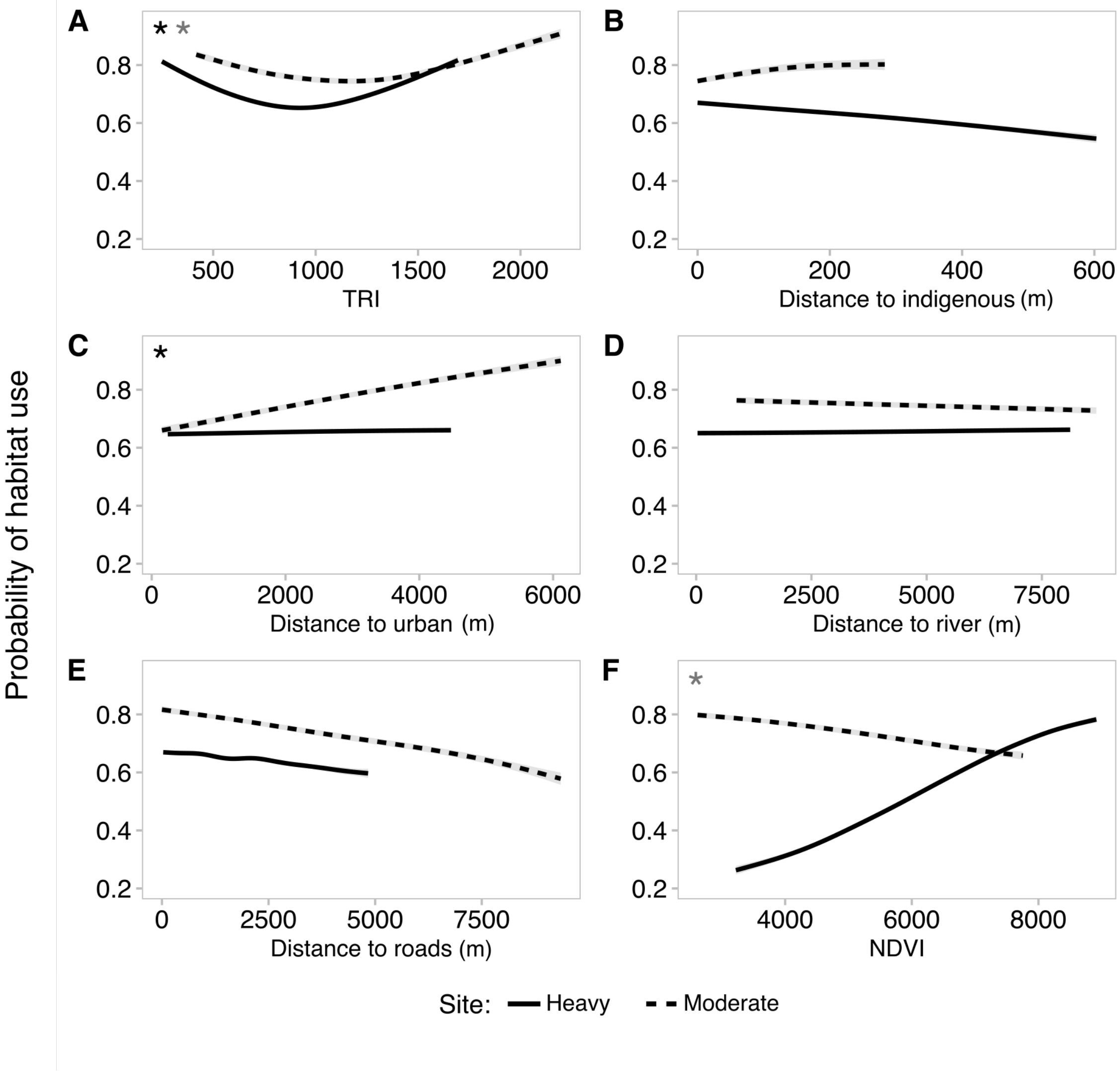

Figure 2.6. Generalised Additive Model (GAM) plots relating predicted station-level probability of habitat use for chacma baboons across the two sites: heavily (Site 1) and moderately (Site 2) transformed (*see* Figure 2.1). Each GAM had large percentages of deviance explained, 98.6% and 99.8% for the moderately and heavily transformed sites, respectively. The x-axis is the range of the environmental variable (TRI: Terrain Ruggedness Index and NDVI: Normalised Difference Vegetation Index) and the y-axis is the predicted probability of habitat use by baboons. Stars in the top left corners represent significant beta responses (based on 95% Bayesian Credible Intervals) derived from the two multi-species occurrence models, where grey stars represent the heavily transformed site (Site 1) and black stars represent the moderately transformed site (Site 2).

2.4. Discussion

I analysed camera-trapping data using a multi-species occurrence model and examined the influence of different intensities of grassland-afforestation on mammal species richness and habitat use. I demonstrated that areas experiencing lower levels of transformation had higher species richness and overall habitat use, with use increasing with ruggedness and in transitional zones. Community habitat use in the highly transformed site also increased with TRI and increased closer to indigenous vegetation patches. However, contrary to my predictions, the mammal community showed increased use of road networks in the plantation matrix and was not influenced by proximity to urban disturbances. Following my predictions, chacma baboon had greater occurrence within moderately transformed landscapes. Within a highly transformed plantation matrix, baboons were strongly influenced by environmental factors, such as terrain ruggedness (TRI) and plant productivity (NDVI). These results provide a baseline understanding of the distribution and composition of the mammal community in this commercially important land use. My results showed that intensively farmed commercial plantations can support a high mammal species richness, but that maintaining large tracts of natural habitat is necessary, especially with respect to specialist species most vulnerable to anthropogenic impacts.

Only two species were not detected under heavy transformation, and therefore overall species richness estimates were similar between the two sites. However, finer-scale species richness, at the camera station level, varied significantly both within and between the two study sites, revealing the differential impacts of land conversion on species across spatial scales (Brockerhoff et al., 2001). Transforming natural habitats for human use alters not only the number of species in an ecosystem but also their relative abundance in space (Hillebrand et al., 2008). This is further showcased in my results where, under heavy transformation, the mammal community was more restricted and revealed increased habitat use closer to the indigenous corridors. For example, samango monkey and serval had low estimated habitat use in heavily transformed areas but a high probability of detection. This suggests that these species were only located in certain areas (most likely indigenous corridors) where they were detected frequently. It is unclear from my results whether these natural pockets are providing adequate habitat for permanent occupancy or if these areas are predominantly used for dispersal through plantations. I removed species with fewer than 10 detections to minimise bias and enhance the reliability of estimates associated with small sample sizes. As a result, this approach may lead to conservative evaluations, as many "rare" species (i.e., those with fewer than 10 detections) were primarily found in the moderately transformed site. Consequently, the actual difference in richness between the sites may be more pronounced than indicated by these analyses.

In general, habitat specialists and narrow-ranging mammals have reduced probabilities of using modified habitats (Cravino and Brazeiro, 2021; Iezzi et al., 2020). This may explain why common duiker and vervet monkey had greater estimated habitat use within the heavily transformed site but grey rhebuck and klipspringer were only detected in large tracts of natural habitat (moderately transformed site; Table A.1). “Generalist” species that are behaviourally flexible and have broad dietary niches, such as common duiker, vervet monkey and chacma baboon, can better adapt to environmental changes and threats associated with anthropogenic modification (Fehlmann et al., 2021; Hoffman and O’Riain, 2012b). These generalist species are able to thrive and dominate a variety of habitats, such as plantations (Hillebrand et al., 2008) more so than typical “specialist” species. Since species were not evenly distributed through the study sites, my results warn against simply comparing overall species richness between areas as species dominance and community stability may be overlooked and potentially bias conservation assessments. I recommend that indigenous patches shared within plantations should not only contain delineated riverine passages but also reflect the original habitat, in this case, grassland, to better support specialist species. Additionally, further research should explore how the management of these indigenous patches, such as patch size or location, could improve the conservation and dispersal value of these green corridors (Perring et al., 2018).

The lower species richness of medium and large mammals in plantations shown in this study is consistent with findings from other regions (Cravino and Brazeiro, 2021) and for other taxa, including birds and invertebrates (Armstrong and van Hensbergen, 1994, 1995, 1996). Despite this, plantations have been shown to have less of an impact on native fauna than other agriculture operations, such as food crops (Baker et al., 2016). Plantations typically extend over thousands of hectares and thus have fewer human barriers (e.g. fences) and a much slower rotation/turnover than other agricultural practices. Plantations tend to have low levels of human disturbance (Betts et al., 2021), especially when compared to annual crops and even protected reserves. For instance, the moderately transformed site showed a higher detection of human activities and domestic animals than the heavily transformed site (214 captures in Site 2 vs. 107 in Site 1; Table A.2). Therefore, mid-aged and mature plantations can offer both refugia from other more intensive land use (e.g. crops), human disturbance and provide dispersal corridors to a variety of organisms (Root and Betts, 2016; Smith et al., 2013). However, this benefit is diminishing as rotation periods for certain tree species have significantly decreased, particularly in tropical and subtropical regions, often to just one or two decades. Although longer rotations still differentiate timber plantations from annual crops, shorter rotation periods limit the establishment of mature ecosystems and reduce habitat stability, undermining the ecological benefits of plantation landscapes. Furthermore, while the large spatial scale of plantations can link fragmented habitats, it may also restrict connectivity and habitat quality for species that require specific conditions found in more diverse, smaller-scale systems.

Only two species had probabilities of habitat use $\geq$0.50 under heavy transformation, namely common duiker and chacma baboons. Duiker has previously been found to be abundant on highly disturbed land in both drylands (Drouilly and O'Riain, 2019; Woodgate et al., 2018) and natural forests (Hou et al., 2021; Lwanga, 2006). Multiple primate species have succeeded within plantations benefiting from additional forest habitat, food and possible buffering from humans, predators, such as leopards, and other agroecosystems (Estrada et al., 2012; Hoffman and O'Riain, 2011; McCarthy et al., 2017; Spehar and Rayadin, 2017). In the Western Cape region of South Africa, chacma baboons have been shown to thrive in commercial plantations, achieving very high densities relative to surrounding natural habitat (Hoffman and O'Riain, 2012b; Hoffman and O'Riain, 2011). In the main forestry region of Mpumalanga, where the study was located, chacma baboons have been found to damage commercially planted trees through the behaviour of bark-stripping

(Germishuizen et al., 2017; McNamara, 2005; Peerbhay et al., 2018), which impairs growth and kills trees, reducing both the commercial value of timber and overall production rates (Nadel et al., 2012). Bark-stripping of *Pinus* plantations, in particular, is reported to be increasing and resulting in unsustainable levels of damage to trees and ultimately timber products (Peerbhay et al., 2018). Bark-stripping by baboons is not limited to South Africa, severe damage to plantations in Zimbabwe has resulted in an estimated loss of wood volume of approximately 50% and revenue losses of US$24 000 to US$32 000 per ha in bark-stripped compartments (Katsvanga, 2011). There are numerous theories as to why baboons strip bark from plantation trees (*see* Chapter 1), but only a limited understanding of baboon habitat use within plantations and how different land management practices may influence this use. I explore the relevance of these variables to baboon habitat use within plantations (*see* Chapter 3) and how they may influence bark-stripping behaviour (*see* Chapter 4). Given their reputation for frequently damaging planted trees, the high estimated probability of habitat use in heavily transformed areas ($\geq$0.50) by baboons in my study is a cause for concern. Although baboons showed greater habitat use in moderately afforested regions, they exhibited the highest probability of habitat use in heavily afforested areas compared to all species, except the common duiker. Additionally, despite lower overall habitat use in plantations, baboon use still correlates with significant damage (Germishuizen et al., 2017; McNamara, 2005; Peerbhay et al., 2018). Consequently, a better understanding of how baboons use plantations and how this influences their relative abundance is important for efforts that seek to manage bark-stripping damage and reduce production losses.

Terrain ruggedness (TRI) was the only covariate that strongly predicted community-level habitat use at both sites. Rugged and rocky areas restrict access to vehicles and hence preclude planting and subsequent mechanical harvesting. These rugged areas are often left as isolated pockets of natural vegetation that provide suitable habitat for the mammal community to occupy, resulting in high levels of habitat use in the vicinity. This would also explain the increased community-level habitat use closer to indigenous vegetation within the heavily transformed site. Unfortunately, inferring preference for such habitat is confounded by the fact that flatter lower-lying areas are invariably more transformed by urban and agricultural land uses, most of which also actively exclude a variety of mammal species (Hoffman and O'Riain, 2012b; Hoffman and O'Riain, 2011). However, critically interpreting this relationship is challenging due to the way distance was measured, where stations within indigenous vegetation were assigned a value of zero. Therefore, more research is needed to better identify the important habitat characteristics influencing community-level habitat use. Contrary to my predictions, community-level habitat use was greater in areas further from indigenous vegetation in the moderately transformed site. This suggests that even though the mammal community are utilising large tracts of natural land more than plantations, these transitional zones (i.e., where grassland meets plantation) may still provide valuable resources. Transitional areas tend to be more diverse in plant structure, species and age composition than core plantations or natural habitats, and thus, could provide refuge from potential predators and humans, act as a microhabitat offering shelter from climatic extremes and for increased foraging opportunities (Hoffman and O'Riain, 2011).

Despite my predictions, neither the distance to rivers nor urban areas were significant predictors of habitat use at either site. Small rivers are abundant within the study area and there are numerous human settlements (e.g., worker villages and equipment depots) interspersed within the plantation, and thus species are seldom far from either landscape feature possibly explaining their lack of predictive power of habitat use. Within the moderately transformed site, the community could be sufficiently buffered from disturbance from the surrounding urban or agricultural matrix. In this chapter, I did not differentiate between types of rivers (seasonal vs. perennial) or urbanisation, which may be an important factor, and thus, this is expanded upon in the following studies presented in this thesis.

Baboons in the moderately transformed site had significantly decreased habitat use in proximity to urban areas. With lower levels of human activity and fewer human settlements, it is likely that baboons in the moderately transformed site are less habituated to human presence and hence more likely to avoid human settlements. Additionally, the bounds of the study area transition towards cropland, which actively exclude and persecute baboons (Findlay and Hill, 2020), this may also account for the negative association with more urbanised areas. By contrast, baboon habitat use was not affected by distance to urban areas within the heavily transformed site where human activity linked to plantation management is consistently high and there are numerous human settlements interspersed through the plantation. Once baboons are habituated to the close presence of people they invariably learn to exploit the abundant human-derived foods found in urban areas (van Doorn and O'Riain, 2020; Fehlmann et al., 2021).

Baboon habitat use increased significantly with increasing NDVI within the highly transformed site, suggesting that baboons are attracted to more productive compartments within plantations. Similar results were noted by Katsvanga et al. (2009a) in Zimbabwean plantations and Germishuizen et al. (2017) in Mpumalanga. NDVI is a complex variable to disentangle within plantations as it can be related to an array of interacting factors such as tree age, species and pruning regimes (Feng et al., 2021). While NDVI can be a useful tool in timber plantations to assess productivity, understanding what baboons are utilising based on NDVI values is challenging. For example, different tree species may exhibit distinct reflectance patterns, leading to varying NDVI values and differing baboon foraging behaviour. I noted a general negative association between NDVI and baboon habitat use in the moderately transformed site and attribute this to baboons preferring natural grassland habitats over plantations. Plantations generally have higher NDVI than grassland, especially during the austral winter (Chamaille-Jammes et al., 2007), when the study was conducted. Baboons foraging in grassland habitats during the winter months typically consume invertebrates and subterranean food sources, e.g., bulbs and corms (Alberts et al., 2005), which will not be fully reflected by NDVI estimates.

Numerous studies have shown the negative effects of roads on biodiversity due to increased access to poachers (Haines et al., 2012) and higher rates of wildlife-vehicle collisions (Jamhuri et al., 2020). Despite these risks, some species (e.g., American marten *Martes americana*, golden jackal *Canis aureus* and red fox *Vulpes vulpes*) have been shown to habitually use unpaved logging roads (Ng et al., 2021; Turk et al., 2021) as open habitat better facilitates travel, provides resources along road edges, and reduces the risk of predation due to increased visibility. As a result of the influence of transportation and differing light intensity, the composition of plant communities in the vicinity of roads can be transformed (Saunders et al., 2002). This was observed at the heavily transformed site with increased community-level habitat use along road networks. This increased use along roads does require special management attention. While the majority of roads in plantations are unpaved with limited use, increased accessibility to a variety of habitats does increase the poaching risk. Enforcement of speed limits to reduce wildlife-vehicle collisions, controlling road access, and running snare sweeps near roads may help mitigate these risks.

In this study, I focus on how the level of transformation of natural habitats for commercial plantations affects mammalian diversity. The original goal, conceived at a stakeholder workshop in Mpumalanga in 2012 (Nadel et al., 2012), was to compare land used for commercial plantations with undisturbed natural habitat while controlling for area and key environmental variables (e.g., rainfall and altitude; Nadel et al., 2012). However, the few remaining large tracts of natural grassland in the region are mostly restricted to high altitudes (Carbutt et al., 2011), with lower rainfall and greater temperature extremes than the escarpment, where the majority of plantations are currently cultivated. Given various interests in the effects of plantations on mammal diversity, I opted to compare two equal-sized sites that were similar environmentally but with clear differences in the level of transformation of natural habitat. It is recommended that future studies be designed in ways that can make appropriate comparisons between agricultural plantations and high-altitude "pristine" or baseline grasslands, while also taking into account variations in environmental covariates that may influence biodiversity. Accurate comparative baseline data will provide important information for the development of conservation strategies and policies aimed at maintaining biodiversity in the face of ongoing anthropogenic activities.

The trade-off between timber production and biodiversity conservation is a significant challenge facing the forestry industry (Betts et al., 2021). Timber production is a key driver of forest management decisions and can have significant impacts on the structure and function of forest ecosystems. Furthermore, biodiversity outcomes are not only influenced by the configuration of the landscape but also by the amount of natural habitat available, which is directly linked to timber yields. Therefore, quantifying timber yields alongside biodiversity assessments will provide a more complete understanding of the trade-offs and synergies between timber production and biodiversity conservation, and is an important step in answering the key question of which landscape configuration (sharing, sparing or Triad; Betts et al., 2021) maximises biodiversity outcomes for a given level of timber production. This information can inform forest management decisions aimed at achieving sustainable forest use and conservation objectives. Future studies will also benefit from including longitudinal data to monitor the change, abundance, and resilience of the mammalian community to afforestation over time and improve our understanding of how management, and the timing of management, impact biodiversity (Perring et al., 2018). Additionally, these studies could help identify potential sink-source population dynamics within plantations, which could significantly influence land management and the planning of green corridors.

My findings indicate that maintaining natural grassland habitat, as well as riparian corridors within plantations (i.e., a land-sharing type approach), benefits local biodiversity in what was once a grassland-dominated landscape. However, delimiting natural areas may result in reduced timber production for a given area, and therefore to maintain yields the industry would have to extend its footprint, potentially leading to greater biodiversity reductions at regional levels than the current practice of intensively converting grassland habitat. Given that plantations are effectively green corridors that facilitate movement throughout the region (Werema and Howell, 2015; and suggested by my results), it is entirely possible that a land-sparing approach combining large patches of grassland in a mosaic with intensively used plantation patches provides the best compromise to produce the required volumes of wood while preserving meaningful biodiversity outside of formally protected areas. Currently, 500 000 ha of forestry-owned land are permanently unplanted (SANBI, 2013) and are set aside as protected reserves. However, a robust empirical comparison between baseline biodiversity data in protected grassland areas to those within plantations and modified corridors is still needed, especially in relation to timber yields and management strategies.

As agricultural landscapes increase globally to meet the demands of the rapidly growing human population, it is essential to evaluate how species diversity is affected within human-altered landscapes (Kshettry et al., 2020). Under intense land transformation, the mammalian community was found to be characterised by predominantly generalist species, most notably chacma baboons. Therefore, indigenous pockets within the plantation matrix could provide critical refugia and movement corridors for wildlife outside of protected areas that are almost completely excluded from urban, industrial and other uses of agricultural land, all of which are expanding rapidly in this region. The significant impact of roads on habitat use also highlights that the proportion of habitat cover is not the only factor determining mammalian diversity within plantations. Further research should also explore how improvements to yields and harvesting practices (Runting et al., 2019), land tenure security (Griscom et al., 2018) and restricting access to roads may influence biodiversity. Finally, more research must be carried out to determine the optimal size and spatial configuration of protected grassland units and how to manage species that thrive within plantations but threaten the crop itself.

CHAPTER 3

The spatial ecology of chacma baboons in commercial forestry plantations

Abstract

Non-human primates, such as baboons, exhibit a strong ability to adapt to human-altered environments, effectively exploiting novel resources across urban and rural landscapes. Understanding how baboons use human-modified landscapes is important for mitigating negative interactions through effective management strategies. In this chapter, I investigate the spatial ecology of chacma baboon troops living within and adjacent to commercial plantations in Mpumalanga, South Africa, where baboons are widely regarded as a pest species responsible for damaging commercial crops. I analysed GPS data from 17 free-ranging troops over a three-year period using integrated Step-Selection, T-LoCoH home range analyses and mixed-effects random forest models. My results reveal a clear preference for plantations, particularly during the wet season. Additionally, troops living in plantations exhibited similar, or smaller, home ranges relative to those living in natural habitats in the same region, and home range areas were not influenced by seasonal fluctuations. Revisitation patterns within home ranges were primarily driven by resource availability within the compartments rather than proximity to compartment edges and were significantly influenced by plantation compartment characteristics including tree age, the size of the compartment, tree species within the compartment and compartment productivity. This chapter challenges previous assumptions about baboon avoidance of pine compartments which provide access to reliable water sources and abundant natural and exotic plant food sources; and underscores the importance of considering multiple factors in comprehending baboon habitat selection dynamics and their interactions with human-modified environments. If baboons did not damage trees through bark-stripping, then commercial plantations might offer them a critical refuge from rapidly expanding food crops where there is no tolerance for baboons. Further research is thus important to understand why baboons damage trees and whether it is possible to reduce such damage while allowing baboons to persist in plantations.

3.1. Introduction

Habitat selection and resource use are important components of an animal's ecological niche, affecting dispersion and individual fitness, but can also have significant impacts on ecosystems and human livelihoods (Bloomfield et al., 2020; Kifle and Bekele, 2021; Parker et al., 2021). Therefore, understanding how animals use available habitat at differing spatial scales is essential not only for understanding how animals are distributed (Galán-Acedo et al., 2018; Johnson et al., 2015) but also for determining the necessary measures for successful management aimed at conserving biodiversity and promoting coexistence between wildlife and a range of human activities (Bracken et al., 2022; Fehlmann et al., 2017b; Hoffman and O'Riain, 2012a). It is widely recognised that primates can cause significant damage and loss to a variety of agricultural crops (Estrada, 2006; Hill, 2005; Mukeka et al., 2019), and consequently, are often cited as agricultural pests (Estrada, 2006). In Africa and Asia, primates are responsible for 50—70% of crop damage in agricultural areas surrounding protected areas (Hill, 2005; Naughton-Treves et al., 1998). In addition to these direct costs, primates can impose important opportunity costs by forcing people to invest precious time and money in protecting livestock and crops.

One species that has shown a remarkable ability to adapt to changing/modified landscapes is the chacma baboon, a medium-sized primate found in southern Africa. Chacma baboons, hereafter 'baboons', are known to inhabit a variety of environments, from deserts (Cowlishaw, 1997) to tropical forests (Okecha and Newton-Fisher, 2006), highlands (Stone et al., 2012), coastal areas (Lewis et al., 2018) and urban spaces (Hoffman and O'Riain, 2011). In recent years, they have also been observed to show a preference for non-food crops such as pine plantations (Hoffman and O'Riain, 2012b; Hoffman and O'Riain, 2011; Katsvanga et al., 2009b). Pine plantations offer several potential resources for baboons, including shelter from predators, food in the form of pine seeds and insects, a stable microclimate and green corridors linking natural land with nearby food crops (Henzi et al., 2011; Hoffman and O'Riain, 2012b; Hoffman and O'Riain, 2011).

How baboons utilise plantations remains a subject of ongoing debate, with research suggesting that they both actively avoid pine compartments (Henzi et al., 2011) as well as select for highly productive compartments (Germishuizen et al., 2017; Hoffman and O'Riain, 2012b; Hoffman and O'Riain, 2011; Katsvanga, 2011). However, there is consensus that baboons frequently engage in bark-stripping behaviour on commercially important tree species, resulting in significant costs for the forestry industry (Fergusson, 2005; Katsvanga et al., 2006). The significance of bark-stripping damage becomes pronounced as it accumulates over time, which is particularly concerning for long-lived species such as trees grown to maturity for timber and pulp production. In 2014, baboon damage was estimated to cost the South African forestry industry more than R130 million, or approximately US$12 million (FSA, 2020b). This loss of revenue does not include incremental growth losses due to damage, re-establishment costs, the cost of thinning and clear-felling of damaged trees, or losses of additional processing costs at sawmills. Therefore, in South Africa, baboon damage is one of the greatest threats to the long-term commercial viability of pine plantations (Nadel et al., 2012).

Despite these high costs to the commercial timber industry, research on the extent of damage, the possible drivers of damage and potential solutions is still extremely limited. Previous studies have attempted to derive methods for reliably measuring damage (McNamara, 2005), providing robust estimates of the scale of the economic loss due to damage (Fergusson, 2005), the drivers of bark-stripping behaviour (Katsvanga et al., 2009b; Ndagurwa, 2013), and whether lethal and non-lethal methods can reduce such damage (Katsvanga, 2011). More recent research has focused on efforts to derive indicators of damage that can then be routinely assessed using remote sensing technology to derive damage assessments at the level of compartments, plantations and ultimately the entire industry (Ferreira et al., 2020; Germishuizen et al., 2017; Peerbhay et al., 2018). However, there has been little research on how baboons are using the plantation landscape (*but see* Henzi et al., 2011 and Katsvanga, 2011) and the factors influencing resource selection at varying spatial scales within plantations.

The first objective of this chapter was to investigate the ranging behaviour of baboons within and around commercial plantations and to use these data to explore whether there is a selection for plantation compartments versus "other" vegetation across the geographical range of the study troops. Secondly, I explored the home range size of the troops living predominantly in plantation habitats, and how this may vary seasonally. Finally, using behavioural metrics extracted within the home range, namely, revisitation rates, I explored the specific factors that drive the use of timber compartments by baboons. These data represent an important step in the long-term goal of an improved understanding of the ecology of baboons in plantations.

3.2. Methods

3.2.1. Study area

This study was conducted in the Mpumalanga province of South Africa (Figure 3.1), covering an area of approximately 3000 km^2. Within this region, commercial plantations occupy ca. 2350 km^2 spanning broad altitudinal and climatic ranges (altitude: 400–2100 m above sea level; mean annual precipitation: 630–1600 mm; mean annual temperature: 13–21 °C) and largely comprised of exotic genera such as *Pinus*, *Eucalyptus* and *Acacia* (FSA, 2020a; Shai, 2021). Compartments range in size from under 0.01 km^2 to 1 km^2, with approximately 70% of the land planted and the remaining 30% of land being allocated to roads, infrastructure and natural areas. Other agricultural activities in the area include the production of subtropical fruit crops (e.g., avocado, mango and litchi), as well as macadamia nuts (Fruit South Africa, 2022).

3.2.2. Data collection

I used archived GPS data collected by the forestry company Sappi as part of their long-term monitoring of baboon troops within plantations. GPS data were available for a total of 17 adult female baboons that were collared between 2016 and 2018 (African Wildlife Tracking (AWT) Iridium Nan collars; https://awt.co.za), with recording periods ranging from 314 to 600 days (Table 3.1). I initially screened the GPS data for any conspicuous errors, particularly instances where points fell well outside the defined study area. This step was essential to ensure the integrity and reliability of the data for subsequent analyses and research objectives. The number of sample points collected was adjusted based on the duration of deployment

Table 3.1. GPS collars deployed on individual baboons in 17 different troops across six plantations in the Mpumalanga region of South Africa. Plantations grouped by region (*see* Figure 3.1). Data include the date on which the collar was affixed and then removed, the total number of days the collar was active, and the number of GPS data points recorded.

Region	Collar ID	Plantation	Fit Date	Remove Date	No. Active Days	No. GPS Points
1	NAN00236	Mooifontein	25/03/2017	12/07/2018	474	1102
	NAN00242	Mooifontein	30/12/2016	07/07/2018	554	1832
	NAN00243	Mooifontein	09/01/2017	08/07/2018	545	1949
2	NAN00254	Houtboshoek	31/07/2017	12/07/2018	346	471
	NAN00255	Houtboshoek	11/08/2017	12/07/2018	335	579
	NAN00256	Houtboshoek	24/08/2017	11/07/2018	321	445
3	NAN00241	Glenthorpe	27/12/2016	22/11/2017	330	521
	NAN00248	Glenthorpe	18/01/2017	10/07/2018	538	1943
	NAN00246	Sjonjona	10/03/2017	12/07/2018	489	1417
	NAN00251	Sjonjona	26/02/2017	11/07/2018	500	1711
4	NAN00245	Ndubazi	12/03/2017	10/07/2018	485	1667
	NAN00247	Ndubazi	02/03/2017	12/07/2018	497	1679
5	NAN00237	Highlands	18/11/2016	11/07/2018	600	1233
	NAN00238	Highlands	04/12/2016	22/11/2017	353	1127
	NAN00239	Highlands	05/12/2016	12/07/2018	584	1990
	NAN00240	Highlands	19/04/2017	11/07/2018	448	742
	NAN00249	Highlands	12/01/2017	22/11/2017	314	4139

(number of sample days); which varied due to satellite connection issues and collar errors. As baboons are group living and females are typically philopatric (Clarke et al., 2008; Henzi and Barrett, 2003), I assumed that GPS data provided a proxy for the movement of the entire troop (Hoffman and O'Riain, 2012b). Collars were programmed to record a GPS point every four hours in each 24-hour daily cycle, with recording times varying between individuals based on deployment time.

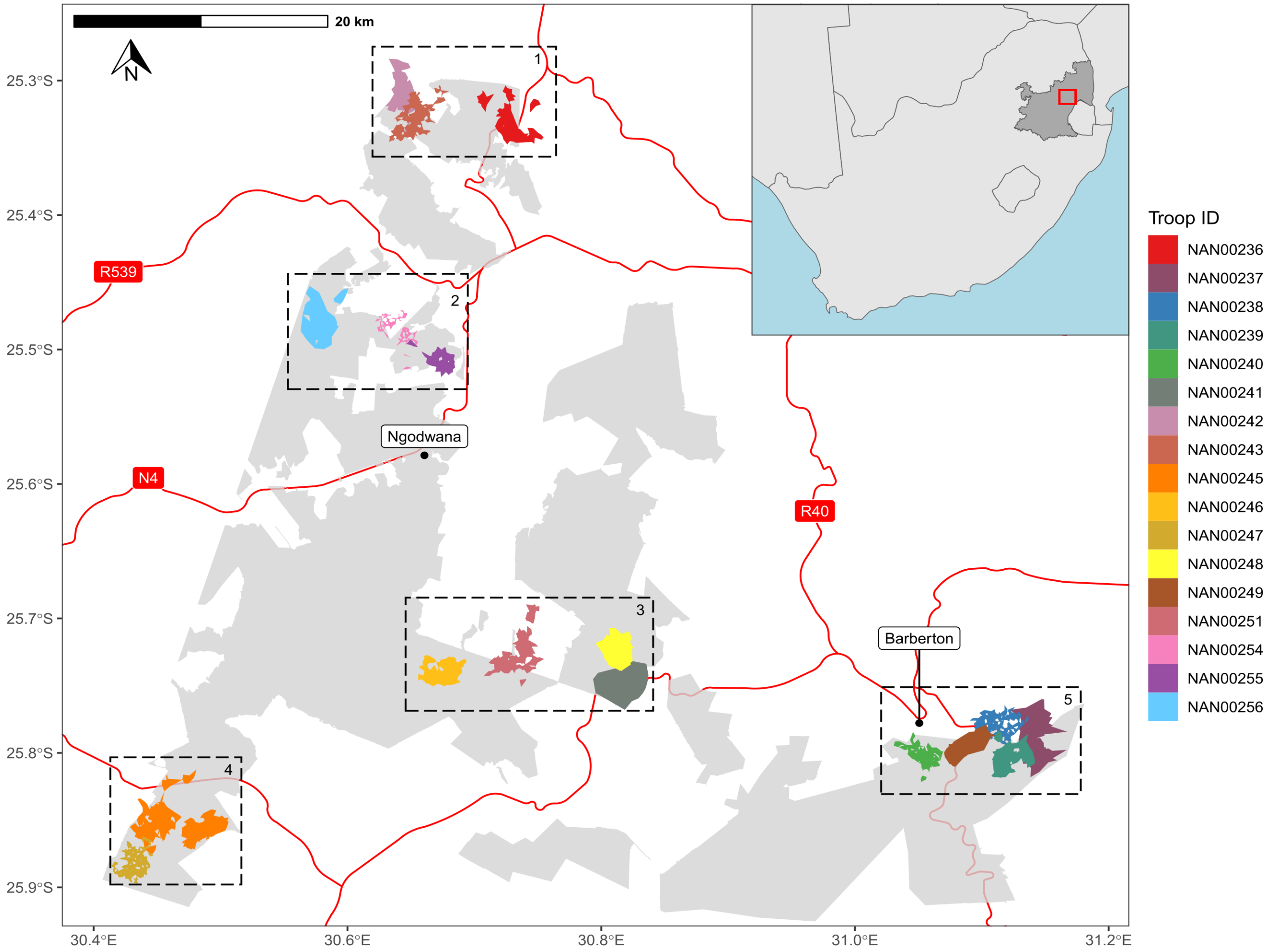

Figure 3.1. Home ranges (95% utilisation distribution) for 17 chacma baboon troops across a plantation matrix (grey polygons) in Mpumalanga province, South Africa. Each troop is represented by a different colour. Red lines are the main roads within the region. Home ranges are grouped into five regions enclosed by rectangles with dashed sides. Inset: Mpumalanga province of South Africa, highlighted in dark grey, with the red square demarcating the general location of the study area. Detailed maps of the different regions can be found in the supplementary materials (Figure B.1 – B.1).

3.2.3. Step-Selection Functions

I constructed integrated Step-Selection Functions (iSSF) following Muff et al. (2020), using an Inhomogeneous Poisson Process model with stratum-specific fixed intercepts to identify population-level habitat and movement selection by troops across the plantation matrix, while accounting for individual variation. This approach allowed for an assessment of the probability of habitat features being ‘used’, relative to what was ‘available’ in the landscape (Signer et al., 2019). To establish a uniform sampling rate, I resampled the movement data such that relocations were all approximately 8 hours apart, with a tolerance of 1 hour (Signer et al., 2019). As I was interested in troop habitat selection and movement through different habitats, I removed GPS locations occurring after sunset and before sunrise, after resampling, to exclude sleeping site selection.

‘Available’ locations were simulated using parametric distributions of step lengths (i.e., the Euclidean distance between two consecutive GPS points) and turn angles (the turning angle between headings of two consecutive steps) that were parameterised using the observed step lengths and turn angles of the GPS tracked baboons (Michelot et al., 2019; Thurfjell et al., 2014). As such, 20 available locations for each ‘used’ location were simulated using an exponential distribution for step lengths and a Von Mises distribution for turn angles (Fieberg et al., 2021; Signer et al., 2019). Habitat type was extracted at each ‘used’ and ‘available’ step to determine whether troops were using the habitat characteristic more (interpreted as selection) or less (interpreted as avoidance) than expected by chance (Fieberg et al., 2021; Signer et al., 2019). Habitat type was coded as “plantation” or “other”, as visualised in Figure 3.1. “Other” vegetation included natural habitat both within (e.g., riparian corridors) and adjacent (e.g., open grassland) to plantations. To determine if plantation habitat also influenced baboon movement, habitat type was extracted at the beginning of a step and included in the model as an interaction with both step length and turn angle (Signer et al., 2019).

I created a mixed-effects model framework using the `glmmTMB` package (Version 1.1.7; Brooks et al., 2017) that included a random intercept for each troop and allowed troops to vary in their response to movement and selection, with a random slope for the main fixed effects: habitat type and year. Baboons are known to switch diets between seasons based on changes in food availability and nutritional needs (Alberts et al., 2005; van Doorn et al., 2010; Hill and Dunbar, 2002). To account for this variation, I split the models into wet (spring/summer) and dry (autumn/winter) periods. All models included a selection component: habitat type. I selected "other" vegetation as the reference category in the models, therefore determining how troops responded to plantation areas in comparison to native vegetation. Each model also contained movement terms (step length and cosine of the turn angle) and interaction between habitat type and each movement term to account for general space-use behaviour (Forester et al., 2009; Signer et al., 2019).

3.2.4. Home range estimation

Home range refers to the spatial area within which an individual or a group of animals typically moves and carries out their regular activities (Burt, 1943). It represents the extent of the animal's habitual use of space and is influenced by a variety of factors, including resource distribution, group size, social interactions, predation risk and reproductive requirements. The size and shape of a home range can vary greatly among different species, populations and individuals within a species, depending on ecological and environmental factors (Hoffman and O'Riain, 2012b; Johnson et al., 2015). In the case of baboons, home range is influenced by their dietary needs, social structure, competition for resources and the distribution of preferred habitats (Johnson et al., 2015). Home range serves as an indicator of the spatial scale at which baboons carry out their daily activities and provides valuable insights into their ranging behaviour, habitat selection and interactions with conspecifics and the surrounding environment.

By utilising advanced tracking technologies such as GPS collars, which provide precise and frequent positional data, researchers can track the movements of individual baboons or entire troops and create detailed movement paths (Fleming et al., 2016). Accurate estimation of the baboons' home range not only helps to understand their spatial requirements and resource utilisation but also contributes to broader conservation and management efforts by identifying critical habitats and assessing the impact of human activities on baboon populations (Fehlmann et al., 2023).

The Minimum Convex Polygon (MCP; Mohr, 1947) method is one of the most widely used home range estimation methods (Signer and Fieberg, 2021), especially in primate research. This empirical estimate of home range is produced by connecting the exterior points of an animal's known positions in space to form a convex polygon. However, the MCP method presents several disadvantages: (1) it is highly sensitive to sampling effort, resulting in home-range estimates scaled according to the number of GPS locations collected, (2) it is sensitive to outliers, i.e., occasional excursions or "sullies" can significantly influence the estimated home range, (3) it assumes that the home range is a convex polygon, thus it generally overestimate the home range of the animal by including areas that are not utilised by the animal at all (Anderson, 1982; Börger et al., 2006; Signer and Fieberg, 2021) and it disregards landscape features, such as rivers and physical barriers (e.g., fences; Scull et al., 2012).

In contrast, Time-local-convex-hull (T-LoCoH; Lyons et al., 2013) employs a kernel modelling approach to identify specific areas that animals repeatedly visit, i.e., core areas (Benhamou and Riotte-Lambert, 2012). Here it is assumed that core areas offer higher profitability in terms of food resources or refuges (Lyons et al., 2013) and thus they are visited more often and/or for longer periods of time. In plantations, adjacent compartments can differ substantially in their physical characteristics (e.g., age of trees, species planted, compartment size, etc.), and the transition from plantations to natural vegetation is typically abrupt. These transitions could be perceived as hard boundaries that could potentially interrupt behaviour patterns. T-LoCoH incorporates boundaries into the analyses and thus more effectively captures the influence of compartmental heterogeneity on animal movement than MCP. Study troops' home ranges were estimated using the T-LoCoH method, based upon previous local-convex hull methods (Getz et al., 2007) and implemented in the `R` package '`tlocoh`' (Version 1.40.07; Lyons et al., 2018). Utilisation distributions (UDs) were created by selecting k nearest neighbour points*. These UDs, or hulls, were then merged from the smallest to the largest to form the familiar 50% and 95% UD isopleths. This nearest neighbour selection process was also modified by the time-scaled distance parameter s, which incorporated time (and therefore temporal autocorrelation) into the home range estimate by rescaling the Euclidean distance between two points in space into a time-scaled distance.

T-LoCoH documentation sets out guidelines to manually select k- and s-values (Lyons, 2013). However, these user-defined parameters are highly subjective, and the resulting hulls are sensitive to the values selected (Dougherty et al., 2017). Therefore, to allow for meaningful and unbiased comparisons between troops, a machine learning cross-validation-based parameter selection process, outlined by Dougherty et al. (2018), was used to achieve standardisation between the T-LoCoH parameters (k and s). Data were divided into training and testing datasets. For each troop, the test points were chosen at random from the entire movement path, which resulted in each point having a 0.002 probability of being selected as a test point. To ensure independence between test points, 50 points preceding and following each selected test point were removed from the full dataset, with the remaining data forming the training data. Therefore, the resulting training data sets consisted of approximately 80% of the original data points, while testing points accounted for approximately 20%. To minimise variation in the procedure, this stochastic splitting process was repeated 100 times for each troop movement path.

A grid-based exploration of parameter space was then conducted, whereby each of the training/testing datasets ($I = 1, ..., n$) was analysed at every combination of k and s values on the grid. The test points ($J = 1, ..., m$) were then laid upon the resulting hulls. Probabilities for out-of-sample points were formulated by normalising the LoCoH surface so that the probability of an observation occurring at a particular location could be calculated, which allowed for a natural penalty for high k values. This value was obtained by dividing the number of training hulls that contained the test point location ($g_{I,J}$) by the summed area

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[*] Different methods of nearest neighbour selection are available, for example, the r-method finds all nearest neighbours with a radius r and the a-method finds all neighbours whose cumulative distance is less than or equal to a. See Getz et al. (2007) for more information.

of all training hulls (A_I). Then, the log probability was calculated for each point per training hullset. To avoid log probability values of $-\infty$, test points that were not contained within any hulls were assigned a probability value equal to the inverse of A_I^2, resulting in a substantially lower log probability than that of a test point contained in a single hull. Finally, a single value ($P_{k,s}$) was assigned to each combination of k and s values by summing across all of the test points in all of the training/testing datasets:

$$P_{k,s} = \sum_{I=1}^{n} \sum_{J=1}^{m} log \frac{g_{I,J}}{A_I} \tag{3.1}$$

This grid-based search of parameter space allowed for the identification of the optimal combination of k- and s-values for each troop, which was implemented in the T-LoCoH home range estimation process (Table 3.5).

Despite its shortcomings, MCP techniques remain widely utilised (Kie et al., 2010), particularly in primate research, and thus, I also computed home ranges using MCP methods to enable comparisons with previous research. I calculated both 50% and 95% home range areas using the `ADEhabitatHR` package (Version 0.4.21; Calenge, 2023). Finally, I used Mann-Whitney U tests (`stats` package; Version 4.2.3) to test for significant differences between the home range estimation methods (T-LoCoH vs. MCP).

3.2.5. Revisitations within plantation compartments

Revisitation was extracted from the T-LoCoH analyses by specifying an Intervisit Gap Period (IVG) dictating how much time must pass between two points before they are considered separate visits to the same local hull. As baboons are diurnal animals, I selected an IVG of 12 hours to reflect activity between sunrise and sunset. Revisitation was defined as the number of separate visits to a local hull (NSV), with separation determined by the IVG. Duration of use, defined as the mean number of locations per visit (MNLV) or the number of locations in the same hull within the IVG period, was initially examined but there was not enough variation in the data to run random forest analyses (Figure B.7), i.e., models did not converge and/or had low accuracy (< 0.5% Out-of-Bag (OOB) R^2 values).

I investigated how compartment-level explanatory variables affected revisitation using mixed-effect random forest models (hereafter MixRF; Wang et al., 2016). This combines the flexibility of Random Forests for habitat modelling with the advantages of Generalised Linear Mixed Models (GLMM) for structured data. MixRF iterates between Random Forest models, implemented using the '`ranger`' package (Version 0.14.1; Wright and Ziegler, 2017), to fit fixed effects (environmental predictors (Table 3.2)) and GLMM (`lme4` package; Version 1.1-31, Bates et al., 2015; with `nlopt` optimisation, Johnson, 2007) to fit random effects with individual troop ID nested within the study site, i.e., Plantation. I also incorporated "Plantation" as a fixed effect to account for regional and temporal differences (Ripari et al., 2022). Data were split into training (80%) and testing (20%) sets, with each set containing a sub-sample from each troop. For the random forest component, the optimum number of variables to be randomly selected at each node split (*mtry*) and the number of decision trees (*ntree*) were determined using a grid-optimisation procedure based on their relative OOB root-mean-square deviation (RMSE) values (Table B.2). I used OOB cross-validation to evaluate the model's goodness of fit and predictive power. Variable importance was estimated using the permutation variable importance approach (Breiman, 2001) which considers a variable important if it has a positive effect on the prediction performance of the model (Wright et al., 2016) and estimated their respective significance (p-values) using simple permutation tests (Altmann et al., 2010). I visualised significant numerical variables (p-values < 0.05) using Partial Dependent Plots (PDP), with a '*loess*' smoother, from the `pdp` package (Version 0.8.1; Greenwell, 2017) and categorical variables using Accumulated Local Effects (ALE) Profiles from the `DALEX` package (Version 2.4.3; Biecek, 2018). Computations were performed using facilities provided by the University of Cape Town's ICTS High Performance Computing team: hpc.uct.ac.za.

Table 3.2. Overview of compartment-level covariates used in the mixed-effect random forest models (MixRF) to assess revisitation rates by baboon troops across a plantation matrix in the Mpumalanga region of South Africa. All variables marked with ∗ were sourced from maps supplied by Sappi Forests.

Proxy variable	**Ecological importance**	**Method**	**Range**	**Resolution**
Distance to urban	As proxy for disturbance in the landscape due to settlements. Risk factors due to negative interactions with people.	Euclidean distance to closest urban areas (from 2018 South African land cover map).	0–5262.14 m	100 m (min. areal mapping unit 25 ha)
Distance to agriculture	As proxy for disturbance in the landscape as baboons are aggressively excluded from crops. Risk factors due to negative interactions with people.	Euclidean distance to closest agriculture pixel (from 2018 South African land cover map).	0–5393.16 m	
Distance to roads∗	As proxy for disturbance in the landscape due to roads. Risk of mortality. Could also be an attractant due to visibility, ease of movement and increased foraging opportunities.	Euclidean distance to closest road, including main plantation roads (used more regularly), internal compartments roads (used less frequently) and all roads (including all plantation and national roads).	0–762.81 m	100 m
Distance to rivers∗	Water availability or proxy for natural riparian vegetation.	Euclidean distance to closest river. Rivers were coded according to flow regime (2, 1, 0) and all rivers.	0.01–842.38 m	
Roughness∗	Proxy for terrain characteristics. Terrain ruggedness could alter available food resources or microclimates for baboons.	Terrain ruggedness index (TRI): the maximum difference between a pixel and its 8 nearest neighbours (Wilson et al., 2007).	0–547 m	90 m
Altitude∗	See ‘Roughness’.	Average compartment altitude above sea level.	886–1820 m	Compartment level

continued . . .

Table 3.2 Overview of compartment-level covariates used in MixRF model to assess revisitation rates by troops — *(continued).*

Proxy variable	**Ecological importance**	**Method**	**Range**	**Resolution**
Minimum/Maximum/ Mean Temperature	Baboons avoid temperature extremes and plantations may buffer climate (Hoffman and O'Riain, 2011).	Min/Max/Mean daily air temperature aggregated from ERA5 hourly values (Hersbach et al., 2022).	-3.07–20.92 °C 8.08–35.77 °C 4.59–27.75 °C	0.25° × 0.25° at 2 m height
Total Precipitation	Rainfall drives primary productivity and thus higher rainfall is predicted to increase above-ground biomass (Magandana et al., 2020).	Total daily precipitation aggregated from ERA5 hourly values (Hersbach et al., 2022).	0–0.05 m	0.25° × 0.25° at 2 m height
Site Index (SI)∗	A measure of species-specific site productivity (Kotze et al., 2012). Compartment productivity could influence resource availability for baboons.	Calculated as the dominant compartment height at a reference age, which, in this instance, was 20 years.	11.2–26.3 m	Compartment level
Genus∗	Exotic tree genera in plantations may differ in their levels of palatability and/or the quality of refugia for baboons.	Planted tree genera.		Compartment level
Species ∗	See 'Genus'	Species or hybrid planted.		Compartment level
Plantation∗	Plantation-level management varies spatially and temporally.	Plantation name.		Plantation level
Age∗	Exotic tree age may differ in their palatability and/or the quality of refugia for baboons.	Calculated as difference from Datetime of GPS location and date planted.	0–32 years	Years
Distance to compartment edge∗	Usage of a compartment may vary spatially, with increased usage along the edges (Henzi et al., 2011).	Euclidean distance to closest compartment edge.	0–371.67 m	
Distance to nearest conservation unit∗	Areas of natural vegetation within plantations could provide important resources for baboons, with increased usage closer to conservation units (CUs; Henzi et al., 2011).	Euclidean distance to closest demarcated/delineated natural area within plantation matrix.	0–367.18 m	

3.3. Results

3.3.1. Habitat selection

During the wet season, troops showed a significantly higher likelihood of being found in plantation compartments compared to other vegetation types (mean odds ratio = 1.37; Table 3.3), but their step lengths and turn angles were similar irrespective of vegetation type. By contrast, in the dry season, there was no significant preference for habitat type, but troops had a significantly greater step length when in plantation compartments (Table 3.3).

Table 3.3. Integrated Step-Selection Function (iSSF) model output for baboon troops (n = 17) seasonal selection response to vegetation type across a plantation matrix in the Mpumalanga region of South Africa. Significant responses (p-value < 0.05) in bold.

Season	Explanatory Variable	Estimate	SE	p-value
Wet	**Plantation**	**0.314**	**0.131**	**0.017**
	Plantation : Step Length	0.031	0.039	0.424
	Plantation : Turn Angle	-0.043	0.060	0.473
Dry	Plantation	0.015	0.092	0.869
	Plantation : Step Length	**0.137**	**0.047**	**0.003**
	Plantation : Turn Angle	-0.095	0.065	0.144

3.3.2. Home range analyses

Estimates of home range area differed depending on the estimation method utilised. The MCP method consistently yielded larger home range area estimates compared to the T-LoCoH method (Table 3.4) at both the 50% (W = 52, p-value = 0.001) and 95% (W = 66, p-value = 0.006) home range isopleth/area. Baboon troops within and adjacent to forestry plantations exhibited a mean home range size of 12.18 km^2 using the MCP method (95% MCP methods; Table 3.4), while the T-LoCoH method yielded a mean home range size of 7.73 km^2 (95% T-LoCoH methods; Table 3.5). Ranging area estimates did not exhibit significant variations between seasons (Figure 3.2). This finding contrasts with the observed seasonal variations in habitat selection and movement patterns and suggests that, despite differences in habitat preference and movement behaviour (Table 3.3), the overall spatial extent of the home ranges remained relatively stable throughout the year.

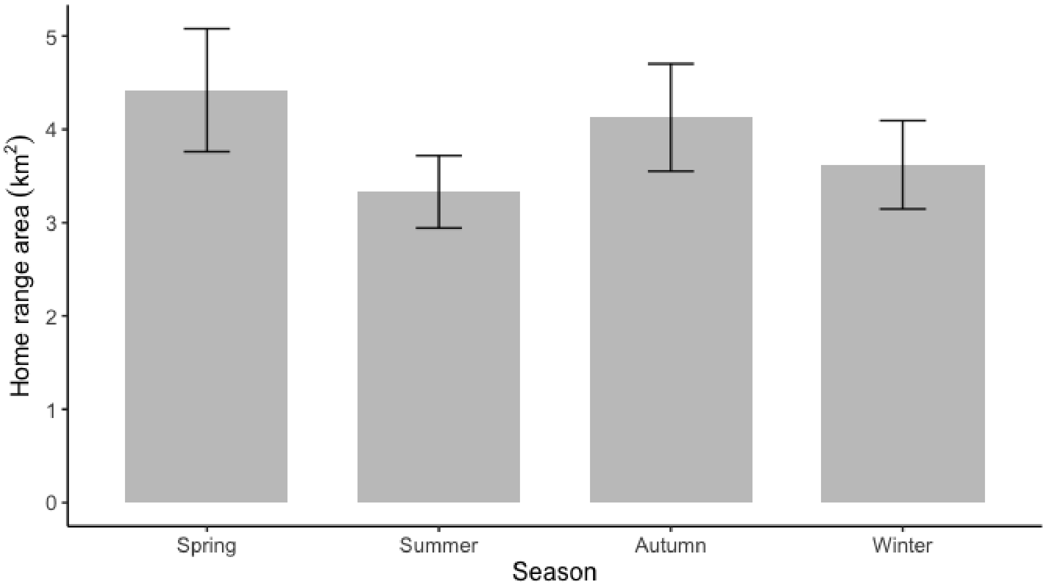


Figure 3.2. Mean (± SE) seasonal ranging area for 17 chacma baboon troops (*see* Table 3.1). Range estimates were calculated using the 95% Time-Local Convex Hull (T-LoCoH) density isopleth.

Table 3.4. Core (50%) and total (95%) home range area (km^2) estimates for 17 chacma baboon troops (unique Collar ID; *see* Table 3.1) across six forestry plantations using the Minimum Convex Polygon (MCP) estimation method.

Collar ID	**MCP**	
	50% (km^2)	95% (km^2)
NAN00236	2.702	17.696
NAN00237	2.702	17.696
NAN00238	3.624	10.410
NAN00239	2.552	9.077
NAN00240	1.084	7.524
NAN00241	4.350	11.818
NAN00242	0.959	9.522
NAN00243	2.365	14.273
NAN00245	8.503	30.689
NAN00246	2.423	7.613
NAN00247	1.674	8.171
NAN00248	1.600	6.445
NAN00249	4.694	11.001
NAN00251	7.313	18.131
NAN00254	3.989	8.705
NAN00255	0.918	5.412
NAN00256	3.069	12.959

Table 3.5. Core (50%) and total (95%) home range area (km^2) estimates for 17 chacma baboon troops (unique Collar ID; *see* Table 3.1) across six forestry plantations using the Time-Local Convex Hull (T-LoCoH) estimation method. Plantations grouped by region (*see* Figure 3.1). Also presented are the optimal combinations of *s*- and *k*-values, implemented in the T-LoCoH home range estimation process, selected using a cross-validation-based approach (Dougherty et al., 2017).

Region	**Collar ID**	**Plantation**	**Cross-validation**				**T-LoCoH**	
			No. points used	**s-value**	**k-value**	**Sum Log Hulls**	**95% (km^2)**	**50% (km^2)**
1	NAN00236	Mooifontein	975	0.0004	15	-5772.157	7.600	0.701
	NAN00242	Mooifontein	1522	0.0047	19	-8267.905	7.092	1.007
	NAN00243	Mooifontein	1780	0.0004	10	-10212.170	7.781	0.875
2	NAN00254	Houtboshoek	471	0.0000	5	-2596.485	3.106	0.181
	NAN00255	Houtboshoek	579	0.0004	14	-3279.175	3.709	0.332
	NAN00256	Houtboshoek	445	0.0013	20	-2743.700	10.171	2.203
3	NAN00241	Glenthorpe	521	0.0094	93	-4116.571	11.771	7.255
	NAN00248	Glenthorpe	1770	0.0100	49	-11073.520	6.689	1.601
	NAN00246	Sjonjona	1300	0.0003	21	-6922.781	6.651	0.779
	NAN00251	Sjonjona	1507	0.0009	9	-8753.128	8.747	1.469
4	NAN00245	Ndubazi	1454	0.0013	9	-8361.655	16.891	1.717
	NAN00247	Ndubazi	1530	0.0001	9	-7870.825	5.572	0.522
5	NAN00237	Highlands	1035	0.0100	21	-11170.350	9.491	3.498
	NAN00238	Highlands	1035	0.0004	9	-5865.975	7.743	1.023
	NAN00239	Highlands	1632	0.0030	24	-9097.282	7.120	1.667
	NAN00240	Highlands	720	0.0100	7	-9343.054	4.896	0.984
	NAN00249	Highlands	3956	0.0030	187	-21477.330	6.339	0.209

3.3.3. Revisitation rates to plantation compartments

The T-LoCoH revisitation rate (NSV) was effectively modelled using a MixRF approach, producing an OOB R^2 fit on the test dataset of 93.13%. Furthermore, the predicted values were closely aligned with the observed values, as indicated by their correspondence along a 1:1 line (Figure B.8). The similarity in the RMSE between the predicted and observed values further supports the model's accuracy (Figure B.8).

In terms of variable importance analysis (Figure 3.3), Plantation (or study site) exhibited the highest ranking by a significant margin. Troops were found to visit a variety of plantation tree species (Figure 3.4D), including *Cedrus deodara* (Cdeo), *Eucalyptus cloeziana* (Eclo), *E. dunnii* (Edun), *E. grandis* (Egra), *E. grandis* × *E. nitens* (Egxn), *E. grandis* × *E. urophylla* (Egxu), *E. macarthurii* (Emac), *Pinus elliotti* × *P. caribaea* (Pech), *P. elliotti* (Pell), *P. greggii* (Pgre), *P. keslya* (Pkes), *P. maximinoi* (Pmix), *P. patula* (Ppat), *P. Pohon* (Ppoh), *P. patula* × *P. tecunumanii* (Pptl) and *P. taeda* (Ptae). Revisitation rates to compartments were more influenced by the species present rather than the compartment genus (i.e., *Pinus* vs. *Eucalyptus*), as indicated by the ALE plot of species (Figure 3.4D). Specifically, revisitation was observed to increase in pine compartments.

Among the environmental variables considered, altitude and distance from rivers emerged as significant factors affecting troop revisitation in the model (Figure 3.3). Revisitation rates displayed an upward trend with increasing altitude (Figure 3.4B). Revisitation rates increased with increasing distances from rivers, regardless of their flow regime (Figure 3.4A and G). Several compartment-specific variables, including tree age, compartment area, tree species and site index, significantly contributed to baboon revisitation patterns (Figure 3.3). Notably, revisitation rates were higher in compartments older than 10 years (Figure 3.4C) and those with a higher site productivity (SI > 18; Figure 3.4F). Furthermore, compartments with SI of approximately 10 exhibited elevated revisitation rates. Conversely, revisitation displayed an inverse relationship with compartment area, with baboons more frequently visiting smaller compartments (< 20 ha or 0.2 km^2; Figure 3.4E).

To gain insights into the influence of edge effects on revisitation rates, three "edge" proxies were incorporated into the analyses: distance to the nearest road, distance to the nearest conservation unit/natural zones (CU) and distance to the edge of the compartment. Among these proxies, only distance to main plantation roads emerged as having a significant impact on the model (Figure 3.3), with revisitation rates increasing with increasing distance from main roads, peaking at approximately 2 km (Figure 3.4J). Proximity to the nearest CU did not significantly contribute to the model (Figure 3.3). Revisitation rates increased with increasing distances from both agricultural and urban areas (Figure 3.4H and I). This finding indicates that troops were observed to revisit areas located farther from agricultural and urban landscapes, potentially suggesting a preference for more remote locations. It's important to note that most variables showed deviations in their smoothed line for extreme values due to a lack of data (Figure 3.4).

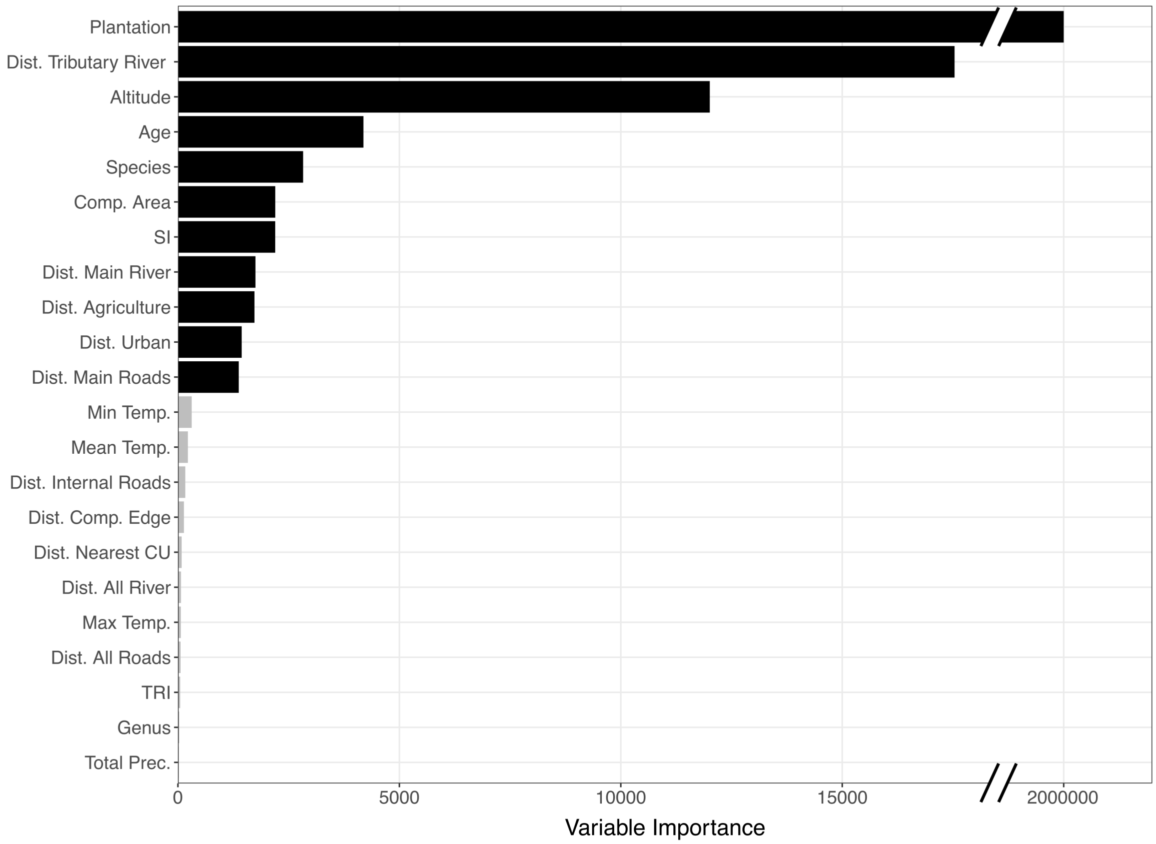


Figure 3.3. The importance of explanatory variables for predicting compartment-level revisitation rates (NSV) of 17 baboon troops. Black bars show significant (p-value < 0.05) variables determined by a permutation (n = 100) approach (Altmann et al., 2010). Plantation (or study site), represented by the broken bar and axis, had a substantially larger importance value compared to the second highest ranked variable, i.e., Distance to (Dist.) Tributary River. Variable abbreviations include: Compartment (Comp.), Site Index (SI), Temperature (Temp.), Conservation Unit (CU), Terrain Ruggedness Index (TRI) and Precipitation (Prec.).

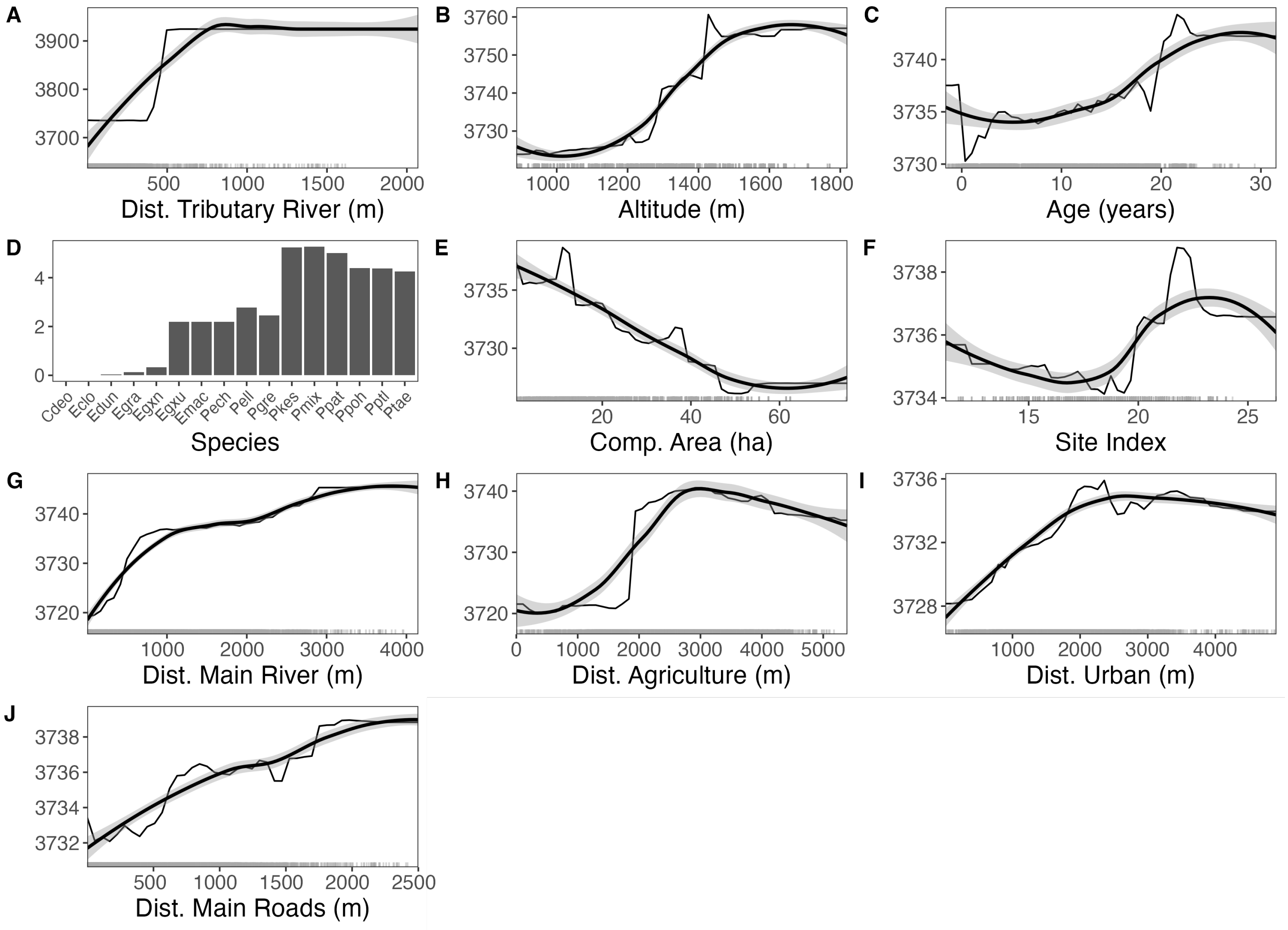


Figure 3.4. Partial dependence (i.e., marginal effects) plots of plantation compartment revisitation rate (NSV) by 17 chacma baboon troops for significant variables (p-values < 0.05; *see* Figure 3.3) while accounting for the average effect of the other predictors in the model. Species variable is visualised using Accumulated Local Effects Profiles. The thin jagged line shows the partial dependence function, while the bold line shows the '*loess*' smoothed estimate with standard error confidence levels in grey. Rug plots indicate the frequency distribution of each variable. Variable abbreviations include: Distance to (Dist.) and Compartment (Comp.).

3.4. Discussion

3.4.1. Habitat selection

During the wet season, baboons exhibited a clear preference for plantation compartments, supporting my initial predictions, and contradicting previous findings of Henzi et al. (2011) who stated that baboons avoided pine compartments, particularly in the wet season. Moreover, according to Brown et al. (2005), baboons were proposed to venture into plantations primarily when resources within their natural habitats were limited. However, the observed preference for plantations during the most productive seasons (i.e., spring and summer) challenges this notion, indicating that resource availability within plantation compartments may potentially surpass that of natural habitats. These discrepancies in behaviour underline the context-specific nature of animal behaviour and may stem from differences in study locations, environmental conditions, or specific baboon populations.

The troops showed elevated rates of movement through plantations during the dry season and no preference for plantations or other habitat types. This could be a response to declining food availability, which has been observed in other primates where extended travel and increased feeding time become necessary to reach widely dispersed food sources (Byrne et al., 1993; Clarke et al., 2002; Gursky, 2000). Similar findings were reported for chacma baboons in the Cape Peninsula, where movement rates and daily distances travelled peaked during the dry summer months when primary productivity was lower (Lewis, 2015). Longer step length in plantations during the dry season may reflect the homogeneous understory and accessibility of roads, which together, facilitates movement relative to natural habitats.

Previously, it was proposed that plantation-dwelling baboons rely solely on the remaining natural habitat patches between pine compartments (Henzi et al., 2011). However, my findings challenge this theory, with baboons actively selecting plantation compartments over natural habitats, both within (riparian corridors) and adjacent (open grassland) to plantations, during the wet season (spring/summer).

Recognising this preference for plantations is crucial for addressing the management challenges associated with mitigating bark-stripping damage. Additionally, it challenges the popular narrative that plantations are ‘green deserts’, as both baboons and other common species, like the common duiker, seem to thrive in these environments with very high occupancy rates (Chapter 2; Pretorius et al., 2023).

3.4.2. Home range

As predicted, the MCP method consistently yielded larger home range estimates compared to the T-LoCoH method (Table 3.4; Li et al., 2010). Despite this, the popularity of MCP methods in previous studies provides a rationale for its use as it allows for comparisons across study sites. For instance, Henzi et al. (2011) used the MCP method to estimate mean home range sizes of 14.55 km^2 for two troops living in and adjacent to plantations in Mpumalanga, while Anderson (1982) and Slater et al. (2018) found mean home range sizes of 24.6 km^2 and 26.1 km^2 ± 12.14 SD for troops in more natural habitat (Suikerbosrand Nature Reserve). Other studies have reported mean home range sizes of 15.19 km^2 across KwaZulu-Natal Province (Stone et al., 2012). However, my estimate of 12.18 km^2 (MCP method) aligns more closely with home range sizes observed in natural environments alongside plantations, such as Blyde Canyon Nature Reserve in Mpumalanga (10.2 km^2 ± 2.3 SD; Marais, 2009), and even baboons that frequent urban and agricultural land areas (11.0 km^2 ± 6.80; Hoffman and O'Riain, 2011). Given the significant differences found between the MCP and T-LoCoH methods, caution is essential when comparing findings across studies, especially as methods like Kernel Density Estimation (KDE) gain popularity. Researchers should carefully consider what methodologies were employed to ensure valid comparisons and interpretations of home range estimates.

While Henzi et al. (2011) argue that plantations are marginal habitats for baboons, my results, namely that troops living in plantations have similar or smaller home ranges relative to those living in natural habitats, do not support this theory. Plantations have been shown to offer relatively stable environments with diverse food resources and abundant refugia to baboons (Hoffman and O'Riain, 2011). It is an established trend that when primates have access to high-quality food resources they typically have smaller home ranges, e.g., samango monkey (Nowak et al., 2014), vervet monkey (Saj et al., 1999), yellow baboon (Altmann and Muruthi, 1988) and Sumatran orangutan (*Pongo abelli*; Campbell-Smith et al., 2011).

Henzi et al. (2011) found that baboons in plantations exhibited smaller home ranges in the dry seasons compared to the wet seasons in Mpumalanga Province. Similarly, Lewis (2015) observed seasonal fluctuations in home range size for baboons on the Cape Peninsula, with a decreased area used in the wet/winter months. These patterns of home range size variation are often associated with changes in food availability, such as alterations in plant phenology (Kunz and Linsenmair, 2007; Whiten et al., 1991). Baboons typically expand their home ranges when resources are scarce, requiring them to travel further to meet their nutritional needs (Hemingway and Bynum, 2005). However, in this study, I did not observe significant changes in ranging size between seasons, despite the previous observations of variations in habitat selection and movement patterns across wet/dry periods. It is possible that because plantations are a slow-growing crop with a very long rotational period they effectively mute seasonal variation in the environment, which is reflected in a consistent range area. In addition, rivers, streams and wetlands are protected from exotic plantation trees, and abundant in the area, relieving baboons from the need to range extensively for water and potentially reducing the size of their home ranges (Amoroso et al., 2020; Johnson et al., 2015).

3.4.3. Plantation compartment usage

Baboons, like many other primates, exhibit selective foraging behaviour and preferentially utilise specific areas within their home ranges based on resource availability and quality (Alberts, 2019). The specific plantation a troop was ranging in was found to be the most important variable determining troop revisitation rate. Plantations subsume a range of management practices including controlled burning, the removal of alien vegetation (e.g., Bugweed; *Solanum mauritianum*; Atkinson et al., 2014), thinning of damaged trees and ultimately the harvesting of whole compartments. Each of these activities can have significant effects on the ecological dynamics and resource availability within plantations which is why, when subsumed together under 'Plantation', they provide the best predictor of revisitation rate.

Controlled burning involves the intentional setting of fires to reduce the fuel load in plantations and so reduce the risk of wildfires (Waldrop and Goodrick, 2012). Controlled burns can alter vegetation structure and composition, leading to changes in food availability and foraging opportunities for baboons. In some cases, controlled burning may enhance the growth of preferred food sources (Herzog et al., 2016). On the other hand, if controlled burns result in the loss of important food resources or disrupt the vegetation structure that baboons rely on, revisitation rates may decrease in the affected compartments. Similarly, the removal of alien vegetation, which refers to the eradication or management of non-native plant species for ecosystem management within natural pockets (Currie et al., 2009) or vegetation that competes with stocked trees (Mead, 2005; South et al., 2001), can impact baboon revisitation rates. Alien vegetation often competes with native plants for resources and can alter the composition and structure of the plant community. By removing alien vegetation, plantation managers aim to restore native plant communities and enhance habitat quality (Richardson and Van Wilgen, 2004). In some cases, the removal of alien vegetation can result in the proliferation of preferred food sources or improve the overall vegetation quality, and as such, baboons may exhibit higher revisitation rates in those areas. However, the opposite may also be true, for example, the fruiting bodies of Bugweed are a favoured plant food source for baboons (Hoto, 2003), which if removed is likely to reduce an important food item.

Altitude, roads and the habitat surrounding plantations can lead to differences in baboon revisitation rates. Baboon troops selected for higher altitudes in this study. Compartments located at different altitudes may experience different climatic conditions and vegetation types, which can influence resource availability and utilisation by baboons (Hill et al., 2003; Whiten et al., 1987). Higher altitudes may offer different food sources or provide more favourable microclimates, potentially affecting baboon behaviour and revisitation rates. Lower altitudes, both in and around plantations, tend to be characterised by increased human activities, including the presence of main roads, forestry infrastructure such as sawmills and equipment depots, workers' villages and a range of other anthropogenic activities. Consistent with this, revisitation decreased in proximity to both urban and other agricultural activities, which are more prevalent at lower altitudes with flatter land. Plantations situated near agricultural areas may experience increased negative interactions with humans due to the proximity of valuable crops or livestock (Hill, 2005, 2018). Revisitation peaked at approximately 2 km from agricultural and urban areas, which could indicate a balance between resource exploitation and risk avoidance, as noted in troops inhabiting urban areas (Fehlmann et al., 2021, 2017b).

Troops avoided main roads within the plantations which are associated with high levels of disturbance from vehicle and foot traffic. This finding contrasts with Chapter 2, where baboon habitat use increased closer to roads in heavily transformed plantation landscapes, though this relationship was not significant. These contradictory results may arise from my not differentiating between road types in Chapter 2. In this chapter, I specifically separated the impacts of main roads and internal compartment roads. Consequently, I found that troops avoided main roads, which are more frequently used for plantation management, while they were not significantly affected by smaller internal roads. Apart from altitude, none of the other environmental covariates, including temperature and rainfall, had a significant influence on baboon revisitation rates within the plantation landscape. Plantations provide a relatively stable microclimate (Hoffman and O'Riain, 2012b; Karki and Goodman, 2015) and may buffer baboons from temperature extremes that would be more likely in exposed indigenous grasslands. Trees also provide shelter from rainfall with baboons resting in the canopy during periods of sustained heavy rainfall (Thys de Wet, *pers. comm.*).

Revisitation rates were greater in compartments with pine than *Eucalyptus* species. Pine species with the greatest revisitation contributed on average approximately 48% of baboon home range areas (Table B.1). Previous research has reported higher understory plant diversity in pine compartments compared to *Eucalyptus* plantations (Lomba et al., 2013, 2011; Vaz et al., 2019). The greater plant diversity in pine compartments likely provides baboons with enhanced foraging opportunities compared to the more simplified and homogeneous structures found in *Eucalyptus* compartments. Pine compartments are also known to possess more complex and heterogeneous forest structures (Sánchez Meador et al., 2009), which can offer a wider variety of food resources and microhabitats for baboons. In contrast, *Eucalyptus* compartments tend to exhibit simplified structures due to self-pruning mechanisms and the competitive dominance of *Eucalyptus* species over other trees (Lomba et al., 2011). While some pine species were visited frequently, it is noteworthy that three specific pine species, despite contributing an average of 20% to the baboon home range areas (Table B.1), did not receive as many visits as other species. This suggests that the selection of compartments is likely influenced by a complex interplay of factors, including species, age and compartment complexity.

Distance to conservation units (CUs) adjacent to pine compartments did not influence revisitation rates, which is contrary to the findings of Henzi et al. (2011). Rather, revisitation rates were more closely linked to the utilisation of plantation compartments, aligning with the observations made by Katsvanga (2011) and Germishuizen et al. (2017). Additionally, revisitation rates increased with increasing distance from tributary rivers within the plantation landscape. Rivers and streams are abundant within this forestry region of Mpumalanga, which was originally selected for planting due to its high rainfall (Armstrong and van Hensbergen, 1999). Most rivers are delineated with natural riverine vegetation to enhance water preservation and create green corridors of natural vegetation (FSA, 2021; FSC, 2017). While these riverine zones are important for ecological connectivity (Pretorius et al., 2023) and maintaining water resources, their abundance in the region means that distance to water is unlikely to significantly limit baboon movement patterns and habitat selection. These results suggest that baboons in plantations may rely less on the proximity to natural vegetation strips, such as delineated riverine areas, and instead prioritise the resources available within the compartments. Consequently, the prevailing theory that baboons are confined to natural pockets and move through compartments solely to find other patches of natural vegetation (Henzi et al., 2011) is not supported by my data. Additionally, the absence of a significant association between revisitation rates and the proximity to CUs challenges the previous notion that plantations are sub-optimal habitats for baboons (Henzi et al., 2011), and that they are driven into these areas due to surrounding habitat changes and conflicts.

Revisitation rates were higher in smaller compartments and those with trees older than 10 years. Smaller compartments tend to be found in areas with steeper and more rugged terrain, where accessibility for delineation, planting and mechanical harvesting is limited. Additionally, compartments with trees older than 10 years are typically less disturbed than those with younger trees that are still subject to thinning and pruning which both require intense labour activities and hence human disturbance (Mead, 2005; Rolando and Little, 2009). Older trees are also taller and have more structurally developed trunks with stronger branches which can be used as perching sites for sleeping or as a temporary refuge from potential predators (Estrada, 2006; Estrada et al., 2012). Furthermore, older compartments may offer a more developed understory with a greater diversity and abundance of exotic and natural food resources (Norton, 1998).

Site Index (SI), a measure of species-specific site productivity, provides insights into the growth potential and quality of a tree species within a compartment (Kotze et al., 2012). As expected, revisitation increased in compartments with a higher SI for the same species. Compartments with higher SI values tend to support healthier and more productive trees and may provide better foraging opportunities for baboons. This preference for compartments with greater SI aligns with previous studies investigating bark-stripping behaviour in plantation settings. Germishuizen et al. (2017) demonstrated that the predicted risk of bark-stripping is elevated in compartments older than 5 years, particularly on high-productivity forestry sites with SI > 25. Similarly, Katsvanga et al. (2009a,b) found that resource availability played a crucial role in bark-stripping by baboons in pine plantations, emphasising that areas situated on high-productivity forestry sites are more susceptible to damage. Interestingly, higher revisitation rates were also observed in compartments with a low SI ($SI \approx 10$). Compartments with a lower SI tend to have shorter and less dense vegetation compared to compartments with higher SI values. The reduced compartment height and diameter at breast height (DBH) in these compartments could offer greater availability of grasses, herbaceous plants, or low-lying shrubs (Rolando and Little, 2009) that serve as important food sources for baboons.

3.5. Limitations and conclusions

This study had several limitations that may influence both the resolution and interpretation of my main findings. Firstly, the GPS locations of baboons were recorded every four hours, limiting my ability to examine fine-scale habitat selection through revisitation and duration of visit analyses.

Secondly, there was no attempt to estimate troop size by the Forestry collaring team. Previous research has demonstrated that daily path length increases with troop size and decreases with greater food availability (Hoffman and O'Riain, 2012b). While the impact of human-modified habitat use has also been shown to override the effect of group size at a local scale (Hoffman and O'Riain, 2011; Johnson et al., 2015), the lack of these data limits my ability to determine density, which is a key attribute of the spatial ecology of a species. Density and group size provides important insights into population dynamics and resource utilisation by social species, which ultimately may lead to more informed management strategies in human-modified habitats. However, Henzi et al. (2011) showed that although troop size of plantation baboons were double the size of troops living in an adjacent natural area, the population density did not differ significantly (3 individuals/km^2).

Despite these limitations, which were largely beyond my control, the data presented here reveal that baboons strongly favour plantation landscapes. The analysis of troop home range revealed that plantation-dwelling baboons exhibit comparable area utilisation to that observed in natural and urban environments, countering the theory of plantations as marginal habitats. Furthermore, compartment usage patterns demonstrate baboon's active utilisation of plantation landscapes, with a preference for older, more productive compartments, while disregarding proximity to compartment edges, such as natural vegetation strips. This study challenges existing paradigms and underscores the importance of considering multiple factors in comprehending the dynamics of baboon habitat selection and their interactions with human-modified environments. Further research, focusing on damage-causing behaviour such as bark-stripping, is essential to make informed decisions regarding habitat management, resource allocation and the implementation of mitigation measures within the plantation landscape.

CHAPTER 4

Bark-stripping by chacma baboons in commercial pine plantations

Abstract

Bark-stripping behaviour by baboons poses a significant threat to the long-term sustainability of the forestry industry in southern and east Africa. Despite the impact of bark-stripping, the function of this behaviour remains poorly understood. This lack of understanding is partly attributed to the historical persecution of baboons in human-modified landscapes throughout the region, which has made habituation for close behavioural observations difficult. However, recent advances in the use of accelerometers in bio-logging devices affixed to animals offer promising prospects, providing fine-scale information on rare behaviours that are traditionally challenging to record. In this chapter, I explored the efficacy of accelerometry in accurately identifying and quantifying bark-stripping behaviour, leveraging tri-axial acceleration data collected from a sample of n = 11 wild chacma baboons. Additionally, I investigated potential environmental predictors of both the duration and frequency of bark-stripping events. Using machine learning (random forest models) trained on video-labelled data, I identified the behaviours of free ranging baboons with high precision (98.3 ± 0.02%) and recall (95.9 ± 0.04%). Applying this model across n = 816 collar days, I estimated that individuals spend on average 9% of their daily activity engaged in bark-stripping, with no clear effect of either age or sex. Bark-stripping bout frequency increased significantly with daily maximum temperature and was notably higher in pine compared to *Eucalyptus* compartments. Additionally, bark-stripping frequency and duration increased closer to human settlements and on steeper slopes, possibly linked to vigilance strategies. Bark-stripping behaviour was strongly associated with residency time within an area and occurred more frequently in compartments with greater tree productivity. Using accelerometry to reliably measure the frequency and duration of rarely observed bark-stripping behaviours is an important step in understanding the drivers of baboon impacts on plantations and ultimately mitigating this persistent conservation conflict.

4.1. Introduction

Bark-stripping, a behaviour observed in various mammal species, causes significant damage to both indigenous and exotic commercial trees in plantations (Baxter and Hansson, 2001; Reimoser, 2003). Previous investigations into bark-stripping behaviour have focused on temperate mammals, with limited attention to primates and their specific behaviours in tropical and subtropical forest plantation systems (Di Bitetti, 2019; Estrada et al., 2012; Gill, 1992a,b). Primates, including chacma baboons, black capuchin monkeys and samango monkeys, have been identified as significant contributors to bark-stripping in natural forests and exotic plantations across various continents (Beeson, 1987; Di Bitetti, 2019; Harris and Chapman, 2007). In southern Africa, chacma baboons are widely recognised as prolific bark-strippers of trees within commercial pine plantations (Bigalke and van Hensbergen, 1990; Germishuizen et al., 2017; Henzi et al., 2011; Katsvanga, 2011; Ndagurwa, 2013).

Damage inflicted by baboons on pine plantations poses a significant threat to the long-term sustainability of the forestry industry (Nadel et al., 2012), compounding existing challenges such as fire, insect infestations and diseases. The direct damage caused by bark-stripping diminishes available yield, disrupting production models and complicating foresters' efforts to anticipate and mitigate these losses. Furthermore, the compromised trees become susceptible to fungal infections (Maganga and Wright, 1991), weakening the entire compartment's resilience against various environmental stressors and resulting in widespread wood degradation (Cukor et al., 2019). This damage also alters stem growth patterns, increasing handling costs and reducing wood recovery efficiency. Moreover, the diverted resources for repair slow down the growth rate of affected trees, ultimately reducing the final wood volume (Cukor et al., 2019; Vacek et al., 2020). Should bark removal exceed 75% of the trunk's circumference (known as ring-barking), the entire tree or its crown may perish, posing a significant threat to the entire forest resource production chain (McNamara, 2005). In both Zimbabwe and South Africa, the economic impact of baboon bark-stripping is significant. For instance, in Zimbabwe, the estimated economic loss attributed to this behaviour in 2004 was approximately US$1.8 million. Subsequent years saw wood volume losses of around 50% and resulted in revenue losses ranging from US$24 000 to US$32 000 per ha by 2011 (Katsvanga, 2011). In South Africa, the Forestry Stewardship Council (FSC) estimated a financial loss of approximately R130 million (approximately US$12 million) over a two-year period (FSC, 2017). These figures, however, do not encompass additional losses such as reduced growth, re-establishment costs, thinning, clear-felling expenses, or processing costs at sawmills. The decline in plantation productivity due to bark-stripping damage is alarming, especially considering the projected 54% rise in global wood consumption by 2050 (Mishra et al., 2022). This could result in a considerable expansion of land allocated to plantations (Brockerhoff et al., 2013), highlighting the need for heightened plantation productivity that can meet escalating wood demands.

A comprehensive review of 18 studies on primate bark-stripping behaviour revealed that the activity is not ubiquitous within groups or populations (Di Bitetti, 2019). Similarly, not all baboon troops within a population exhibit bark-stripping, suggesting it may be a learned behaviour (Gwenzi et al., 2007; Katsvanga et al., 2009b), with tree products linked to bark removal gradually incorporated into a group's diet (Beeson, 1987; Bigalke and van Hensbergen, 1990; von dem Bussche and van der Zee, 1985). When present, bark-stripping is not a predominant activity, accounting for only about 1% of an individual's activity budget (Katsvanga, 2011), with larger or bolder individuals engaging more frequently in this behaviour (Katsvanga, 2011). While it is evident that bark-stripping is not universally practised within groups or populations (Di Bitetti, 2019), finer details remain elusive. Specifically, we lack insights into the triggers that prompt baboons to engage in bark-stripping (theories around this discussed in Chapter 1), the fine-scale spatial extent of damage, how bark-stripping is associated with baboons' use of plantation compartments and which sex and age classes are most involved in this behaviour. Given the challenges associated with detecting bark-stripping and the limitations of traditional methods, including direct observations of often heavily persecuted individuals (Biro, 2013; Crofoot et al., 2010; Jack et al., 2008; Merrick and Koprowski, 2017), there is a pressing need to explore new and innovative approaches to study this damage-causing behaviour.

Bio-logging devices have found extensive application in behavioural ecology research, across species, capturing information on elusive or concealed behaviours that pose challenges for conventional recording methods (Campbell-Smith et al., 2010; Fehlmann and King, 2016; Naughton-Treves, 1998). Bio-loggers reduce potential adverse effects linked to the presence of observers, including biases in data acquisition and direct impacts on the study species, such as altering their perceived landscape of fear (Nowak et al., 2014). Additionally, they circumvent issues related to habituation arising from prolonged observations (Boyer-Ontl and Pruetz, 2014; Strier, 2010). The data retrieved from bio-logging devices has proven instrumental in evaluating diverse aspects of a species' biology and physiology, including estimating activity patterns, habitat utilisation, energy expenditure, body temperature and sleep cycles, as well as monitoring mortality and reproductive events (Brown et al., 2013; Campera et al., 2019; Chimienti et al., 2021; Christensen et al., 2023; Fehlmann et al., 2017b; Reinhardt et al., 2019; Schmidt et al., 2020).

Bio-logging devices have undergone rapid advancements in recent years, including reductions in size, enhanced battery life, an augmented array of integrated sensors and an expanded capacity to concurrently record various types of data, like GPS, accelerometers, magnetometers, pressure sensors and acoustic recorders (Hughey et al., 2018; Williams et al., 2020). These devices may also be applied to group living species providing detailed and simultaneous data from multiple individuals. GPS technology, a fundamental component of bio-loggers, delivers precise spatial and temporal data (x, y coordinates) regarding an animal's location, enabling comprehensive analyses of individual responses to human-modified landscapes (McFarland et al., 2013; Wilmers et al., 2015) and in the context of conspecifics. Utilising bio-loggers in tandem with GPS devices on chacma baboons within commercial plantations presents a unique opportunity to delve into both intrinsic (e.g., age and sex) and extrinsic (e.g., tree species/age, slope) factors that may influence baboon bark-stripping behaviour. Previous studies have demonstrated the efficacy of bio-logging devices on chacma baboons in identifying various behaviours, ranging from general activities such as walking, running and foraging (Fehlmann et al., 2017b), to more subtle behaviours like grooming (Christensen et al., 2023). This indicates the potential for bio-logging technology to also capture bark-stripping, offering valuable insights into this damage-causing behaviour.

The frequency and duration of bark-stripping behaviour hold significant importance due to its potential effects on tree damage. For example, increased instances of bark-stripping could lead to more trees being affected, while longer durations may indicate more severe damage, such as ring-barking. Various factors, including climatic variables and individual characteristics, can influence bark-stripping patterns. Primates can respond to changing weather conditions by seeking shelter from temperature extremes (Duncan and Pillay, 2013; Hill, 2006a; McFarland et al., 2019) or rain (Cui et al., 2006; Hanya et al., 2018; Majolo et al., 2013) and engaging in more sedentary behaviours (Campos and Fedigan, 2009; Hill, 2006b; Majolo et al., 2013). For instance, as temperatures rise, baboons have been observed to engage in significantly higher levels of resting and grooming (Hill, 2006a,b). Commercial plantations offer a relatively stable microclimate (Hoffman and O'Riain, 2012b; Karki and Goodman, 2015), potentially shielding baboons from temperature extremes more prevalent in exposed indigenous grasslands. Trees within these plantations also provide shelter from rainfall (Cui et al., 2006), with baboons seeking refuge in the canopy during sustained heavy downpours (Thys de Wet, *pers. comm.*). As such, it is hypothesised that in plantations, baboons may seek shelter in compartments during hot days or heavy rain, leading to increased sedentary behaviour that could increase the chances of bark-stripping in these areas. Furthermore, individual traits such as sex and age have been shown to influence baboon behaviour in anthropogenically modified landscapes (Bracken et al., 2023; Fehlmann et al., 2017b) and these can be readily measured by affixing bio-loggers to multiple individuals within a troop.

Plantation-specific variables may further shape bark-stripping behaviour. Previous research has shown the importance of tree species, age and compartment productivity in determining damage patterns (Germishuizen et al., 2017). The palatability of tree species is likely to affect bark-stripping, with pines, particularly certain species such as *Pinus patula* (Germishuizen et al., 2017), expected to experience higher levels of damage compared to *Eucalyptus*. Bark-stripping is also expected to increase with compartment age as trees become structurally larger, allowing for increased climbing and perching opportunities. Age has also been associated with sap nutrients and bark "stripability" (Gill, 1992a; Kuiters et al., 2006), suggesting that bark-stripping should increase as trees mature. Additionally, results from Chapter 3 suggest that baboons spend more time in smaller compartments, which could potentially increase the likelihood of bark-stripping occurrences in these areas. Germishuizen et al. (2017) found that baboon damage was higher on upper slopes and with increased compartment productivity, therefore, I hypothesise that bark-stripping behaviour will increase with slope due to increased vantage-point perching sites and in more productive compartments due to increased foraging opportunities. Furthermore, the study troop was observed to occasionally raid the local workers' village and vacation rental when visitors were present, during which humans would employ noise (such as shouts and whistles) and their physical presence to deter the baboons. Previous studies have linked increased bark-stripping activity with sites that have been supplemented with food (e.g., corn; Bigalke and van Hensbergen, 1990; Henzi et al., 2011), as such, it is predicted that plantation baboons will take advantage of abundant human-derived foods found around urban settlements within plantation matrices with bark-stripping increasing in the vicinity of this anthropogenic food source.

In this chapter, my primary aims revolve around understanding key aspects of baboon bark-stripping behaviour within commercial timber plantations. Firstly, I aim to leverage accelerometry data from bio-logging devices to predict all instances of bark-stripping behaviour by chacma baboon individuals within a single study troop. Through the development and validation of random forest models, I aim to differentiate bark-stripping movements from other activities, such as locomotion and foraging, and to establish a reliable methodology for identifying and quantifying this behaviour. Finally, I aim to explore the influence of climatic factors, such as temperature and rainfall, as well as plantation-specific variables, such as tree species, compartment age and productivity, on the frequency and duration of bark-stripping events. Understanding the drivers of tree damage is important for proposing effective management strategies, mitigating economic losses, and ensuring the long-term sustainability of commercial pine plantations in southern Africa.

4.2. Methods

4.2.1. Study site and troop

The study was conducted in the Ehlanzeni district of Mpumalanga province (Figure 4.1), South Africa, approximately 7 km from Sappi Ngodwana Pulp Mill and 48 km from Mbombela (formerly Nelspruit and the provincial capital). The region predominantly features commercial tree plantations, primarily comprising exotic genera such as *Pinus* and *Eucalyptus* (FSA, 2020a; Shai, 2021). The mean altitude of the area is 1390 m, with an average annual precipitation of 1068 mm and mean temperatures ranging between 13 to 22 °C. These plantations, spanning compartment sizes ranging from 0.82 ha to 77.6 ha, are primarily managed for the production of pulp (Bennett and Kruger, 2013). Within the confines of a commercial plantation, approximately 70% of the land is dedicated to tree cultivation, while the remaining 30% serves various purposes including roads, infrastructure, firebreaks, rugged terrain, and delineated riparian vegetation (FSA, 2021).

Data was collected between October 2021 and May 2022 on a troop of wild chacma baboons situated in the central region of Houtboshoek plantation (Figure 4.1), a Sappi-owned property, located within the Houtboshoek valley. Land surrounding the plantation was mostly comprised of private small holdings and small-scale macadamia/citrus farming. The troop consisted of approximately 30 baboons, with 15 adults and approximately 8 sub-adults and 7 juveniles. Their home range encompassed plantation compartments, natural delineated areas and a small area of human settlements, which included a workers' village, forestry offices and a recreational facility (vacation rental; Figure 4.1).

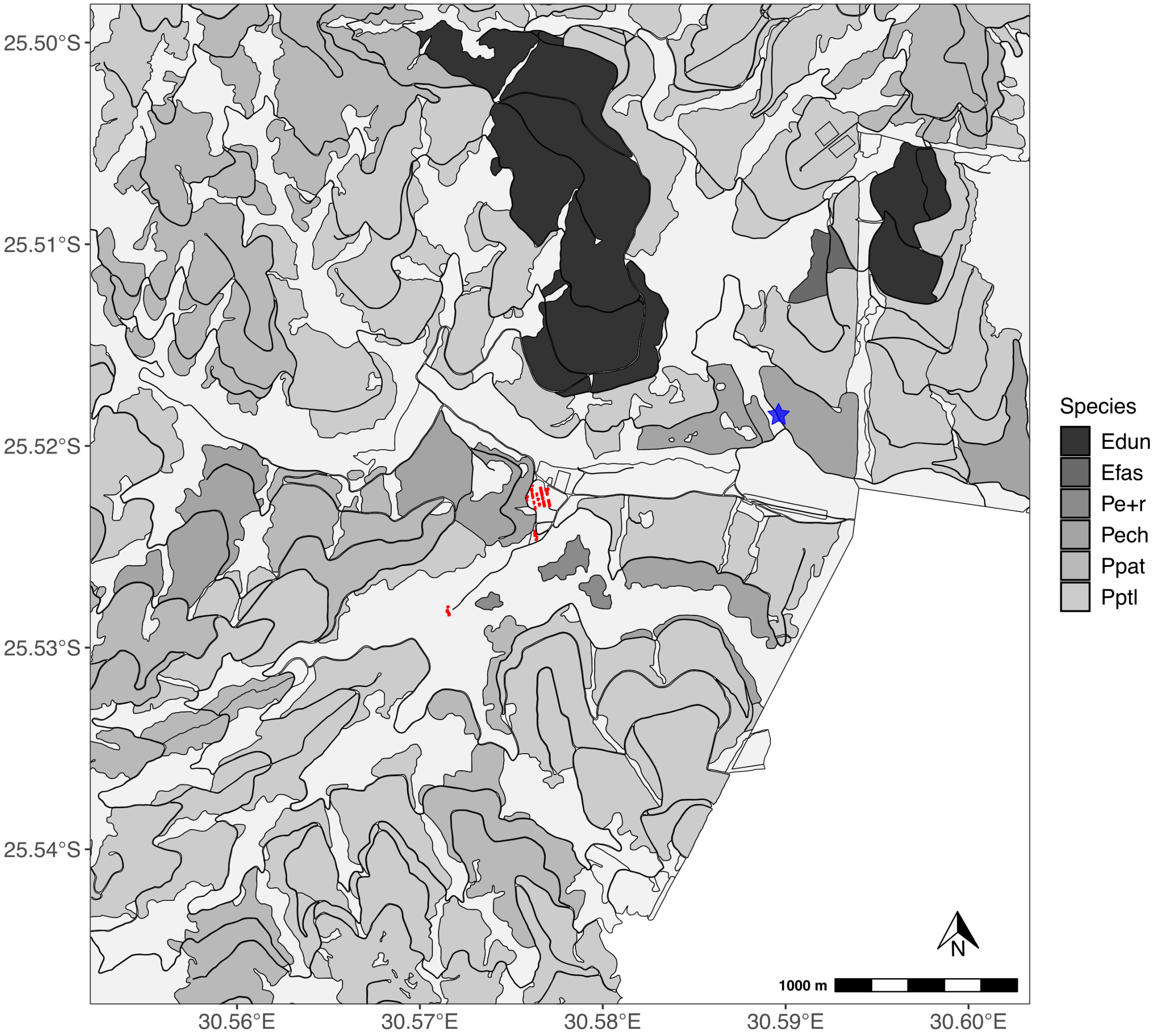


Figure 4.1. Study area of the collared chacma baboon troop. Houtboshoek plantation compartments are colour-coded by planted species. Light grey areas represent other forestry-owned land, including roads, infrastructure, firebreaks, and delineated natural areas. Red areas indicate urban human settlements within the plantation, with the troop capture site marked by the blue star.

4.2.2. Collars

I equipped 18 adult and sub-adult individuals (comprising 5 adult males, 10 adult females and 3 sub-adult males) with custom designed F2HKv3 collars from the SHOAL group (Sociality, Heterogeneity, Organisation And Leadership group) located at Swansea University, UK. Each collar contained a Daily Diary (Wilson et al., 2008) containing a tri-axial accelerometer (recording at 40 Hz per second). The collars were also equipped with GiPSy 5 GPS tags manufactured by TechnoSmArt in Italy, recording GPS coordinates at a rate of 1 Hz (1 fix per second), as well as a drop-off mechanism (version CR-7, Telonics, Inc.) to reduce the need for recapture. The GPS data was utilised to capture fine-scale positional information, allowing me to link predicted behaviours with specific locations within the plantation matrix, based on shared timestamps. GPS recordings were restricted to daylight hours between 06:00 and 18:00 local time, to coincide with peak active foraging periods. All devices were oriented so the *z*-axis corresponded to 'heave' (up-down motion), *x*-axis to 'surge' (forward-back motion) and *y*-axis to 'sway' (left-right motion). Before deployment, each device was calibrated to the exact time, orientation of the axes and to correct accelerometer and magnetometer offsets.

Due to troop preference for plantations during the wet season (Chapter 3), I fitted the collars to baboons during the rainy period to maximise the chances of detecting bark-stripping behaviour. Collars were fitted to the baboons between 18/10/2021 and 19/10/2021 in collaboration with a forestry capture team and a local certified veterinarian. Upon entering food-baited cages, baboons were anaesthetised using Ketamine (dose adjusted for body mass) in accordance with accepted protocols (described by: Fehlmann et al., 2017a) and following approval by the Faculty of Science Animal Ethics Committee (SFAEC; 2020/V15/JOR/A). Collars weighed on average 367.33 g (± 11.85 g) accounting for on average 2.2% of an adult baboon body mass (Christensen et al., 2023) and their deployment on baboons was also approved by Swansea University's Ethics Committee (IP-1314-5). Once a baboon has fully recovered (subject to the professional opinion of the veterinarian, e.g., no signs of ataxia), they were released at the capture site. No baboons died or sustained injury during the capture process and no injuries resulted from wearing the collars.

Out of the 18 collars deployed, 13 collars were successfully retrieved; data from five collars were not recovered after release because of battery failure, and two collars experienced accelerometer data recording failures. As a result, data from a total of 11 baboons (comprising 2 adult males, 6 adult females and 3 sub-adult males) were included in the analysis. The data covered an average duration of 74 ± 59 days, ranging from 9 to 212 days.

4.2.3. Description of bark-stripping behaviour in baboons

Baboon bark-stripping behaviour includes three distinct behaviours which are described below.

1. **Bark-stripping with teeth** (BS_teeth): The baboon, while seated on the ground or on tree branches (Figure 4.2), leans forward, biting the tree bark with its head orientated perpendicular to the trunk's vertical direction. Subsequently, the baboon pulls the bark backwards stripping it from the trunk, using its feet and hands for stability. This behaviour involves a sitting position, an initial backward neck jerk upon bark detachment and a gradual backward head movement during bark removal. Periodically, the baboon may make smaller bites with its upper and lower incisors on the cambium layer (Figure 4.3).
2. **Bark-stripping with fingers** (BS_fingers): In a sitting position, the baboon may use its fingers to assist in removing bark (Figure 4.2). This behaviour would typically include a small backwards movement upon bark release from the underlying cambium.
3. **Processing of stripped bark** (Processing_BS):
    - (a) After removing bark, the baboon may discard it and, with arms bracing against the trunk, begin to lick the exposed/wet tree trunk with upward movement of the head and/or upward scrapes of the incisors on the cambium layer (Figure 4.3). This behaviour is characterised by rapid up and down movements of the head/neck region.
    - (b) Following bark removal, the baboon may hold the bark strip using its hands and/or feet to secure it (Figure 4.4). While seated, the baboon then licks the inner surface, scrapes it with its' incisors or makes small bites similar to the action describes in

(a). However, the body posture differs from (a) as it involves sitting and processing rather than bracing against the trunk with its arms.

(c) The baboon may also descend from the tree and process fallen bark (Figure 4.5), following the same actions as described in (b).

Multiple baboons can simultaneously engage in bark-stripping activities on different trees or even on different positions of the same tree. In some cases, previously stripped trees may be revisited, with baboons either removing the bark covering a healed section or creating new wounds on a different part of the same tree. This can lead to extensive bark removal over large sections of the trunk, ending at the next node or whorl of branches (Figure 4.6) or extending across multiple whorls of side branches (Figure 4.7).

Figure 4.2. Male baboon using its fingers to remove bark from a pine tree while sitting on the branches of a node.

Figure 4.3. Vertical incisor scrapes on the cambium surface with horizontal bite marks.

Figure 4.4. Male baboon processing a strip of bark.

Figure 4.5. Stripped pieces of bark on the ground in a compartment of trees all the same age and species.

Figure 4.6. Extensive bark-stripping damage, exhibiting ring-barking between multiple branch whorls, while leaving residual bark patches at nodes.

Figure 4.7. Multi-nodal ring-barking that has extended across branch whorls and includes incisor scrapes (vertical white lines).

4.2.4. Video collection and processing

Despite six months of on-foot tracking efforts, successful habituation of the study troop was limited, with most members maintaining a distance of at least 20 meters. This hindered the collection of continuous and clear video footage of collared individuals, crucial for accurately labelling behaviours and cross-referencing with accelerometer data. Where video-follows were possible, I would dictate date, time, approximate GPS location, individual ID (based on unique colour ID bands attached to the collars) and provide detailed descriptions of behaviours, following a predefined ethogram (Table C.1). I labelled behaviours for individuals (n = 9) at time steps of one second, leading to a sample size of 28 779 s or 7.99 hrs (mean ± SD = 34.26 mins ± 60.35 mins), for n = 15 labelled behaviours. All three processing behaviours (Processing_BS) associated with bark-stripping (see 4.2.3 above) were merged, as behaviours (a) and (c) had significantly less than 100 s of observations. Furthermore, aggression behaviours (give and receive), play and climbing were removed from the dataset as they had less than 100 s of observations. If an individual baboon was shifting from one behaviour to another (e.g., from sitting to walking), the adjustment period (typically less than 2 sec) was assigned to whichever behaviour most closely matched the transitional behaviour. Some videos contained multiple collared individuals, i.e., some video footage was used to label the behaviours of more than one individual. This comprehensive list of behaviours, with timestamps and individual ID, was loaded into ‘Daily Diary Multiple Trace’ software (DDMT; Wildbyte Technologies Ltd., Swansea, UK; http://www.wildbytetechnologies.com) and saved as ‘marked events’.

4.2.5. Computing variables from acceleration data

To classify specific behaviours, variables that are commonly used to detect behaviours from acceleration data (Bracken et al., 2022; Christensen et al., 2023; Fehlmann et al., 2017a; Sakai et al., 2019) were extracted or derived from the raw tri-axial acceleration and magnetometry data (Table 4.1). These variables were either based on static acceleration (Shepard et al., 2008), which describes the orientation of the device relative to gravity, and thus, the posture of the animal, or dynamic acceleration, which describes the body movement of the animal (Gleiss et al., 2011). From the tri-axial magnetometry, five variables were included, calculated using each of the three orthogonal axes independently or by combining all three axes to provide a measurement of full body motion (Chakravarty et al., 2019; Williams et al., 2017; Table 4.1).

To align with my behavioural sampling (i.e., video footage) at a frequency of 1 Hz and to detect behaviours at this rate, I calculated mean values over a one-second interval for the set of 29 variables encompassing magnetic orientation, as well as static and dynamic acceleration data across all individuals. Mean magnetic heading was calculated using a circular mean function (Gunner et al., 2021; Pewsey et al., 2013):

$$\bar{\theta}_p = a\tan 2(\frac{1}{n}\sum_{j=i}^{n}\sin(h_j \cdot \frac{\pi}{180}, \frac{1}{n}\sum_{j=i}^{n}\cos(h_j \cdot \frac{\pi}{180})) \tag{4.1}$$

where n is the total number of magnetic heading measurements, h_j is the unsmoothed heading values and $\bar{\theta}_p$ the arithmetic mean after converting degrees to Cartesian coordinates.

Acceleration data were time-matched with the 'marked events' using DDMT. The position of the Daily Diary component of the collar was specified to correct the position of acceleration channels (i.e., x = surge, y = sway, z = heave) relative to the ground, using the initial collar calibration before collar deployment, to create accelerometer and magnetometer offsets within DDMT. Visual inspection showed appropriate matching, i.e., the accelerometry data showed different signatures for different behaviours.

Table 4.1. Overview of accelerometry and magnetometry variables that were used or calculated for the random forest model.

Variable	**Description**	**References**
Static acceleration (stX, stY, stZ)	The static acceleration of each axis, representing device orientation and thus individual posture. Calculated as the running mean of acceleration for each axis over 1 second.	
Pitch, Roll and Heading	To define the orientation of the plane and determine its upright position, the 3D orientation with respect to gravity was transformed into angles. The *x*-axis represents ‘sway’ movement (Pitch), the *y*-axis corresponds to ‘surge’ movement (Roll) and the *z*-axis represents ‘yaw’ movement (Heading). Pitch and Roll angles were computed as the arcsine of the *x* and *y* axes, respectively, with a running mean calculated over a 1-second interval. The running mean for Heading was determined using a circular mean function (Equation 4.1)	(Gunner et al., 2021; Wilson et al., 2008)
Absolute Angular Velocity	The rate of change of three channels: pitch, roll and heading, calculated as the square root of the sum of the squared values of each channel.	(Sakai et al., 2019)
Dynamic acceleration (dynX, dynY, dynZ)	The dynamic acceleration along each axis representing the body movement of the animal. Calculated by subtracting static acceleration from the raw acceleration for each respective axis.	(Fehlmann et al., 2017a)
Overall Dynamic Body Acceleration (ODBA)	A measure of the total body acceleration. The sum of the absolute dynamic acceleration of all three orthogonal axes.	(Halsey et al., 2011; Wilson et al., 2020)
ODBA smoothed (ODBA.sm)	To reduce noise and minimise fluctuations in the ODBA signal, ODBA smoothed was calculated as a running mean over a 3-second period, effectively reducing variations in ODBA at a frequency of 40 Hz.	

continued . . .

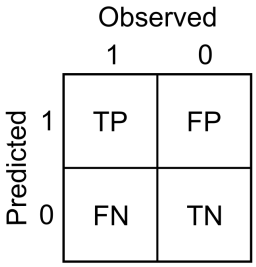
Table 4.1 Overview of accelerometry and magnetometry variables — *(continued).*

Variable	**Description**	**References**
Vectorial Dynamic Body Acceleration (VeDBA)	An alternative metric for total body acceleration, offering values more closely aligned with the actual experienced acceleration. In contrast to ODBA, this measure is not influenced by device orientation. It is determined by taking the square root of the sum of the squared values of each acceleration axis.	(Bidder et al., 2012; Qasem et al., 2012)
VeDBA smoothed (VeDBA.sm)	VeDBA smoothed was calculated as a running mean over a 3-second period, effectively reducing variations in VeDBA at a frequency of 40 Hz.	(Gunner et al., 2022)
Vectorial Static Body Acceleration (VeSBA)	An additional measure of the total body acceleration. The sum of the absolute static acceleration of all three orthogonal axes.	
VeSBA smoothed (VeSBA.sm)	VeSBA smoothed was calculated as a running mean over a 3-second period, effectively reducing variations in VeSBA at a frequency of 40 Hz.	
Partial dynamic body acceleration (PDBAX, PDBAY, PDBAZ)	The absolute values of acceleration, representing the amplitude of acceleration along each axis. Calculated as the absolute positive value of acceleration	(Fehlmann et al., 2017a)
Power spectrum density (PSD) for first and second associated maximum frequency (PSD1X, PSD1Y, PSD1Z; PSD2X, PSD2Y, PSD2Z)	Amplitude and frequency of oscillations were assessed through Fast Fourier Transformation (FFT) analysis. PSD was estimated at the first and second maximum PSD, along with their corresponding frequencies, for each second. This analysis was conducted at intervals of 3 seconds, encompassing 1 second before and 1 second after the target interval.	
Magnetic smoothed (magX, magY, magZ)	The magnetic orientation of the device in relation to the Earth's magnetic field measured along three axes, and smoothed over 120 data points, equivalent to a 3-second interval.	(Chakravarty et al., 2019; Williams et al., 2017)
Magnetic vectoral sum smoothed (Mag.Vec.sum)	The sum of vectorial magnetometry along three axes represents the overall absolute change in magnetic orientation smoothed over a 3-second interval.	

4.2.6. Model fitting using random forest models

Random forest models were constructed to predict behaviour among plantation baboons, using accelerometry and magnetometry variables (Table 4.1). All analyses were executed in `R` (Version 4.2.3; R Core Team, 2021), employing the `randomForest` (Version 4.1-1.1; Breiman, 2001; Liaw and Wiener, 2002) and `caret` packages (Version 6.0-94; Kuhn, 2008). These models utilise classification trees to categorise accelerometer signals into distinct behaviours, establishing decision rules based on the chosen variables (Cutler et al., 2007; Fehlmann et al., 2017a; Sakai et al., 2019). The data were first divided into training (70%; 20 096 s or 5.58 h) and validation datasets (30%; 8587 s or 2.39 h; Breiman and Spector, 1992). Both datasets were stratified based on baboon ID and behaviour, ensuring that each unique behaviour and ID were adequately represented in both datasets. The random forest model used 1000 iterations, representing the number of classification trees sampled, with each tree constructed from a random subset of data (bootstrap method). This method mitigates against over-fitting and challenges associated with imbalanced datasets, which could be prevalent in observations of individuals more inclined toward rest than activity (Fehlmann et al., 2017a; Sakai et al., 2019; Shuert et al., 2018).

In assessing variable importance for behaviour classification, the Gini index was used to measure the probability of misclassification for randomly selected observations (Breiman, 2001). This process involved continuous subdivision of observations at each classification node until the Gini index ceased to decrease (Fehlmann et al., 2017a). The mean Gini decrease was then calculated to determine the significance of each variable, with higher values indicating greater importance in classifying behaviours (Shuert et al., 2018). The proportional error of each model (i.e., number of misclassifications/number of observations based on the number of trees) was evaluated for each behaviour, 'Out-Of-Bag' error estimates, and considering observations not included in the bootstrapped sample or tree, were examined for each model to assess overall model performance. Model performance was evaluated using confusion matrices that were produced for the model on the validation dataset. The confusion matrix, also known as the error matrix, is depicted by a matrix describing the performance of a classification model on a set of test data (Figure 4.8). From this, the model accuracy, precision and recall were calculated using the number of true positives (TP, correctly classified positive behaviours), false positives (FP, incorrectly classified positive behaviours), true negatives (TN, correctly classified negative behaviours) and false negatives (FN, incorrectly classified negative behaviours; Christensen et al., 2023; Fehlmann et al., 2017a).



		Observed	
		1	0
Predicted	1	TP	FP
	0	FN	TN

Figure 4.8. Confusion matrix visualisation depicting matrix of true positives (TP), false positives (FP), false negatives (FN) and true negatives (TN).

Model accuracy was calculated as the percentage of true positives and true negatives (Ferdinandy et al., 2020):

$$\text{Accuracy} = \frac{TP}{TP + FP + TN + FN} \tag{4.2}$$

Precision was defined as the proportion of positive classifications that were true compared to false positives:

$$\text{Precision} = \frac{TP}{TP + FP} \tag{4.3}$$

Finally, recall was defined as the proportion of positive classifications that were true compared to the false negatives:

$$\text{Recall} = \frac{TP}{TP + FN} \tag{4.4}$$

4.2.7. Activity budgets based on acceleration data

To obtain activity budgets for each baboon across their respective collar periods, the predicted model output from all baboons was applied to the accelerometer dataset (816 days, n = 11 baboons), for daylight hours. Sunrise and sunset data were extracted from the `R` package `bioRad` (Version 0.7.3; Dokter et al., 2019) based on a central GPS location within the study area. I produced two separate activity budgets, one detailing the specific behaviours predicted from the random forest model, and one using more traditional behavioural groupings: locomotion (walking + running), foraging (foraging + feeding), rest, social (grooming (receive + give)) and bark-stripping (BS_teeth + BS_fingers + Processing_BS). I assessed significant variations in the mean time allocated to bark-stripping across different sexes and age groups using unpaired two-sample t-tests. I verified model assumptions utilising the Shapiro-Wilk normality test and F-test to examine homogeneity in variances. All statistical analyses were performed using base `R` functions.

4.2.8. GPS data preparation

Utilising GPS data, necessary for aligning fine-scale positional information and predicted behaviours within the plantation matrix, posed substantial challenges due to the rugged terrain and dense plantation forest canopy (Hance et al., 2021). Consequently, the GPS recording observed in this study was less frequent than in previous studies conducted in more open or less obstructed environments, e.g., fynbos (Bracken et al., 2022; Christensen et al., 2023; Fehlmann et al., 2017a) or farm pastures (Riaboff et al., 2020; Sakai et al., 2019). The obstructed canopy hindered the GPS unit's ability to establish and maintain a consistent satellite connection, resulting in sporadic data collection and unreliable location tracking (Hance et al., 2021). Moreover, the continuous search for a GPS signal in challenging terrain significantly drained the device's battery, limiting the duration of data collection. Consequently, only a small subset of individuals (n = 3; one adult male, one adult female and one sub-adult male) yielded sufficient GPS data for further analysis. Each of these individuals provided approximately 10 days of GPS locations which could be paired with accelerometer data for subsequent analysis of the frequency and duration of bark-stripping bouts. Given the limited availability of GPS data, I used the "best" data from the adult female (as females are philopatric; Clarke et al., 2008; Henzi and Barrett, 2003) as a representative sample of the troop's movement (Chapter 3; Hoffman and O'Riain, 2012b).

I then applied data processing steps to eliminate erroneous fixes. These steps involved the removal of relocations outside the study area and consecutive 1-second GPS fixes that would have been physically implausible for baboons to traverse due to excessive speed or abrupt changes in direction. I adopted methodologies described by Bjørneraas et al. (2010) and thresholds were adopted from Bracken et al. (2022) for identifying outliers, considering a predefined threshold distance of 250 m and criteria for trajectory anomalies (e.g., high speed or sharp turning angles). Through these processes, 0.3% of GPS fixes were excluded. In instances where GPS fixes were absent or removed, and the duration of missing values did not exceed 10 seconds, I employed interpolation functions adopted from Bjørneraas et al. (2010) to interpolate the missing path. The interpolation process was applied to 0.02% of the data. All analyses were executed in `R` (Version 4.2.3; R Core Team, 2021). After applying data processing steps, the GPS data from the selected individual were used to estimate the positional data of each troop member, linking individual positions with predicted bark-stripping events for each baboon within the troop.

4.2.9. Frequency and duration of bark-stripping and environmental variables

Following methods by Christensen et al. (2023), bark-stripping bouts were extracted by identifying consecutive minutes of the same behaviour. If the majority of the seconds within a minute was spent bark-stripping (BS_teeth, BS_fingers, or Processing_BS), the minute would be classified as "bark-stripping". If the next minute was also spent bark-stripping, this would be stitched to the first, and so forth until a minute was identified as a new behaviour at which point the bout was considered to have ended. Bout frequency was calculated as the number of bouts per day and durations as the number of minutes spent bark-stripping per day.

Climate variables

Weather data for the study was sourced from the Machadodorp weather station (South African Weather Service — SAWS) located approximately 30 km from the field site (Climate number: 10211, 25.7158 °S, 30.2303 °E). The selection of this station was based on proximity and its hourly data recording, which was crucial for the study's temporal resolution. Malfunctions at the weather station resulted in no weather data for 44 days out of the maximum collar duration of 212 days. Climate variables were estimated at a "per day" rate, where maximum temperature (°C) was the maximum temperature recorded that day. Rainfall was estimated as the number of rain hours in a day, which denotes an hour during which rain was recorded, though not necessarily continuously (median and range of rain per hour: 0.6 mm; 0.2–87.6 mm). Rainfall occurred on n = 103 out of the n = 198 study days (with a median and range of rain hours per day: 1 h; 0–21 h).

Plantation variables

To integrate bark-stripping bouts with spatial covariates, a gridded study area was established. Each GPS location was encircled by a circular zone (buffer) spanning 150 m^2, approximating the average troop spread (Hoffman and O'Riain, 2011) and encompassing areas potentially utilised by troop members at that time. Buffers were merged into a single area which defined the "accessible area" of the troop over the 10-day study period. Subsequently, a grid system was constructed over this accessible area, consisting of cells measuring 0.023 km^2 (150 m $\times$ 150 m; Figure 4.9). Bark-stripping frequency within each grid cell was determined by counting the number of bark-stripping bout GPS locations; cells devoid of such bouts were assigned a value of zero. Bark-stripping duration was calculated as the sum of bark-stripping minutes spent within each cell.

Plantation covariates were then extracted for each grid cell. In instances where multiple compartments overlapped within a cell, the compartment that comprised the higher proportion of that cell was selected. Additionally, the distance from the centroid of each cell to the nearest human settlement was computed. Like in Chapter 3, compartment productivity was estimated using Site Index (SI), a measure commonly used in forestry for species-specific site productivity (Kotze et al., 2012). Grid usage was estimated as the proportion of time that the troop spent within a given grid cell over the 10-day period.

Statistical Analyses

The influence of both climatic variables and plantation characteristics on bark-stripping behaviour was examined using generalised linear mixed models (GLMMs). GLMMs were constructed using the `glmmTMB` package (Version 1.1.7; Brooks et al., 2017). All continuous data were standardised to a mean of zero and a standard deviation of one. I tested the collinearity between covariates using Pearson's correlation with a threshold of $|r|$ = 0.7 (Dormann et al., 2013). No covariates were highly correlated with each other. Model fit was evaluated for the global models by residual diagnostics, using the `DHARMa` package (Version 0.4.6; Hartig, 2022) to identify potential outliers, dispersion issues, and zero-inflation concerns.

For the analysis of climate factors, the response variables considered were: 1) number of bouts per day and 2) mean bout duration per day (Table 4.2). Fixed predictor variables included the number of rain hours per day, maximum daily temperature (°C), and the intrinsic variables of age and sex. A GLMM with a poisson error distribution was applied for bout frequency and a quasi-poisson error distribution for bout duration, to account for increased dispersion (Table 4.2). Both models used a log-link function and a quasi-Newton optimiser (i.e., BFGS). Additionally, to account for repeated measures from the same individual, individual ID was included as a random intercept. Temporal autocorrelation in the residuals was addressed by incorporating a first-order autoregressive covariance term (AR1) into the model, and an offset term was used for number of recording days per individual (Table 4.2).

For the analysis of plantation factors, fixed predictor variables were thus: (1) the proportion of each grid cell covered by plantation (m^2), (2) the species of tree, (3) the age (years) of the trees, (4) distance (m) to nearest human settlement, (5) mean slope (degrees) of the cell, (6) the total area (km^2) of the compartment, (7) species-specific site productivity (compartment SI) and (8) the proportion of time (seconds) the troop spent within each grid cell (Table 4.2). A GLMM with a negative binomial error distribution was applied for bout frequency and a quasi-poisson error distribution for bout duration, both distributions utilised a log-link function and a quasi-Newton optimiser (i.e., BFGS). Finally, random intercepts were included for individual ID to account for repeated measures (Table 4.2).

Post-hoc pairwise comparisons were performed to determine any differences in bark-stripping frequency and duration among tree species using the package `emmeans` (Version 1.10.1; Lenth et al., 2024).

4.3. Results

4.3.1. Acceleration ethogram

Variables relating to total body acceleration were found to be consistently important in the model, being included in seven of the top ten variables (Figure 4.10A). Mean partial dynamic body acceleration along the *x*-axis (PDBAX; forward-back motion) was found to be the most important variable for distinguishing between behaviours (Figure 4.10A). Mean PDBA for the other two axes (*y* and *z*) were not found to be as important, ranked 20th and 26th respectively. PDBAX were different between locomotion behaviours (running, median [1st and 3rd quartile]: 0.68 g* [0.49 g–0.79 g]; walking: 0.15 g [0.12 g–0.19 g] and all other behaviours such as foraging (0.04 g [0.02 g–0.06 g] and rest (0.02 g [0.01 g–0.02 g]; Figure C.1).

In the context of bark-stripping behaviours, both BS_fingers and BS_teeth exhibited similarities in the patterns observed for VeDBA.sm and ODBA.sm. This is evidenced by the overlapping interquartile ranges and medians for both variables which fall within each other's range, indicating a substantial portion of shared values between the two variables (Figure C.1). In contrast, Processing_BS was distinct in terms of body acceleration variables, with no overlap between the 1st and 3rd quartiles when compared to BS_fingers and BS_teeth (Figure C.1). A similar, though weaker, relationship was observed for PBAX, with the median value of Processing_BS not falling within the interquartile ranges of BS_fingers

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*Unit "g" refers to acceleration due to gravity.

Table 4.2. Complete list of the four generalised linear mixed models (GLMM) structures used. Each response variable is listed with the error distributions, full list of explanatory variables, random effects and temporal autocorrelation parameters detailed for the specific models.

Response	**Distribution**	**Explanatory**	**Random effects**	**Temporal autocorrelation**
Climatic impacts				
1: Frequency	Poisson	Maximum temperature Number of rainfall hours Sex Age	ID	Yes
2: Duration	Quasi-poisson	Maximum temperature Number of rainfall hours Sex Age	ID	Yes
Plantation impacts				
3: Frequency	Negative binomial	Grid area covered Compartment Species Compartment age Distance to human settlement Mean slope Compartment area Site Index Grid usage Sex Age	ID	No
4: Duration	Quasi-poisson	Grid area covered Compartment Species Compartment age Distance to human settlement Mean slope Compartment area Site Index Grid usage Sex Age	ID	No

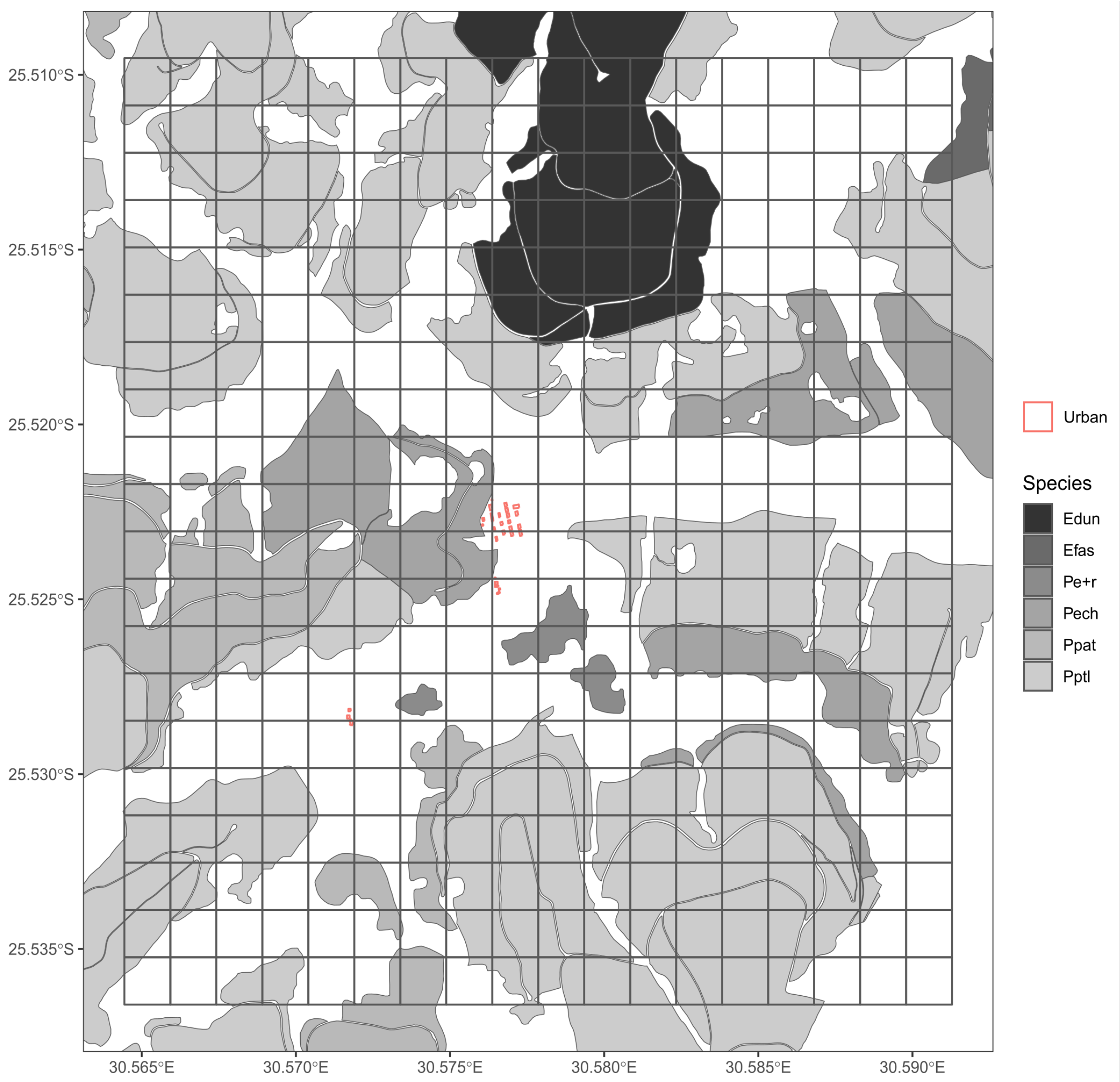

Figure 4.9. Grid system used to define the “accessible area” to the troop over the 10-day study period. Each cell within the grid system covers a 0.023 km^2 (150 m × 150 m) area. Plantation covariates were extracted per grid cell. Compartments are colour-coded according to planted species and red areas demarcate human settlements (urban) within the plantation.

and BS_teeth. Notably, BS_fingers and BS_teeth exhibit the highest median PBAX values among all sedentary behaviours, excluding scratching. For Acc_y and Pitch, a shift in the relationships between behaviours was evident. BS_fingers and Processing_BS had increased similarity, once again characterised by their overlapping interquartile ranges and medians. BS_teeth deviated slightly from this pattern, with its median value not falling within the interquartile ranges of BS_fingers and Processing_BS (Figure C.1). As such, BS_teeth shows different body position patterns compared to the other bark-stripping activities.

4.3.2. Model performance

The random forest model reached a mean (± SD) precision of 98.3% (± 0.02%) and a mean recall of 95.9% (± 0.04%) across all behaviours. The recognition (or extraction) of bark-stripping behaviours showed a high precision (> 95%) and recall (> 95% for Processing_BS; > 90% for BS_teeth and > 85% for BS_fingers) (Figure 4.10C). Examining bark-stripping behaviours in the confusion matrix (Table 4.3), BS_fingers exhibited a degree of misclassification with various other behaviours, which is to be expected given its lower recall in the model. Processing_BS and BS_teeth tend to be misclassified as foraging (Table 4.3), but at a very low rate, given their high precision and recall in the model (Figure 4.10C).

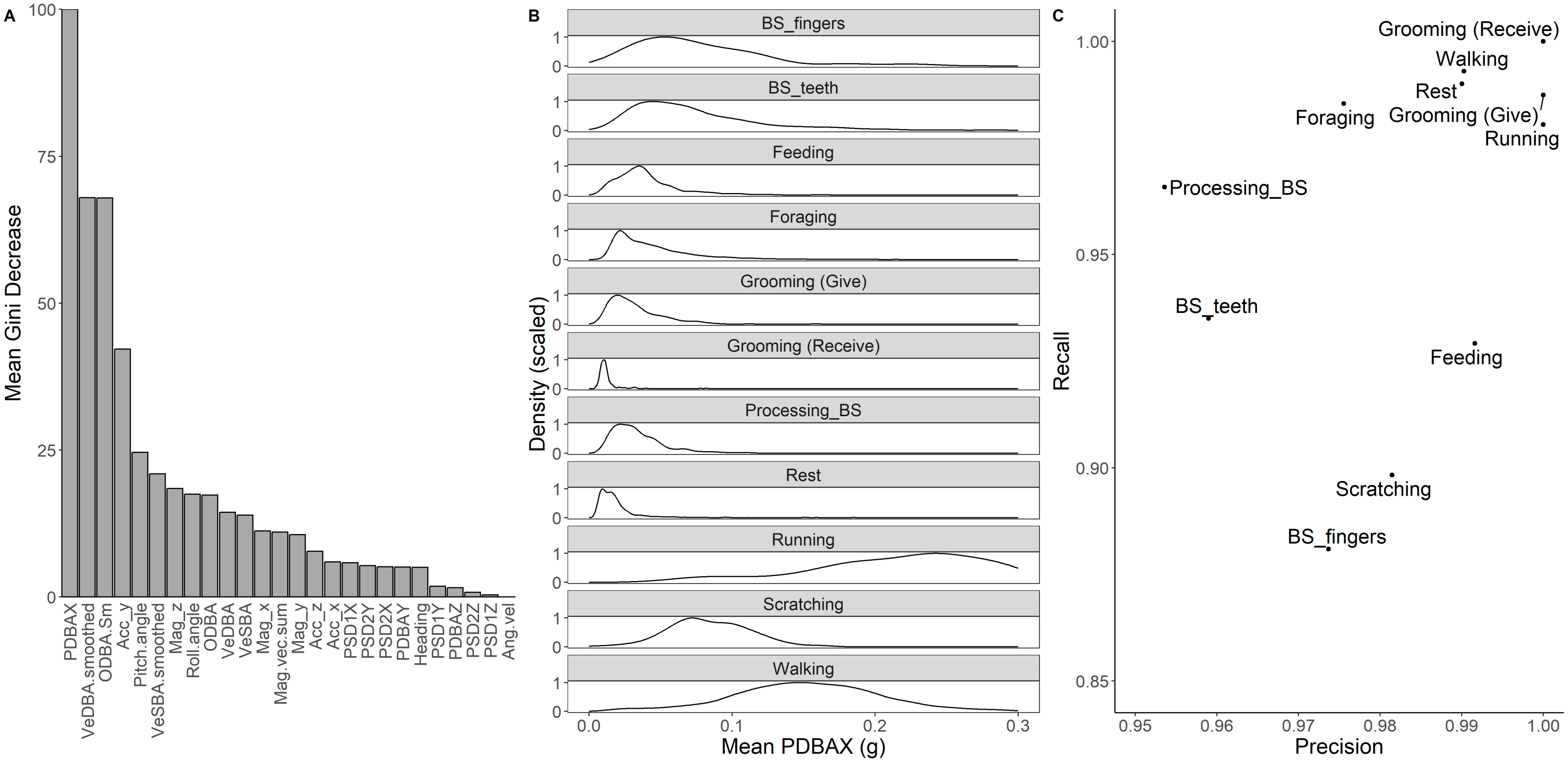

Figure 4.10. Random forest model results. **(A)** Variable importance for the identification of baboon behaviour. Variables are ordered according to the mean decrease in Gini index (see “Methods” for more details). **(B)** Scaled density histogram plots for major behaviours as a function of mean partial dynamic body acceleration (PDBAX), which scored the highest mean decrease in the Gini index (i.e., was most important to classification of behaviours). **(C)** Precision and Recall for all identified behaviours.

Table 4.3. Confusion matrix comparing the predicted (Pred.) behaviour from the model and observed (Obs.) behaviour from video recording showing the quality of extraction of different behaviours. Observed behaviours are organised in columns and predicted behaviours are in rows, values in bold represent the true positives (TP) correctly classified by the model.

	BS_fingers	BS_teeth	Feeding	Foraging	Grooming (Give)	Grooming (Rec.)	Processing_BS	Rest	Running	Scratching	Walking	Total Pred.
BS_fingers	**37**	0	0	0	0	0	3	0	0	0	2	42
BS_teeth	0	**187**	0	10	0	0	0	0	0	0	3	200
Feeding	0	0	**118**	9	0	0	0	0	0	0	0	127
Foraging	0	6	1	**1755**	0	0	1	2	0	0	16	1781
Grooming (Give)	0	0	0	0	**235**	0	0	2	0	1	0	238
Grooming (Rec.)	0	0	0	0	0	**62**	0	0	0	0	0	62
Processing_BS	1	1	0	3	0	0	**226**	2	0	0	1	234
Rest	0	0	0	2	0	0	4	**795**	0	0	2	803
Running	0	0	0	0	0	0	0	0	**251**	0	5	256
Scratching	0	0	0	2	0	0	1	0	0	**53**	3	59
Walking	0	1	0	18	0	0	2	2	0	0	**3253**	3276
Total Obs.	38	195	119	1799	235	62	237	803	251	54	3285	7078

Note: Grooming (Receive) shortened to Grooming (Rec.)

4.3.3. Activity budgets

Activity budgets were calculated by applying the random forest model to the acceleration dataset, restricted to daylight hours (total collar days = 410; n = 11, Table C.2). Baboons spent on average (mean ± SD) 25.8 ± 8.5% of their time walking, followed by resting (25.7 ± 15.6%) and foraging (22.8 ± 15.5%). For bark-stripping behaviours, baboons spent on average 6.8 ± 8.3% of their time processing bark strips (Processing_BS), 3.0 ± 2.2% stripping bark with teeth (BS_teeth) and 0.4 ± 0.5% stripping bark with fingers (n = 10, BS_fingers; Table C.2).

When analysing more general activity (Figure 4.11), baboons spent on average (mean ± SD) 27.5 ± 8.7% of their time locomoting, followed by foraging (25.9 ± 18.8%), resting (25.7 ± 15.6%), socialising (16.2 ± 23.7%) and bark-stripping (9.4 ± 8.9%). No significant sex differences were observed for the mean time allocated to bark-stripping (*df* = 9, t = -1.184, p-value = 0.267) and age (*df* = 9, t = -2.213, p-value = 0.054) groups.

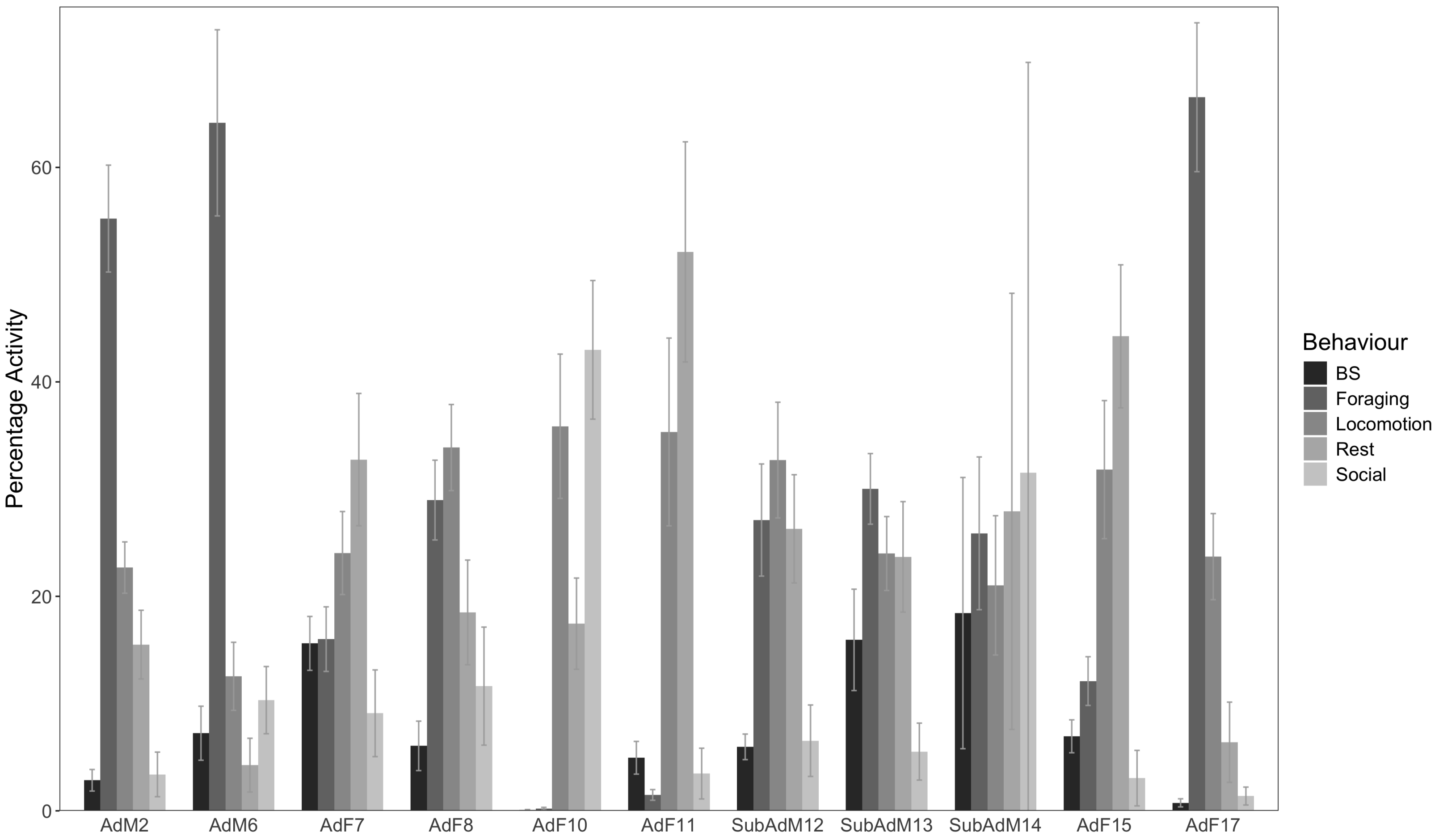

Figure 4.11. Mean percentage of time each individual baboon was engaged in generally defined behaviours based on acceleration data restricted for daylight hours. Error bars represent standard deviation. Individuals are coded by Age-Sex, including adult males (AdM), adult females (AdF), and sub-adult males (SubAdM), followed by their collar numbers.

4.3.4. Predictors of bark-stripping frequency and duration

Model fit for all the global models was found to be adequate, with no significant outliers, dispersion issues, or zero-inflation identified (Figures C.2, C.3, C.4 and C.5). GLMM 3 exhibited some dispersion, as indicated by the standard deviation of residuals fitted versus simulated (Figure C.4B). However, the dispersion parameter was low (0.43), and I therefore accepted the model following the protocols outlined in the `DHARMa` vignette (Hartig, 2022).

The climatic models revealed that temperature was the sole significant factor affecting bark-stripping frequency (GLMM 1; Table 4.4), indicating a positive correlation between higher temperatures and bark-stripping (p-value = 0.045). None of the climate variables predicted bark-stripping duration (GLMM 2), and no effects of age or sex on bark-stripping were found (Table 4.4).

Bark-stripping was recorded in 25 % of the troops "accessible area", accounting for 92 grid cells out of 360 (Figure 4.13). Within the study area, the compartment species and hybrids, identified by their parent species cross, were represented in varying proportions: *P. patula* × *P. tecunumanii* (Pptl) accounted for 34%, *P. elliotti* × *P. caribaea* (Pech) for 8%, *E. dunnii* (Edun) for 6%, *Pinus patula* (Ppat) for 5%, and *P. elliottii* × *P. roxburgii* (Pe+r) and *Eucalyptus fastigata* (Efas) for less than 1%. The *post-hoc* pairwise comparison test revealed statistical significance between five combinations of tree species and bark-stripping frequency (Figure 4.12A): Edun and Ppat (p-value = 0.004), Pe+r and Pech (p-value = 0.005), Pe+r and Ppat (p-value < 0.0001), Pe+r and Pptl (p-value = 0.003) and Pech and Ppat (p-value = 0.033). Similarly, for bark-stripping duration, five combinations of tree species showed statistical significance (Figure 4.12B): Edun and Pe+r (p-value = 0.002), Edun and Ppat (p-value < 0.001), Pe+r and Pech (p-value < 0.0001), Pe+r and Ppat (p-value < 0.0001) and Pe+r and Pptl (p-value < 0.0001).

Ppat exhibited the highest bark-stripping frequency and duration among all other species, and significantly greater than Edun and Pe+r. Pine species Pech, Ppat and Pptl were associated with more frequent and longer duration bouts of bark-stripping compared to Edun and Pe+r. Notably, there were no significant differences observed between Pech, Ppat and Pptl for either bark-stripping frequency or duration.

Both bark-stripping frequency and duration showed significant increases in grid cells where the troop spent greater amounts of time, i.e., increased grid usage, as well as in older compartments and closer to human settlements (p-value < 0.001; GLMM 3 and 4; Table 4.4 and Figure 4.13). Bark-stripping frequency was found to increase in smaller and more productive compartments (p-value < 0.05; GLMM 3; Table 4.4), whereas bark-stripping duration was found to increase on steeper slopes (p-value < 0.001; GLMM 4; Table 4.4). Proportion of cell covered by plantation (i.e., a proxy for edge effects) did not exert significant influence on bark-stripping frequency or duration. No significant differences based on sex or age were detected in either bark-stripping frequency or duration (Table 4.4).

Table 4.4. Results from the generalised linear mixed models (GLMM) investigating the effects of climatic and plantation variables on bark-stripping bout frequency and duration. Species include *Eucalyptus fastigata* (Efas), *Pinus elliottii* × *P. roxburgii* (Pe+r), *P. elliotti* × *P. caribaea* (Pech), *P. patula* (Ppat) and *P. patula* × *P. tecunumanii* (Pptl). *Eucalyptus dunnii* (Edun) reference category for tree species variables. Significance levels are indicated with stars: ∗∗∗ p-value < 0.001, ∗∗ p-value < 0.01, ∗ p-value < 0.05. All model terms, error distributions and temporal autocorrelation are listed in Table 4.2.

Response	**Predictor**	**Estimate**	**Std. error**	**z-value**	**p-value**	
Climatic impacts						
1: Frequency	Intercept	-2.93938	0.49137	-5.982	< 0.001	
	Maximum temperature	**0.04605**	**0.02295**	**2.007**	**0.0447**	∗
	Rainfall hours	0.01238	0.01925	0.643	0.5199	
	Sex (Male)	1.20972	1.04502	1.158	0.247	
	Age (Sub-adult)	-1.15686	1.10292	-1.049	0.2942	
2: Duration	Intercept	-3.72588	0.89087	-4.182	< 0.001	
	Maximum temperature	0.02575	0.03074	0.838	0.402	
	Rainfall hours	0.03528	0.02567	1.374	0.169	
	Sex (Male)	2.46114	1.78069	1.382	0.167	
	Age (Sub-adult)	-1.21373	1.91545	-0.634	0.526	
Plantation impacts						
3: Frequency	Intercept	-4.73266	0.91084	-5.196	< 0.001	
	Species_Efas	-9.11533	55.90949	-0.163	0.870489	
	Species_Pe+r	**-2.68436**	**1.13972**	**-2.355**	**0.018509**	∗
	Species_Pech	0.56983	0.84386	0.675	0.499509	
	Species_Ppat	**2.33085**	**0.64897**	**3.592**	**< 0.001**	∗∗∗
	Species_Pptl	1.07316	0.76735	1.399	0.161956	∗∗∗
	Grid area covered	0.02357	0.07512	0.314	0.753725	
	Compartment age	**1.08406**	**0.21461**	**5.051**	**< 0.001**	∗∗∗
	Distance to human settlement	**-0.26863**	**0.09255**	**-2.903**	**0.003702**	∗∗
	Mean slope	0.09894	0.09890	1.000	0.317114	
	Compartment area	**-0.26898**	**0.10493**	**-2.563**	**0.010364**	∗
	Site Index	**0.55023**	**0.23153**	**2.377**	**0.017475**	∗
	Grid usage	**0.91721**	**0.07305**	**12.556**	**< 0.001**	∗∗∗
	Sex (Male)	0.88691	1.02602	0.864	0.387362	
	Age (Sub-adult)	0.63366	1.10195	0.575	0.565265	
4: Duration	Intercept	-4.32517	0.84817	-5.099	< 0.001	
	Species_Efas	-11.33254	172.27693	-0.066	0.947552	
	Species_Pe+r	**-4.17810**	**1.12560**	**-3.712**	**<0.001**	∗∗∗
	Species_Pech	1.45229	0.80408	1.806	0.070896	
	Species_Ppat	**2.53896**	**0.62559**	**4.058**	**< 0.001**	∗∗∗
	Species_Pptl	**1.93835**	**0.73054**	**2.653**	**< 0.05**	∗∗
	Grid area covered	-0.12691	0.06628	-1.915	0.055524	
	Compartment age	**1.24216**	**0.20937**	**5.933**	**< 0.001**	∗∗∗
	Distance to human settlement	**-0.56407**	**0.09159**	**-6.159**	**< 0.001**	∗∗∗
	Mean slope	**0.27196**	**0.08904**	**3.054**	**< 0.05**	∗∗
	Compartment area	-0.13985	0.09520	-1.469	0.141816	
	Site Index	0.22179	0.21140	1.049	0.294129	
	Grid usage	**0.47851**	**0.02448**	**19.546**	**< 0.001**	∗∗∗
	Sex (Male)	0.44868	0.88335	0.508	0.611503	
	Age (Sub-adult)	0.82480	0.95004	0.868	0.385302	

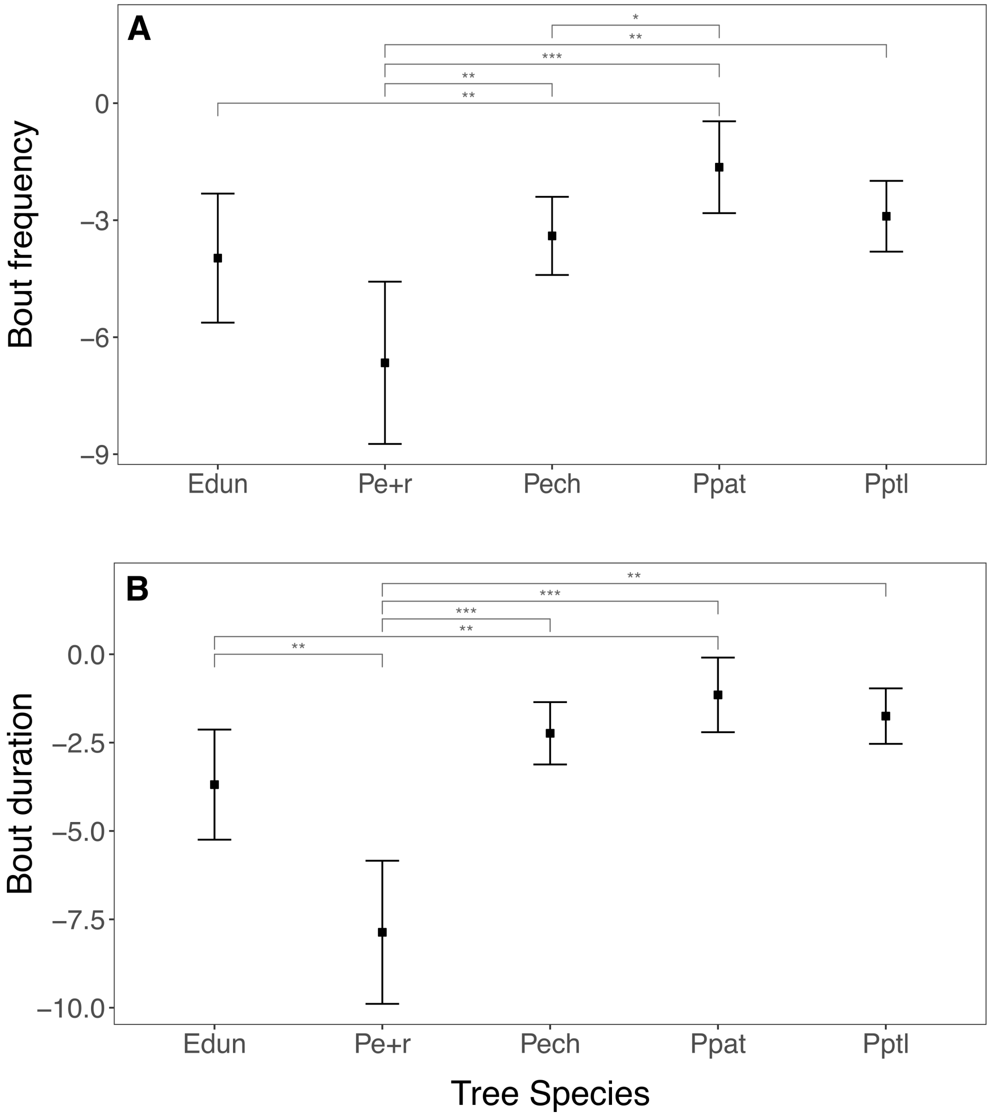

Figure 4.12. Boxplot comparison of (**A**) bark-stripping bout frequency and (**B**) duration across dominant exotic tree species. Species include *Eucalyptus dunnii* (Edun), *Pinus elliottii* × *P. roxburgii* (Pe+r), *P. elliotti* × *P. caribaea* (Pech), *P. patula* (Ppat) and *P. patula* × *P. tecunumanii* (Pptl). Squares represent the marginal means and error bars indicate the 95% confidence interval (CI) of the marginal means. Significance levels for *post-hoc* pairwise comparisons are indicated with stars: $***$ p-value < 0.001, $**$ p-value < 0.01, $*$ p-value < 0.05. *E. fastigata* (Efas) was excluded from the plot due to excessively large CIs, Efas was not statistically different to any other species (p-value > 0.05).

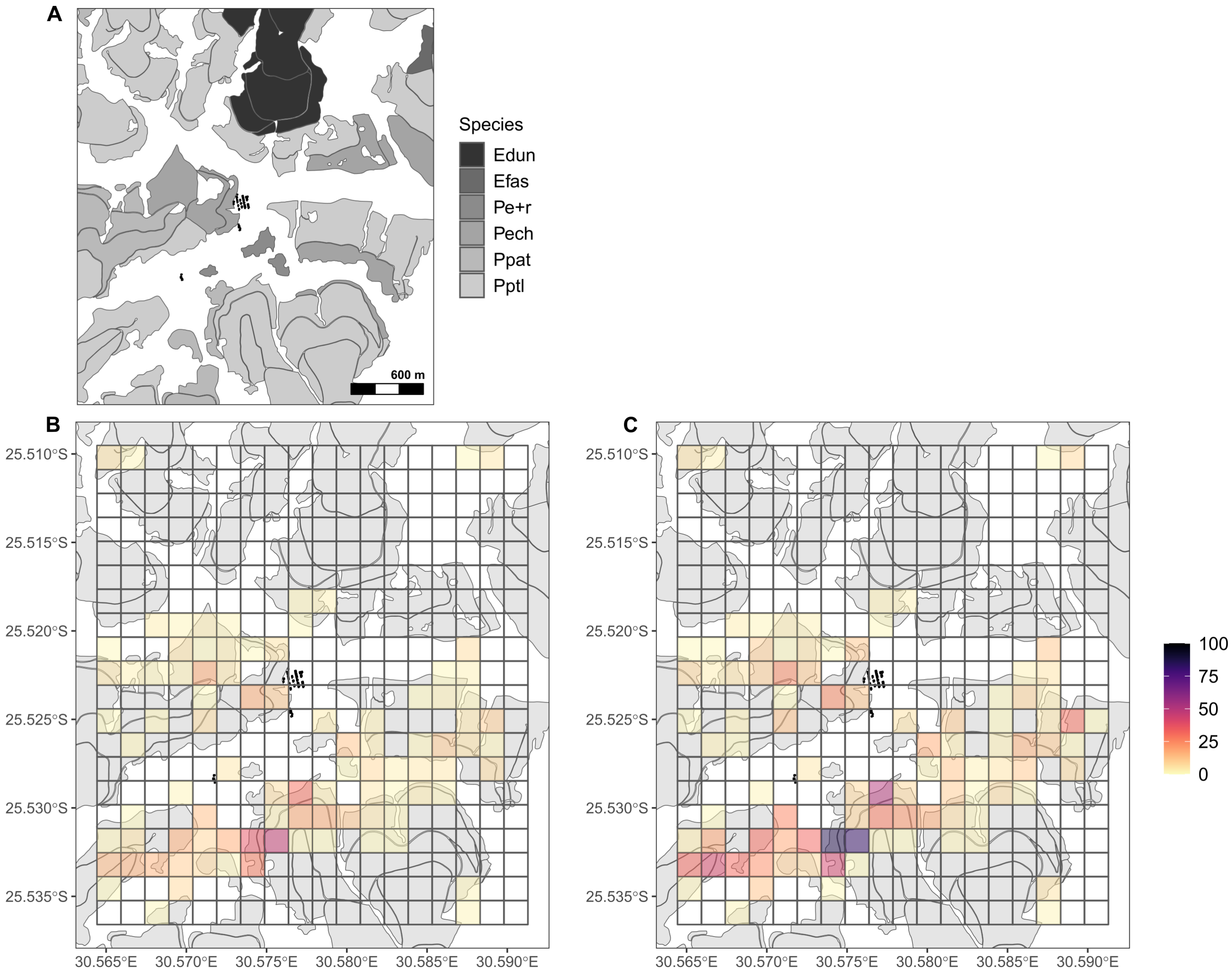

Figure 4.13. Spatial distribution of bark-stripping within the “accessible area” to the troop over the 10-day study period. (**A**) Map illustrating tree species per compartment. (**B**) Frequency and (**C**) Duration of bark-stripping bouts per grid cell (150 m × 150 m).

4.4. Discussion

This chapter focussed on understanding key aspects of baboon bark-stripping behaviour within commercial timber plantations. Firstly, by leveraging accelerometry data from bio-logging devices, my study aimed to accurately predict instances of bark-stripping behaviour among chacma baboon individuals. Central to this was the development and validation of random forest models capable of distinguishing bark-stripping movements from other activities such as locomotion and foraging. This study is the first to identify bark-stripping behaviour in baboons using tri-axial accelerometer data with high precision (98.3%) and recall (95.9%). Although bark-stripping behaviours were performed infrequently, I showed that they could be successfully identified and incorporated into activity budgets alongside other key behaviours.

Furthermore, this study explored the influence of climatic factors and plantation-specific variables on the frequency and duration of bark-stripping events. Contrary to initial hypotheses, intrinsic factors such as age and sex did not dictate bark-stripping occurrences; instead, extrinsic variables such as temperature, compartment age and the availability of anthropogenic food sources emerged as prominent influencers. A higher frequency of bark-stripping was found in smaller, more productive compartments, while the duration of these behaviours tended to increase on steeper slopes.

4.4.1. Acceleration ethogram for bark-stripping behaviours

The use of random forest models allowed for the identification and quantification of bark-stripping behaviour, collectively providing movement metrics specifically associated with bark-stripping activities. By utilising these metrics, researchers can not only measure the occurrence of such damage-causing events but also delve further into their spatial-temporal dynamics. Distinguishing between BS_fingers and BS_teeth from Processing_BS was facilitated by their shared characteristic of elevated patterns in body acceleration variables (e.g., VeDBA.sm and ODBA.sm). This distinction is understandable given that BS_fingers and BS_teeth entail more vigorous activity, involving the active extraction of bark from the trunk. Conversely, Processing_BS involves less energetic movement, similar to feeding behaviour where the baboon remains relatively sedentary around a food source. Similarly, disparities between active bark-stripping behaviours (BS_fingers and BS_teeth) and Processing_BS were evident in PBAX values. PBAX, which reflects the amplitude of acceleration along the *x*-axis (back-and-forth), aligns with the characteristic short, jerking movements associated with separating bark from the trunk using fingers or teeth.

BS_teeth exhibited distinctive accelerometer patterns in Acc_y and Pitch compared to the other bark-stripping behaviours. Acc_y, representing dynamic acceleration along the *y*-axis (left-and-right), corresponds to the lateral body movements made during bark removal, particularly when the baboon rotates its head sideways to position its incisors under the bark layer before biting and pulling. Such lateral head movements are characteristic of BS_teeth but are unnecessary for BS_fingers and Processing_BS, where the bark manipulation is primarily executed by the hands or fingers. Likewise, in terms of Pitch, which reflects head position relative to the *x*-axis, notable differences were apparent. During BS_teeth, the baboon typically positions its head forward toward the trunk to secure its teeth for bark extraction. In contrast, for BS_fingers and Processing_BS behaviours, head positioning tends to remain relatively stable, as bark manipulation is primarily executed by the hand/fingers or feet.

4.4.2. Activity budgets

Time budgets reflect the prioritisation of various activities by animals, with food availability and energy content playing pivotal roles in shaping their daily activity patterns (Alberts et al., 2005; Dunbar, 1992). In my study, locomotion, foraging and resting emerged as the predominant activities, underscoring their significance in the daily routines of baboons living within and immediately adjacent to plantations. Similar results were recorded for baboons living in plantations in Zimbabwe (Katsvanga, 2011) with most time allocated to foraging (33.94%) and locomotion (32.90%), and less time dedicated to resting (11.87%) and social interactions (13.19%; Katsvanga, 2011).

By comparison, troops living predominately within natural habitat within the same region allocated 62.3% of their time to foraging, 24.3% to movement and 10.2% to resting (Marais, 2009). Marked variations in time allocated to foraging and resting for troops living predominately in plantations versus natural habitat may reflect differences in food availability. For instance, Altmann and Muruthi (1988) comparing activity budgets and feeding behaviours among semi-provisioned baboons feeding from garbage dumps and wild-feeding groups in Amboseli National Park, Kenya, showed that semi-provisioned baboons spent only 20% of their time foraging and nearly 50% resting, whereas wild-feeding baboons allocated approximately 60% to foraging and 10% to resting. Similarly, baboons that accessed human derived food in both agricultural and urban areas spent less time locomoting and foraging and more time resting than natural foraging troops (Hoffman and O'Riain, 2011). Thus, with plantation baboons allocating about 25% of their time to resting, they occupy an intermediate position between semi-provisioned and wild-feeding baboons. The findings of this study, along with those of Katsvanga (2011), suggest that food resources are not limiting within plantations, contradicting the suggestions of Henzi et al. (2011) who proposed that plantations lack sufficient forage for baboons and are thus primarily used as corridors between patches of natural habitat.

In my study, social behaviours exhibited very large standard errors, which could be associated with a lack of ground-truthed video data to accurately train the model for this behaviour, as well as possible sex and age differences in grooming behaviours. For example, significant differences in grooming patterns between male and female baboons or between different age groups (such as adults vs. sub-adults) could lead to larger standard errors in the data. Random forest models have demonstrated success in predicting social behaviours, such as grooming (Christensen et al., 2023). However, achieving this often demands a considerably larger volume of video footage than what was collected during my study season. Moreover, such modelling is typically confined to adult individuals and does not extend to sub-adults, as is the case in this study. My study only included grooming as a social behaviour, as observations of aggression and playing were too sparse ($< 100\,\mathrm{s}$) to be included in the model. Given that these are active behaviours, it can be assumed that they would have been subsumed into locomotion behaviours, potentially contributing to the high estimated locomotion activity relative to foraging. While this could also help explain some of the variation in other behaviours, such as foraging, the standard deviations around these estimates remain consistent with previous studies using accelerometer collars to create activity budgets for baboons (Christensen et al., 2023).

Although bark-stripping was among the least observed behaviours, the estimated time allocation in my study (9%) was substantially higher compared to previous studies (Henzi et al., 2011; Katsvanga, 2011). For instance, Katsvanga (2011) reported an average of < 1% of time dedicated to bark-stripping (through pre-rainy, rainy and post-rainy seasons), while Henzi et al. (2011) estimated that pine cambium accounted for 3.5% of annual foraging effort (4.7% in the wet season). I included all behaviours related to bark-stripping, including the processing of stripped bark, a distinction that has not been used in other studies to date. While most primate studies include processing of food material in active foraging estimates, this aspect has not been previously emphasised in relation to bark-stripping behaviours. If I exclude bark processing behaviours from bark-stripping estimates, the time spent bark-stripping is still greater (i.e., 2.5%) than estimated in other studies (Katsvanga, 2011). This variance may stem from differences in methodology; while traditional direct observation methods often struggle to capture all instances of rarely performed behaviours, especially when obscured by dense canopies or in young trees prior to the first pruning, bio-logging collars used in this study can record all instances of the behaviour.

The relatively high proportion of time allocated to bark-stripping activity in this study suggests that baboons are deriving some benefit from the behaviour. The sweet and palatable nature of pine cambium exudate has been proposed to provide both hedonistic (Bigalke and van Hensbergen, 1990; Rogers et al., 1994) and nutritional (Erasmus, 1993; McNamara, 2005) value to baboons that may separately, or together, provide an incentive for bark-stripping. At a forestry stakeholder workshop, both scientists and managers hypothesised that boredom during extended periods of inactivity (e.g., heavy sustained rainfall) and anxiety (e.g., crossing busy roads or approaching areas frequented by people) may drive bark-stripping behaviour as a displacement activity (Nadel et al., 2012). My findings supported these theories, showing that bark-stripping was associated with elevated temperatures rather than rainfall. Plantation compartments may offer cooler microclimates, where baboons can engage in lower-energy activities like bark-stripping." Moreover, my findings indicated heightened bark-stripping activity near human settlements. It remains unclear whether this behaviour is primarily driven by anxiety, such as the anticipation of conflict when accessing anthropogenic food sources. Through personal observations of damage events, bark-stripping did not appear to be associated with anxiety. However, further research is required to conclusively eliminate stress as a driving factor.

While some studies have identified age differences in crop raiders, such as sub-adult baboons being more likely to forage on crops in certain contexts (Strum, 2010), more recent research indicates that crop foraging is undertaken to some extent by all age-sex classes, typically initiated by adult individuals of either sex or sub-adult males (Hockings et al., 2009; Priston et al., 2012; Schweitzer et al., 2017). This contrasts the findings of Katsvanga (2011) who suggested selective participation by baboons in plantations and Di Bitetti (2019) who reviewed bark-stripping behaviour in other primates and concluded that not all individuals within a group or population engaged in the activity. Katsvanga (2011) did stress that their conclusion may have been influenced by detection bias with larger, bolder individuals more likely to be observed engaging in the behaviour. My personal observations confirmed the acceleration data with bark-stripping activities performed by most members of the troop. Such behaviour is difficult to record when performing either scan samples or focal follows used in previous observational studies. Furthermore, accelerometer collar data are not influenced by other factors such as dense foliage which limit visibility and hence the recording of behaviours in the canopy of plantations (Katsvanga, 2011). While it is noteworthy that all collared individuals, regardless of age or sex, participated in the behaviour, it is essential to consider the frequency of occurrence among different groups. In the activity budget analyses, individuals dedicating the most time to bark-stripping were dispersed across various ages (adults and sub-adults) and sexes. This suggests that no particular demographic group is predominantly responsible for observed damage. However, it is crucial to delve deeper into the frequency and distribution of bark-stripping incidents among demographic categories to accurately assess its overall impact. For example, while variation in bark-stripping was not statistically significant across age-sex groups, notable differences were observed among individual baboons (Figure 4.11), with time allocated to this activity ranging from approximately 1% to 19% of their daily budgets, regardless of age or sex (collar 10 was an outlier in this regard). Additionally, a negative correlation between time spent foraging and bark-stripping suggests that cambium may serve as an alternative food resource that some individuals exploit more than others, regardless of age or sex, while others prioritise traditional food sources over bark-stripping. Therefore, further research is necessary to investigate how other individual/group characteristics may influence bark-stripping behaviour.

4.4.3. Predictors of bark-stripping frequency and duration

Bark-stripping frequency (but not duration) increased with higher daily maximum temperatures. This pattern aligns with the observed behavioural responses of baboons to intense thermal loading, wherein they seek shade and engage in more sedentary activities such as resting and grooming (Hill, 2006a). Similarly, Stelzner and Hausfater (1986) found that travel rates in yellow baboons were influenced by ambient temperature at a microhabitat level, with baboons slowing down on hot days when traversing more shaded areas.

Thus, increased temperatures may drive baboons to seek shelter within plantation compartments, particularly during the hottest part of the day, and while sedentary and situated within, or beneath, the tree canopy, they may engage in more bark-stripping behaviour. Accelerometer data revealed that energy expenditure (derived from VeDBA and ODBA) patterns linked to bark-stripping closely resembles that of sedentary behaviours such as resting, feeding and grooming. Consequently, this suggests that bark-stripping could be categorised as a sedentary activity undertaken by baboons when in shaded compartments.

Among the tree species studied, pine species (*P. patula*, *P. elliottii* × *P. caribaea* and *P. patula* × *P. tecunumanii*) were associated with more frequent and longer duration bouts of bark-stripping relative to *E. dunnii* and *P. elliottii* × *P. roxburgii*. Previous research has highlighted the susceptibility of certain pine species to baboon damage (Germishuizen et al., 2017), likely due to higher concentrations of sugar and protein (McNamara, 2005), or the ease with which bark can be removed (Erasmus, 1993). Damage to *Eucalyptus* trees by chacma baboons is comparatively less severe in both frequency and extent when contrasted with pine damage, potentially due to *Eucalyptus* bark containing higher concentrations of phytoestrogens, which can induce behavioural changes and fertility suppression in primates (Wasserman et al., 2012a,b). Furthermore, differences in the structural composition of pine versus *Eucalyptus* compartments could contribute to variations in baboon behaviour. Pine compartments typically exhibit higher understory plant diversity compared to *Eucalyptus* (Lomba et al., 2013, 2011; Vaz et al., 2019), potentially offering baboons greater foraging opportunities. Additionally, *Eucalyptus* trees employ self-pruning mechanisms (Lomba et al., 2011), which may limit perching availability for bark-stripping. Personal observations corroborate this, with damage to *Eucalyptus* species predominantly occurring at ground level (Figure 1.3).

Bio-loggers that provide high-resolution GPS and accelerometer data have been used to assess activity budgets and specific behaviours of chacma baboons within other human-modified landscapes, including commercial food crops (Walton et al., 2021) and urban land use (Bracken et al., 2023, 2022; Fehlmann et al., 2017b). Baboons tend to avoid agricultural and urban areas protected by guards, which are considered potential high-risk zones. In Cape Town, Fehlmann et al. (2017b) revealed that baboons employed a "sit-and-wait" tactic to minimise spatial overlap with guards, enhancing their access to anthropogenic food sources. Additionally, Bracken et al. (2023) showed that baboons alter their movement patterns and behaviours when navigating high-risk urban areas in Cape Town. Proximity to human settlements emerged as a significant factor influencing bark-stripping behaviour, with an increased frequency and duration observed nearer to such settlements. Therefore, plantation baboons may adopt this "sit-and-wait" strategy, waiting near anthropogenic feeding opportunities where they engage in bark-stripping, a relatively low-energy activity. In the plantations within the Tokai region of the City of Cape Town, bark-stripping was initially observed when baboons were prevented from accessing vineyards for the first time (Nadel et al., 2012). Surprised by the presence of guards armed with catapults and rocks, the troop retreated to the plantation edge, where they climbed trees and began to observe their surroundings. After approximately an hour of this behaviour, the baboons commenced bark-stripping in the trees they had taken refuge in, causing considerable damage to all trees in that area within three hours (M. Justin O'Riain, *pers. obs.*). While this study did not formally measure the availability of anthropogenic food sources, the observed patterns in bark-stripping provide valuable insights into how baboons may adapt to and exploit resources within human-modified landscapes. These findings underscore the significance of utilising bio-logging collars to record fine-scale movements and activity patterns of wildlife exploiting resources in human-modified landscapes, often under the threat of deterrence. Quantifying the impacts of wildlife is a critical component of mitigating conservation conflicts, as it allows for an improved understanding of drivers of negative interactions, and hence, provides an opportunity for improved management of both the animals and human-modified landscapes.

A significant predictor of both bark-stripping frequency and duration was the proportion of time spent by the troop in a grid cell. This aligns with observations from Bigalke and van Hensbergen (1990) and Henzi et al. (2011) who noted that damage was higher near sleeping sites and areas that were used to pre-bait before capturing baboons. Baboons may engage in bark-stripping behaviour more frequently and for longer durations in areas where resources are abundant or easily accessible. Increased residency time may allow them to thoroughly exploit available resources, including bark from trees, leading to higher levels of bark-stripping activity. This pattern aligns with the hypothesis that baboons target areas with higher resource availability for foraging activities, as evidenced by the increased bark-stripping frequency observed in more productive compartments. Compartments with higher Site Index (SI) values are known to support healthier and more productive vegetation, potentially providing better foraging opportunities for baboons (Kotze et al., 2012). This finding is consistent with Germishuizen et al. (2017), who identified an increased risk of damage in sites with higher SI values. Additionally, Chapter 3 revealed significantly greater revisitation rates by troops to compartments with higher SI values. Given that baboons devote approximately 9% of their time to bark-stripping, suggesting that this behaviour may have fitness consequences, it follows that highly productive trees could be particularly appealing or beneficial for them. Therefore, it is important to consider the potential role of sap flow and nutrient content in bark, which could attract baboons to certain compartments for nutritional purposes. On the other hand, bark-stripping duration was not significantly influenced by compartment productivity. This suggests that once baboons initiate bark-stripping behaviour, the duration of a stripping event may be influenced by factors other than resource abundance. For example, bark thickness or palatability may impact how long baboons spend engaged in bark-stripping activities, regardless of compartment productivity. Future research could further investigate this association by focusing on specific locations such as sleeping sites or spatially important resources, and examining how these factors influence bark-stripping behaviour.

Longer residency time in an area offers ample opportunities for various social interactions, including grooming, mating and territorial behaviours, which could potentially influence bark-stripping activity. Furthermore, social hierarchies and group cohesion likely play a role in determining both the locations and timing of bark-stripping events. Katsvanga (2011) observed that bark-stripping coincided with foraging and social interactions, a finding I corroborated through direct observations. Bark-stripping events were frequently linked to social interactions, including agonistic behaviour such as chasing individuals away from recently damaged trees. Moreover, younger individuals often competed for and processed bark dropped on the plantation floor by individuals bark-stripping in the trees (Figure 4.5). Various playful behaviours, such as climbing and tumbling down branches, were also observed to coincide with bark-stripping events. Future research should delve deeper into understanding how these complex social dynamics intersect with bark-stripping, shedding light on the underlying mechanisms and motivations driving this behaviour.

Bark-stripping frequency increased with compartment age. As trees mature, they tend to grow taller and develop more structurally robust trunks with stronger branches, capable of supporting baboons during bark-stripping bouts. Moreover, older compartments may boast a more developed understory, characterised by a greater diversity and abundance of both exotic and natural food resources (Norton, 1998). This finding is consistent with the results presented in Chapter 3, where higher revisitation rates were observed in compartments with trees older than 10 years. Bigalke and van Hensbergen (1990) observed that baboon damage became significant after trees reached the age of four years, with notable reductions observed in the Western Cape when trees reached twenty years, attributed to the protective thickness of their bark. Although this study did not examine how bark-stripping varies throughout a tree's lifespan, the strong relationship between revisitation patterns (as discussed in Chapter 3) and bark-stripping implies that bark-stripping may increase as trees mature but subsequently decline once the bark becomes too thick (i.e., a humped distribution). This observation was further supported by Germishuizen et al. (2017) and Ferreira et al. (2020), who found that damage increased in older trees (up to 20 years) within research plots. Older trees, which may have been previously damaged, could be revisited (Katsvanga, 2011; Nagaike, 2020; Welch and Scott, 2017), with baboons exploiting prior wounds as access points through the resilient, thick bark. The recurrence of baboons returning to trees over time could lead to cumulative damage throughout a tree's lifespan. For future damage assessments, it will be important to investigate how bark-stripping frequency changes with tree age. Specifically, research could explore whether frequency increases continuously with age or follows a pattern where bark-stripping initiates at a certain age and remains constant thereafter, indicating an all-or-nothing threshold response.

Bark-stripping frequency exhibited a negative relationship with compartment size, indicating a higher incidence of bark-stripping in smaller compartments. This trend aligns with increased troop revisitation rates in smaller compartments observed in Chapter 3. Smaller compartments are often situated in areas with rugged terrain, where limitations in accessibility for planting and mechanical harvesting are common. The increased bark-stripping frequency observed in smaller compartments may be attributed to the concentrated distribution of resources within these areas. However, despite the higher bark-stripping frequency in smaller compartments, there was no significant increase in bark-stripping frequency closer to compartment edges, contrasting with previous findings that observed localised patterns of baboon damage concentrated at compartment edges, such as roads and fire breaks (Bigalke and van Hensbergen, 1990; Henzi et al., 2011). Moreover, the distance to natural areas adjacent to pine compartments did not impact troop revisitation rates (Chapter 3), indicating that baboons in plantations may prioritise resources within compartments (including cambium) over proximity to natural vegetation strips (Germishuizen et al., 2017; Katsvanga, 2011). Consequently, the prevailing theory that baboons are restricted to natural pockets and traverse compartments primarily to access other patches of natural vegetation (Henzi et al., 2011), with bark-stripping predominantly occurring at these edges, finds little support in my data. This discrepancy could also stem from a visibility bias, where bark-stripping within compartments is more difficult to detect compared to the same activity along the perimeter. The utilisation of accelerometer collars in this study allowed me to overcome these observer biases, enabling a more accurate estimation of bark-stripping rates and locations.

Bark-stripping duration exhibited significant increases on steeper slopes. Consistent with this finding, damage assessments conducted by Germishuizen et al. (2017) revealed higher baboon damage on upper slopes. These locations provide a vantage point with an open area ahead, potentially facilitating baboons' monitoring of their surroundings (Katsvanga, 2011). Elevated locations are known to be important for other primate behaviours, such as sleeping site selection, as they offer a vantage point to spot terrestrial predators (Bidner et al., 2018). Additionally, increased visibility from elevated positions may create perceived safer environments for baboons, allowing them to dedicate extra time to bark-stripping for longer periods. Furthermore, it is proposed that baboons may climb trees on steep slopes to enhance their field of view, allowing them to observe potential threats such as neighbouring troops or forestry staff involved in silvicultural activities. If danger is perceived, the entire troop may ascend nearby trees to monitor the threat and subsequently engage in bark-stripping after an extended period of vigilance within the tree canopy. This aspect becomes especially relevant when considering proximity to human settlements, as baboons can better survey the area and make decisions based on raiding risks.

Traditionally, mitigation strategies for managing damage-causing behaviours in wildlife populations often focus on identifying and targeting specific individuals believed to be primarily responsible for such behaviours (Erasmus, 1993; Katsvanga, 2011; Nadel et al., 2012). However, the findings of this study largely negate such an approach given the apparent ubiquity of the behaviour in the region and the finding presented here that all collared individuals engage in the behaviour. This insight has significant implications for the design and implementation of mitigation strategies, which will be expanded upon in the final Synthesis chapter of this thesis (Chapter 5).

4.5. Limitations and future research

An interesting finding of this study was the differential relationship between the frequency and duration of bark-stripping in relation to temperature as compartment size. While bark-stripping frequency increased with rising temperatures and reduced compartment area, the duration of stripping events did not show a similar trend. In these cases, bark-stripping may be a by-product of baboons being in the area, such as being limited to shaded regions or selecting smaller compartments to forage. As a result, baboons may "sample" the cambium; however, the suitability or palatability of these trees for bark-stripping could restrict the duration of stripping bouts. To draw meaningful conclusions about why these two metrics vary in relation to compartment attributes, further data on the nutritional attributes of cambium and inner bark would be necessary. However, this analysis was beyond the scope of the current study and presents a significant challenge for future research.

The results presented in this chapter offer only a snapshot of bark-stripping behaviour within a single troop, cautioning against broader extrapolation. GPS battery life in this study was substantially shorter than anticipated and shown in other studies using this technology (Bracken et al., 2022; Christensen et al., 2023; Fehlmann et al., 2017a; Riaboff et al., 2020; Sakai et al., 2019). I attribute this to the dense canopy of plantation compartments limiting connectivity and the constant searching between GPS devices and satellites depleting the battery faster than expected (Hance et al., 2021). Unfortunately, the limited GPS data restricted my ability to analyse fine-scale bark-stripping movement patterns linked to specific trees (e.g., movement between trees). Additionally, I was unable to link a substantial amount of accelerometer data with spatial information and therefore, in order to explore bark-stripping bouts with spatial variables, I assigned bark-stripping bouts to grid cells serving as a proxy for troop spread. A limitation of this method was that tree species within a grid cell were assigned based on majority coverage. This could have resulted in bark-stripping bouts being attributed to the dominant species within that grid cell, even if they occurred within a minority species (*see* Figure 4.13), and therefore misrepresenting species preferences. Future research should look into other GPS technologies and varying GPS collection rates that can record data under dense canopies, such as mature plantation compartments, to avoid rapid battery depletion.

My study did not explicitly account for tree species availability within the generalised linear mixed models (GLMM). Although the highest frequency and duration of bark-stripping was observed in *Pinus patula*, accounting for only 5% of the study area, tree species availability should be directly considered in future studies exploring bark-stripping within baboon home ranges. Edge effects estimated by the proportion of the grid cell covered by compartments primarily captured the relationship between compartments and natural areas. However, this approach did not fully account for compartment edges created by thin features, such as roads. Chapter 3 did not identify distance to roads as a significant factor influencing revisitation by baboon troops. Therefore, a similar relationship can be assumed given that residency time (grid cell usage) was a strong determining factor of bark-stripping frequency and duration. However, future studies could further investigate the relationship between baboons and hard edges created by roads and fire breaks to better understand their impact on bark-stripping behaviour.

I was unable to explore the relationship between bark-stripping behaviour and plantation management practices, such as pruning, as the 10-day study period did not align with silvicultural activities in the area. Bark-stripping has been suggested to increase in freshly pruned compartments (Bigalke and van Hensbergen, 1990; Ndagurwa, 2007), and thus, exploring the effects of pruning on bark-stripping behaviour could provide valuable insights into direct triggers of bark-stripping and how forestry management impacts damage.

Climbing behaviours, which could influence the position of bark-stripping on trees, were not included in the random forest model due to sparse observations. The position of bark removal on the tree trunk is important as it impacts the timber's value (Katsvanga, 2011), and thus is an important avenue of future research. The grid area used for plantation models was approximately 8 km^2, roughly equivalent to the average size of a plantation troop's home range (7.73 km^2, as described in Chapter 3). However, direct observations of troop movements during video observation revealed that the troop ranged over a much larger area than the designated grid, indicating that the "accessible area" grid did not fully represent the troop's entire home range. As a result, the 10-day constrained spatial analyses limited the exploration of bark-stripping variations across the troop's total home range area.

Observations of social activities, such as aggression and playing, were too infrequent to be included in the model, with observations being less than 100 s. Consequently, the study only included grooming under social behaviours. It is possible that these active behaviours were subsumed into locomotion behaviours, potentially leading to an overestimation of locomotion relative to foraging, and thereby negatively skewing the prevalence of social behaviours in the study troop. Moreover, the dataset encompassed only 35% of the baboons within the troop, which is notably lower coverage compared to previous studies (Bracken et al., 2022; Christensen et al., 2023; Fehlmann et al., 2017a). This disparity is partly attributed to challenges related to habituation in this study. Therefore, caution is warranted when generalising the findings beyond this specific group, as the behaviour of non-collared individuals may differ from those included in the analysis, particularly juveniles. Future research could also expand on these findings by delving into the social dynamics surrounding bark-stripping events, including investigating the synchronicity in bark-stripping bouts within the troop.

Seasonal variation in activity budgets was not explored within this study. While the battery life of bio-logging collars has greatly improved in recent years, battery demands from additional sensors such as GPS, accelerometers and magnetometers still prevent long-term (across seasons) studies (Hughey et al., 2018; Williams et al., 2020). Activity budgets can vary seasonally due to fluctuations in resource availability and changes in day length. Seasonal differences in bark-stripping populations have previously been noted. For example, in the Western Cape, damage appears to escalate during the dry spring and summer months (Erasmus, 1993), whereas in Malawi, damage appears to peak during the wet season (summer; Darwin, 1982). Future research should explore ways in which to accurately study bark-stripping behaviour across multiple seasons, which could provide valuable insights into the dynamics of this behaviour throughout the year.

4.6. Conclusions

The utilisation of accelerometer collars to detect infrequent damage-causing behaviours constitutes an important advancement in understanding the potential drivers of bark-stripping which may lead to better formulated mitigation strategies. These collars enabled a precise estimation of the total time dedicated to bark-stripping during daylight hours within a baboon troop, which was much higher compared to all previous studies using direct observations. Contrary to expectations, bark-stripping behaviour in baboons does not appear to be dictated by intrinsic factors such as age or sex. Individuals exhibited variation in bark-stripping, with no discernible differences detected among demographic groups. This challenges the prevalent notion that certain individuals (e.g., adult males: Katsvanga, 2011) are largely responsible for such behaviours.

While I was not able to directly test why baboons bark-strip, I was able to confirm that the behaviour is non-random with both climatic and plantation level factors influencing the frequency and bout duration of bark-stripping. The relatively high frequency of bark-stripping, compared to findings in other studies, is consistent with forestry managers' assertions that baboon induced damage in this region of South Africa is extensive throughout commercial plantations and a threat to the sustainability of their industry. The findings of this chapter suggest that damage levels to commercial exotic trees could be offset by planting more *Eucalyptus* species and avoiding planting on steep slopes and in proximity to human infrastructure, suggestions that will be further explored in the final Synthesis chapter of this thesis (Chapter 5). Of concern, given the predicted increase in global and regional temperatures is the clear positive relationship between maximum daily temperature and bark-stripping frequency. Assuming all other variables remain constant, this finding alone predicts increasing levels of damage to plantations throughout southern Africa if this relationship holds for other troops.

The use of accelerometer technology has provided the first detailed data on bark-stripping by baboons in the plantations of Mpumalanga, one of the most important areas for commercial timber products in southern Africa. Prior to this, numerous years and considerable resources have been invested in attempting to habituate baboons in this area to close human observation. However, sustained historical persecution both outside and within plantations, coupled with the hyper-abundant refugia offered by plantations, has made baboons exceptionally difficult to observe in and around plantations. Moving forward, the challenge is to build upon this study by collaring baboons from other troops to establish the broader applicability of these findings. Enhancing the quality of GPS data represents a crucial technological advancement, enabling investigations into whether bark-stripping occurs synchronously within troops and identifying finer-scale spatial predictors of bark-stripping.

CHAPTER 5

Synthesis

The escalating global demand for commercial forestry products has increased the demand for natural land and heightened concerns regarding the associated biodiversity loss (Díaz et al., 2019; IPBES, 2019). Despite the recognition of protected areas as crucial for biodiversity conservation (Brooks et al., 2006), their limited coverage is insufficient to mitigate current rates of biodiversity decline (Williams et al., 2022). Consequently, understanding how human modifications of natural landscapes affect species diversity is important to inform management strategies that may enhance the conservation potential of working lands and foster connectivity between increasingly isolated patches of natural habitat.

In South Africa, the conversion of approximately 1.1 million ha of natural land to commercial exotic tree plantations over the past century reflects the local and global demand for structural timber and fibre (FSA, 2020a). Nowhere is this transformation more evident than in Mpumalanga province, which provides optimal environmental conditions for tree growth (Fergusson, 2005). Intensive management practices undeniably improve production on these plantations (Betts et al., 2021), however, their impact on biodiversity remains uncertain (Armstrong et al., 1998; Barlow et al., 2007).

Commercial tree plantations have been described as "green/ecological deserts" devoid of suitable habitat for local fauna (Barlow et al., 2007; Makino et al., 2007; Matthews et al., 2002). However, others have recognised their potential to support components of natural ecosystems, including native fauna (Brockerhoff et al., 2005, 2001, 2008; Carnus et al., 2006; Pretorius et al., 2023). Most recent studies have focussed on commercial afforestation, most usually with exotic tree species, within previously native forest areas (Betts et al., 2021), leaving notable gaps in our understanding of how biodiversity responds when planting has primarily targeted non-forested environments such as grassland. In this thesis, I aimed to bridge this knowledge gap by first conducting a landscape-level evaluation of biodiversity across plantation-modified lands. I then explored how one of the most abundant and commercially important species, the chacma baboon, uses the mosaic of natural and plantation land types available, and how bark-stripping behaviour varies both amongst individuals within a baboon troop as well as spatially through plantation compartments at the troop level. By exploring aspects of baboon behavioural ecology in these human-modified landscapes, I aimed to improve our knowledge of how land use influences wildlife, how wildlife may adapt and exploit plantations and the possible implications for the forestry industry in southern Africa.

5.1. Biodiversity dynamics in plantation landscapes

The transition to densely planted areas of exotic trees in previously grassland-dominated landscapes has undeniably reshaped the ecological dynamics within large parts of the world (Betts et al., 2021). Despite the perception of plantations as "ecological deserts" (Barlow et al., 2007; Makino et al., 2007; Matthews et al., 2002), my research reveals that overall mammalian species richness between sites of varying levels of transformation was not significantly different (Chapter 2). I attributed these findings to a combination of the many corridors of natural riparian vegetation that have been preserved within plantation landscapes and the novel resources provided within plantations. Linear patches of natural vegetation, similar to hedgerows in cropland, serve as vital refuges and corridors for species within modified plantation landscapes, providing access to natural food, water and serving as corridors between patches of natural habitat (Vanneste et al., 2020). However, to maximise the conservation potential of these riparian corridors, it is imperative that they are expanded, with the explicit goal of linking patches of grassland habitat, essential for specialist species, such as the grey rhebuck and klipspringer. These grassland patches are often in areas that are too steep or rugged for commercial plantations, and they should be preserved and managed to prevent the encroachment of invasive plants linked to plantations.

The delicate balance between conservation and production objectives does prompt consideration of a land-sparing approach, wherein large patches of grassland are maintained outside of intensively managed plantation lands. Currently, 500 000 ha of forestry-owned land are permanently unplanted (SANBI, 2013) and are set aside as protected reserves. These areas consist of a biodiverse mosaic of moist grasslands, wetlands, riparian and natural forests, many of which fall into priority biodiversity areas. Such an approach offers a promising compromise to meet timber production demands while preserving meaningful biodiversity outside of formally protected areas (Werema and Howell, 2015). However, robust empirical comparisons between baseline biodiversity data in protected grassland areas and those within plantations and modified corridors are still needed to fully understand the conservation potential of these reserves. To inform sustainable land use decisions, these comparisons should consider both biodiversity metrics as well as timber yields and silviculture techniques. By integrating strategies such as riparian corridor conservation and maintenance, grassland enhancement and land-sparing practices, it is possible to navigate the trade-offs between conservation and production, ensuring the long-term sustainability of plantation ecosystems while also safeguarding considerable biodiversity outside of formally protected areas.

Another important finding of my research was the increased habitat use of mammal communities along road networks under heightened afforestation pressure (Chapter 2). In other parts of the world, certain species, such as the American marten, golden jackal and red fox, have been observed to habitually utilise unpaved logging roads (Ng et al., 2021; Turk et al., 2021). Notably, even in native vegetation, mammals have also been observed using roads (Hill et al., 2021). This preference for road networks can be attributed to the open habitat, facilitating travel, providing resources along road edges (Saunders et al., 2002) and increasing the detection of potential predators. However, this increased use of roads by mammal species does necessitate special management attention. While most roads within plantations are unpaved and experience limited use, they also increase accessibility to a variety of habitats which could increase the risk of poaching. The enforcement of speed limits to reduce wildlife-vehicle collisions, controlling road access to minimise unauthorised entry, and conducting regular snare sweeps near roads could mitigate these negative impacts.

Finally, the contrasting results between overall species richness, which did not exhibit significant differences across two levels of afforestation, and fine-scale species richness, which demonstrated reduced species richness with increased transformation, underscores the critical importance of considering not only the number of species present in an ecosystem but also their abundance and distribution through a landscape (Chapter 2; Hillebrand et al., 2008; Pretorius et al., 2023). Notably, the differences in species richness recorded at the station level between the two study sites (Chapter 2) indicate varying abundances within the mammal assemblages. This richness may not be sustained in heavily transformed landscapes without the presence of less impacted areas that serve as population sources. While generalist species, such as baboons and the common duiker, thrive in these altered environments, rarer species like the aardwolf, leopard, and oribi likely rely on populations sourced from more intact habitats, reflecting a metapopulation or metacommunity strategy. Therefore, relying solely on comparisons of overall species richness between areas may yield misleading conclusions, as it may not accurately reflect conservation value or sustainability, particularly at different spatial scales (Brockerhoff et al., 2001). This highlights the need to incorporate a comprehensive understanding of biodiversity into future monitoring efforts within plantation landscapes. This includes considering aspects such as species evenness (dominance) alongside species richness to provide a more nuanced assessment of mammalian communities and biodiversity in general.

5.2. Chacma baboons as "ecological winners"

The dominance of species like the chacma baboon and common duiker in heavily transformed plantations underscores the remarkable adaptability of generalist species (Chapter 2). Baboons, known for their behavioural flexibility and broad dietary niches, demonstrate an impressive ability to thrive and dominate in human-modified, homogenised environments (Hillebrand, 2008; Fehlmann et al., 2021; Hoffman et al., 2012). Their capacity to survive across diverse habitats, including plantations (Hillebrand, 2008), positions them as ecological winners in a human-dominated world.

Multiple primate species have successfully established populations within plantations, benefiting from additional forest habitat, food resources and possible buffering from human activities in other agroecosystems (Estrada et al., 2012; McCarthy et al., 2017; Spehar and Rayadin, 2017). Contrary to the assumption of plantations being relegated to marginal habitat for baboons (Henzi et al., 2011), my research suggests a distinct preference for plantation environments, particularly during the wet season (Chapter 3). This preference is likely driven by a higher diversity of resources within the matrix of natural patches and plantation compartments, with the latter having additional benefits including an abundance of refuges in the form of large trees, fewer natural predators and buffering from extreme weather conditions, including high temperatures. Baboon use of plantations was influenced by compartment attributes, with more rugged compartments with higher SI values (i.e., more productive) being preferred. There was no preference for natural habitat within and adjacent to plantations, which were favoured by other mammal species. Troops living in plantations have similar-sized or even smaller home ranges relative to those living in natural habitats (Marais, 2009), which is indicative of lower daily distances moved and the availability of high-quality food resources (Altmann and Muruthi, 1988; Campbell-Smith et al., 2011; Nowak et al., 2014; Saj et al., 1999). Additionally, the ubiquitous presence of surface water in the form of rivers, streams and wetlands within plantations reduces the need for baboons to range extensively for water, potentially contributing to the reduction in home range size (Amoroso et al., 2020; Johnson et al., 2015). Once again, these findings challenge previous assumptions regarding baboon avoidance of pine compartments and are more consistent with the findings of Hoffman and O'Riain (2011), which revealed a clear preference for plantations over natural habitat in the Cape Peninsula of South Africa.

Mid-aged and mature plantations could serve as important refuges for baboons from more intensive adjacent land uses, such as crops, and provide dispersal corridors for a variety of organisms (Root and Betts, 2016; Smith et al., 2013). Given that only 12% of the land in sub-Saharan Africa has protected status (Trimble and van Aarde, 2014), it is increasingly important to improve the management of land outside of protected areas to promote biodiversity. Baboons epitomise this conservation challenge, facing risks attributed to climate change, agricultural and urban expansion and hunting (Hill and Winder, 2019). Among baboon species, the chacma baboon is particularly vulnerable, with forecasts indicating a notable decrease in suitable habitat exacerbated by limited southward movement along the South African coastline (Hill and Winder, 2019; Stone et al., 2013, 2015). Against the backdrop of expanding agricultural systems, where baboons typically encounter zero tolerance and often are subjected to lethal management and exclusion measures, plantations emerge as a potentially important habitat for their future survival outside of protected areas.

5.3. Understanding and managing bark-stripping behaviour in baboons

The conservation potential of plantations for baboons is undermined by the negative impacts baboons have on plantation trees. Not only do baboons remove freshly planted seedlings (Fergusson, 2005) but they engage in bark-stripping throughout their distribution, a behaviour that impedes tree growth and greatly reduces both the quality of the timber and overall compartment productivity (Vacek et al., 2020). Moreover, baboon-induced damage exacerbates existing issues such as susceptibility to fires, insect infestations and diseases (Cukor et al., 2019). These cumulative losses pose a significant challenge to the long-term sustainability of this economically important industry (Gwenzi et al., 2007), with both lethal and non-lethal efforts failing to mitigate this damage, fuelling conflict between stakeholders on how best to address this challenge (Nadel et al., 2012). As the global demand for timber is projected to increase by 54% between 2010 and 2050 (Mishra et al., 2022), there is an increasing need for efficient processes that maximise productivity, tree value and profitability. However, baboon-induced damage undermines these objectives, not only through direct damage to planted trees but also by increasing the susceptibility of trees to infections and subsequent decay, thereby diminishing the quality of timber.

Despite the prevalence of baboon-induced damage to trees, direct observations of bark-stripping by forestry personnel are exceptionally rare, with baboons typically avoiding human presence on foot or in vehicles, likely due to historical persecution. Consequently, only a few studies have attempted to directly observe and quantify baboon behaviour in and around plantations (Henzi et al., 2011; Katsvanga, 2011; Ndagurwa, 2007), with challenges in habituation further limiting close observations in many plantation settings (Thys De Wet, *pers comm.*; this study). As a result, the quantification of bark-stripping events and the identification of potential drivers of bark-stripping behaviour are poorly understood, limiting a scientific basis for deriving methods to prevent or mitigate its frequency and extent. The use of bio-logging collars allowed my research to overcome many of the methodological limitations of previous studies (Henzi et al., 2011; Katsvanga, 2011; Ndagurwa, 2007), allowing for a fine-scale quantification of bark-stripping frequency and duration among different individuals within a troop. Although bark-stripping was among the least prioritised behaviours, with an estimated time allocation of 9% in my study (Chapter 4), it was substantially higher compared to previous estimates (< 1% in Katsvanga (2011) and 3.5% in Henzi et al. (2011)). This is still much less than recorded for other primate species in agroforestry systems, e.g., 20% in Barbary macaques (Ménard and Qarro, 1999), 33% in Sumatran orangutans (Campbell-Smith et al., 2011) and 31–67% in Bornean orangutans (Morrogh-Bernard et al., 2009; Wich et al., 2006). However, the importance of bark in the diet of primates feeding in timber plantations is usually lower (e.g., < 5% of feeding bouts; Di Bitetti, 2019).

In this study, the troops "accessible area" delineated in the bio-logger collared troop (Chapter 4) closely matched the average home range size of other plantation troops (Chapter 3; $7.73\,\mathrm{km}^2$), with approximately 25% of this area being subjected to bark-stripping. However, my study only estimated bark-stripping over 10 days and thus the true physical extent of damage is likely to be much greater over the course of a whole year, although it may vary seasonally. Furthermore, given baboons are long-lived (ca. 20 years, Galbany et al., 2015) and pine trees are typically only harvested between 20 to 45 years of age (depending on intended use; Tadesse and Fonseca, 2022), the scope for substantial cumulative damage is enormous. In this context, there is a pressing need for the forestry industry to quantify baboon damage more systematically and routinely to better understand its true production and economic impacts. These damage assessments should evaluate the impact of bark-stripping from planting through to final harvest, incorporating additional losses from reduced growth, increased susceptibility to insect infestations, disease and fires, as well as re-establishment costs, thinning and clear-felling expenses.

An example of such a comprehensive assessment can be seen in studies examining the economic impacts of browsing by red deer (Ligot et al., 2023). Models have been developed to assess the financial losses caused by browsing damage, incorporating forest dynamics, management strategies and interactions with ungulate populations (Wam and Hofstad, 2007; Ward et al., 2004). These models enable predictions of the costs and revenues associated with different management strategies under varying environmental conditions (Ligot et al., 2023). Similarly, future research could develop models specific to baboon-induced bark-stripping damage, incorporating factors such as their social structure and climbing ability, allowing for a more accurate estimation of its economic consequences on timber production. In this regard, remote sensing techniques represent a promising approach for conducting long-term, spatially extensive damage surveys, offering insights into damage levels across South African plantations (Ferreira et al., 2020; Germishuizen et al., 2017; Peerbhay et al., 2018). Such models would provide valuable insights into the financial implications of baboon damage and inform management decisions aimed at mitigating its effects, in addition to promoting more meaningful stakeholder engagement over this contentious issue.

Damage varies with tree species

Bark-stripping is not a behaviour restricted to exotic tree plantations. Southern African baboons have been found to consume bark from native trees, targeting the bark of kapok trees (*Acacia giraffae*; Hamilton et al., 1978) and naturally invasive species such as black wattle (*Acacia mearnsii*; Pebsworth, 2020). In Uganda, olive baboons have been found to consume the bark of different native tree species (*Albizia coriaria*, *A. zygia*, *Khaya anthotheca* and *Sarcophrynium schweinfurthianium*; Okecha and Newton-Fisher, 2006). In plantations, significant differences were observed in bark-stripping frequency and duration among pine species (Chapter 4), suggesting varying susceptibility to baboon damage. Damage to *Eucalyptus* trees by chacma baboons is comparatively less severe in both frequency and extent when contrasted with damage to pines, corroborated by both personal observations and accelerometer data. It has been suggested that high concentrations of phytoestrogens in *Eucalyptus* bark may deter primates (Wasserman et al., 2012a,b), although some damage has been observed on *Eucalyptus* species in Mpumalanga, typically in the form of frilling (vertical strips pulled up from the base of the tree; *see* Figure 1.3). It is also possible that the suppression of other plant species which results in a denuded understory (Lomba et al., 2013, 2011; Vaz et al., 2019), in addition to their self-pruning mechanisms, make *Eucalyptus* compartments less attractive to baboons for both foraging and roosting purposes.

The reduced bark-stripping behaviour with *Eucalyptus* species in this study is fortuitous given the industries proposed “genus exchange”, in which pines will be replaced by *Eucalyptus* species because of their shorter growth cycles (6–15 years compared to 20–45 years for pine) and short fine-fibre pulp content, which is preferred by paper and cellulose industries (FSA, 2016). Leveraging this reduced preference for *Eucalyptus* by baboons could serve as a practical strategy to minimise bark-stripping damage in plantation landscapes while meeting the demands of the forestry industry. It is hoped that this switch to *Eucalyptus* will greatly reduce the impact of bark-stripping by baboons on commercial plantations, but it may also greatly reduce mammalian biodiversity (Chapters 2 and 3).

Other primate species are known to bark-strip *Eucalyptus* species specifically, including ashy red colobus (*Piliocolobus tephrosceles*), black and white colobus, gorillas and chimpanzees in Uganda (Harris and Chapman, 2007; McCarthy et al., 2017; Wasserman et al., 2012b) as well as black and gold howler monkeys in Argentina (Agostini et al., 2010). Thus, while bark-stripping occurrences are currently lower in *Eucalyptus* compared to pine, both for baboons and black capuchin monkeys (Liebsch and Mikich, 2015; Peerbhay et al., 2018), an increase in the relative abundance of *Eucalyptus* species may, under optimal foraging theory (Pyke et al., 1977; Stephens and Krebs, 1986), see a steady increase in bark-stripping damage on this species. However, this theory is contradicted by the observation that capuchin monkeys continue to target *Pinus* species, despite *Eucalyptus* occupying 2.4 times the area of pines (*see* Figure A1 in Di Bitetti, 2019).

The potential effects of a genus exchange to *Eucalyptus* on water availability is a hotly debated issue, as evidenced by the Department of Water and Sanitation’s (DWS) draft “Genus Exchange Regulations” issued in October 2015 (DWS, 2015). These regulations require plantation managers seeking to exchange their compartment genus to apply for authorisation from the responsible authority. One of the main regulatory changes would be to reduce compartment size when switching from pine to eucalypts. However, Forestry South Africa contested these regulations, citing a commissioned report by Gush (2016), which argued that the DWS overstated the reductions in areas required in these exchanges. Despite ongoing debates, much remains unknown about *Eucalyptus* water use, including the representative tree age for measuring water use as well as the baseline vegetation for comparison with commercial trees (Clulow et al., 2023).

Effective management strategies to mitigate plantation impacts on water quantity and quality could include avoiding planting *Eucalyptus* in recharge and other hydrologically sensitive areas, using longer rotations or planting at lower densities, as well as adhering to water quality best management practices. One possible outcome of this could be the expansion of delineated buffers around riverine areas, which could enhance green corridors within plantations and hold promise for biodiversity (Chapter 2; Pretorius et al., 2023). However, careful monitoring and evaluation are essential to ensure that such actions do not inadvertently lead to an expansion of plantation footprints, which could further encroach upon remaining patches of natural habitat and exacerbate biodiversity loss. Evaluating biodiversity metrics alongside timber yields and management strategies is important for making informed and sustainable land use decisions that balance conservation and production objectives. Thus, while a genus exchange may offer a potential solution for bark-stripping mitigation, it necessitates a thorough examination of ecological and economic impacts before wider implementation.

Hypotheses revisited: new insights on the causes of baboon bark-stripping

The fall-back food hypothesis has long been regarded as a leading explanation for bark-stripping behaviour among primate species, with numerous studies citing it as a contributing factor (see review by Di Bitetti, 2019). This hypothesis, along with the habitat transformation hypothesis, is often intertwined with the notion that plantations represent ecologically impoverished environments due to extensive habitat transformation and ecological degradation (Bremer and Farley, 2010). According to this perspective, plantations fail to adequately meet the nutritional requirements of primate species, compelling them to resort to less preferred yet readily available resources such as bark or cambium. Although several bark-stripping primate species conform to this fall-back food theory, such as capuchin monkeys (Liebsch et al., 2015; Liebsch and Mikich, 2015, 2017; Mikich and Liebsch, 2014a,b) and rhesus macaques (Zhang et al., 2022), findings from my study cast doubt on fall-back food mechanisms as a driver of bark-stripping behaviour in chacma baboons.

Firstly, baboons exhibited a strong preference for plantations during rainy seasons when food resources are typically abundant (Chapter 3; Henzi et al., 2011). Furthermore, bark-stripping activity itself was high during the rainy season (Chapter 4), when abundant resources would prevent the need for diet supplementation. Foraging time (both when excluding bark-stripping and when including it as expected under the fall-back food hypothesis) observed for baboons inhabiting plantations was lower than those in nearby natural habitats (Chapter 4; Marais, 2009), suggesting that plantations offer ample resources for troops. The absence of seasonal fluctuations in plantation troop home ranges (Chapter 3) indicates that plantations provide stable environments in terms of food and water availability, thus obviating the need for fall-back foods during challenging seasons. These observations collectively suggest that bark-stripping behaviour among baboons in plantation ecosystems is unlikely to be primarily driven by the fall-back food hypothesis.

If bark-stripping behaviour in baboons is not driven by a lack of natural food, then the implementation of supplementary feeding to reduce bark-stripping may prove ineffective. Research by Henzi et al. (2011) found that capture sites that were pre-baited with supplementary food (e.g., corn) became hotspots for bark-stripping damage, supported by my findings that bark-stripping frequency and duration increases with troop residency time in a compartment. Thus, provisioning does not appear to be a viable solution for reducing bark-stripping by baboons in commercial plantations, and may even exacerbate the problem by increasing damage at provisioning sites and in the long-term increasing the fecundity and hence density of baboons within plantations (Liebsch and Mikich, 2015). Diversionary feeding to draw animals away from target areas has been found to be successful in reducing bark-stripping damage in bears (Ziegltrum, 2008) and somewhat in deer (Jerina et al., 2008), however most primate studies have found the strategy to be unsuccessful (Di Bitetti, 2019), e.g., black capuchin monkeys in Brazil (Mikich and Liebsch, 2014a).

It is also unlikely that bark-stripping behaviour in baboons is driven by the water availability hypothesis (Di Bitetti, 2019). This theory suggests that primates may consume bark to access moisture present in the sap, particularly in regions prone to drought. For instance, Ciani et al. (2001) demonstrated that Barbary macaques increased bark-stripping in areas lacking sufficient water sources. In the context of baboon behaviour in plantations, distance to water does not appear to influence their habitat use (Chapter 3). Moreover, I recorded high levels of bark-stripping during the rainy season and on days with rainfall (Chapter 4). Additionally, in certain Zimbabwean study areas like the Erin Forest (Ndagurwa, 2007), where rainfall is distributed evenly throughout the year, bark-stripping occurs consistently across all seasons, further undermining the association between bark-stripping behaviour and water scarcity in baboons. The forestry region of Mpumalanga, where my study was conducted, is characterised by abundant rivers and streams, with high rainfall originally motivating the selection of this area for planting (Armstrong and van Hensbergen, 1999). These water bodies are typically bordered by natural riparian vegetation, serving not only to conserve water but also to create green corridors of natural vegetation (FSA, 2021; FSC, 2017). While these riverine zones play crucial roles in ecological connectivity and the protection of water resources (Pretorius et al., 2023), their prevalence throughout the region suggests that water is unlikely to be a limiting resource for baboons, and hence, they are unlikely to strip bark for access to moisture in the cambium.

My study revealed that as temperatures increase, baboons are more likely to engage in bark-stripping behaviour. Thus, in a warming world, assuming all other factors remain constant, bark-stripping would be predicted to increase in commercial plantations. Moreover, climate change is expected to impact the distribution and prevalence of numerous forest pests, including insects, pathogens and weeds (Anderegg et al., 2015; Walther et al., 2009), and will likely modify the occurrence and severity of detrimental abiotic factors like windstorms and wildfires (Allen et al., 2010; Anderegg et al., 2015). Together these predictions pose a significant challenge to the forestry industry, stressing the importance of firstly understanding bark-stripping behaviour and then investigating potential mitigation strategies.

Proximity to human settlements emerged as a significant factor influencing bark-stripping behaviour, with an increased frequency and duration observed nearer to such settlements. Baboons have been shown to adopt a “sit-and-wait” strategy when seeking raiding opportunities in both urban (Fehlmann et al., 2017b) and crop-growing areas (Findlay, 2016; Strum, 1994; Walton et al., 2021). Baboons in plantations may adopt a similar strategy, sitting in trees close to nodes of urban infrastructure and watching for high-speed raiding opportunities. My results reveal that the more time baboons spend in a particular compartment the more bark-stripping occurs, and hence, areas in which baboons are more likely to "sit-and-wait" are predicted to have more damage. This has been observed in Cape Town, where bark-stripping of pine trees was first observed following the exclusion of baboons from neighbouring vineyards where they prefer to forage (Nadel et al., 2012). In response to this temporary displacement, the baboons climbed into pine trees that provided a safe refuge and vantage point for observing the vineyards, and then after an hour began to strip bark prodigiously (M. Justin O'Riain, *pers. obs.*). Bark-stripping in this context could be construed as either hedonistic or displacement behaviour linked to the anxiety anticipating the engagement in risky but high-reward raiding behaviour (Bigalke and van Hensbergen, 1990; Rogers et al., 1994). Bark-stripping has also been shown to be particularly prevalent in the trees surrounding baited capture sites (Henzi et al., 2011) and around large fruiting fig trees and Bugweed bushes in plantations (Thys De Wet, *pers. comm.*). Here it is hypothesised that lower ranking troop members sit in the trees surrounding the spatially discrete high quality food source and wait for an opportunity to access the food patch that is dominated by higher ranking individuals which have priority of access (Kaplan et al., 2011). Effective waste management in all urban nodes adjacent to plantations and limiting access to gardens or small-scale crops on the urban edge could reduce the attraction of urban areas for foraging, and hence, limit baboon use of compartments adjacent to these urban areas.

Bark-stripping behaviour in baboons does not appear to be influenced by intrinsic factors such as age or sex, with all collared individuals participating in bark-stripping. This challenges the suggestion that particular individuals are largely responsible for most damage (Katsvanga, 2011) and that their removal may prevent or reduce damage. While lethal management is the preferred method for some bark-stripping species, such as squirrels (Crowley et al., 2018) and deer (Candaele et al., 2021), this success is largely attributed to the strong link between density and damage (Jerina et al., 2008; Kiffner et al., 2008; Ligot et al., 2013). While efforts to reduce baboon damage through culling whole troops have been shown to reduce damage in the short term, damage levels returned to pre-culling levels in the medium to long term (Katsvanga et al., 2006). Non-lethal measures aimed at reducing baboon populations, such as sterilisation and contraception, have generally been deemed too costly and ineffective as long-term solutions to damage (Di Bitetti, 2019; Liebsch and Mikich, 2015). Clearly, there are no simple lethal or non-lethal solutions to reducing bark-stripping, especially given the finding that the behaviour is performed more often than thought and by both sexes and age classes. Perhaps the transition to *Eucalyptus* can reduce damage in commercial plantations to acceptable levels, but how this impacts biodiversity and water consumption remains an important area for future research.

5.4. Limitations

In Chapter 2, the camera trap survey design prioritised the scale of the sites over seasonality. As a result, all 80 cameras were deployed at one site to estimate habitat use across a larger area, leading to the decision to split the survey over two years. This approach introduced ‘year’ as an uncontrolled variable that is confounded with ‘site’. Nonetheless, both plantations and protected grasslands are considered stable environments over the short term (Betts et al., 2021; Kirkman et al., 2014), and no significant disturbances, such as fires or extreme weather, were reported during the study period. Consequently, I did not anticipate drastic changes in the medium/large mammalian community (Drouilly et al., 2018a). However, for future studies, it may be beneficial to reduce the number of camera stations (i.e., 40 per site), allowing for different surveys to be conducted within the same year to better account for seasonal variations.

The GPS data provided by the forestry company as part of their long-term monitoring of baboon troops within plantations was coarse (Chapter 3) which precluded fine-scale habitat selection analyses. Additionally, the Forestry collaring team did not determine troop size, which together with home range estimation would have allowed for an estimate of baboon density. Density has been shown to provide a good indication of resource availability, with much higher densities in human-modified landscapes including plantations

(Hoffman and O'Riain, 2011). Future monitoring by forestry personnel should strive to estimate troop numbers in addition to home range to allow for density estimates, and an assessment of whether density correlates positively with bark-stripping damage.

A second major limitation linked to tracking devices was the paucity of GPS data obtained by the smart collars used in Chapter 4. Other recent studies using the same technology obtained substantially more data allowing for an analysis of spatial proximity estimates between all collared individuals and an understanding of collective movement and interactive behaviours, e.g., grooming (Bracken et al., 2022; Christensen et al., 2023; Fehlmann et al., 2017a; Riaboff et al., 2020; Sakai et al., 2019). These studies were all conducted in more open habitat (fynbos, pastures), with the forest canopy in this study limiting connectivity between collar GPS devices and satellites. With limited GPS data, I was unable to link GPS locations with individual-specific accelerometer data, and thus, could only assign bark-stripping bouts to grid cells. This approach limited the assessment of fine-scale measures of bark-stripping (i.e., to the level of individual trees or specific areas within a compartment). Future studies should explore other GPS technologies capable of recording data under dense canopies, or varying GPS collection rates to prevent the depletion of batteries associated with constantly trying to link with satellites that are obscured by the tree canopy.

One promising approach to overcome limited GPS connectivity is the application of dead reckoning, a method used to reconstruct animal movement paths by integrating heading and speed estimates over time from a predetermined position (Gunner et al., 2021). This technique could help fill in gaps in the data and create uninterrupted fine-scale movement paths, providing insights into bark-stripping behaviour within the plantation environment. However, periodic ground-truthing by a secondary source is essential to maintain accuracy (Gunner et al., 2021), a practice that was not feasible in our study due to battery limitations. Another potential solution is adopting a two-stage modelling approach, as shown in a study on fisher cats (*Pekania pennanti*, Hance et al., 2021), which faced similar GPS connectivity challenges in dense canopies. This approach involves fitting hidden Markov models to estimate periods of movement and resting, followed by linear Gaussian state space models to estimate the location of each resting event. While successful in determining resting behaviour (Hance et al., 2021), the accuracy of this method in predicting location data for short-term behaviours such as bark-stripping requires further investigation.

A lack of time to adequately habituate the study troop (largely as a result of a reduced field season due to the Covid-19 lockdown) means that many social activities, including aggression, playing and mating, were recorded infrequently and therefore were not included in the random forest model (Chapter 4). A larger dataset improves the accuracy of behavioural predictions and allows for the accurate estimation of even infrequently performed behaviours. While my study may have been skewed against social behaviours and potentially inflated locomotion behaviour due to their inclusion as a single category, the dataset contained sufficient data to accurately predict bark-stripping behaviour, largely because of the distinct acceleration and body position signals associated with bark-stripping. Nonetheless, caution should be exercised when extrapolating findings more generally to other troops living in plantations.

5.5. Future research

The factors underlying baboons' attraction to pine trees remain ambiguous. The sole investigation into the potential medicinal benefits of baboons consuming pine bark and cambium was conducted in the Zimbabwean Highlands by Ndagurwa (2013). Despite the prevalence of bark-stripping pines (*Pinus patula*) in winter, suggesting a potential prophylactic use by baboons, no significant relationship was established between respiratory ailments in baboons and the ingestion of bark and cambium. Another proposed benefit of bark consumption for primates is the enhancement of gut motility due to its high fibre content (Di Bitetti, 2019). However, observations indicate that baboons almost always discard the outer bark, the fibrous component, and exclusively consume the soft inner cambium tissue (*pers. obs.*; Bigalke and van Hensbergen, 1990; Erasmus, 1993). Furthermore, faecal analyses of baboons inhabiting plantations yielded no evidence of bark fibre (Erasmus, 1993; Ndagurwa, 2013). Significant differences in phosphorus concentration and moisture content have been found between baboon-damaged and undamaged trees

(McNamara, 2005), however, it is not clear if this is due to baboons selecting trees with higher nutrient concentrations, or if there is just a change in resource allocation towards the wounded area of the tree. Personal field observations of bark-stripping events revealed individuals extracting small pieces from various trees before settling on a particular tree to strip more determinedly, often then resulting in extensive damage or ring-barking to that tree. This suggests that individual trees, despite sharing similar characteristics such as species, age and terrain, may possess distinct attractants, leading to significant damage to that one tree. Monkeys, such as brown capuchins and blue monkeys (*Cercopithecus mitis*), have been shown to have a preference for the largest and healthiest pine trees and those with the widest phloem layer (Liebsch and Mikich, 2015; Maganga and Wright, 1991), and it is possible that a combination of taste and smell could inform baboons as to which trees are most likely to satisfy these criteria. Future research should explore these potential attractants, examining their connection to compartment productivity and age, which my study has shown to be linked with bark-stripping behaviour.

One potential strategy to address the effects of tree damage caused by bark-stripping is the application of chemicals that reduce the rotting of damaged bark. Chemicals, such as gels, are already utilised during pruning to prevent fungal infection and promote wound closure (Katsvanga, 2011). However, implementing this approach also involves significant financial and time investments. Moreover, there are challenges associated with locating damaged trees and applying chemicals in large-scale plantations. Remote sensing, currently employed for damage assessments (Ferreira et al., 2020; Germishuizen et al., 2017; Peerbhay et al., 2018), could offer a viable avenue for addressing these challenges. Plantation managers could efficiently identify areas of tree damage and prioritise chemical application, potentially mitigating the impacts of bark-stripping on tree health. Nevertheless, further research and development are needed to optimise this approach for practical implementation in plantation management strategies.

Exploring the genetic manipulation of trees to alter their chemical composition represents a promising avenue for future research in mitigating baboon bark-stripping. By decreasing palatability or enhancing chemical defences in planted trees, genetic engineering could potentially reduce or even prevent bark-stripping incidents. However, it's crucial to weigh the significant monetary and time costs associated with genetic manipulation against potential benefits. Additionally, there may be a trade-off between tree growth and chemical production, potentially impacting profitability (Mikich and Liebsch, 2014b). While potential reductions in profit should be balanced against losses from damage, it's also essential to consider market acceptance, as not all markets are receptive to genetically modified trees or their products. This line of research presents an intriguing possibility for addressing the issue of baboon bark-stripping, but it requires careful consideration of ecological and economic implications before implementation.

Anecdotal reports from foresters in Mpumalanga, as documented by Bigalke and van Hensbergen (1990) and personal experience talking with foresters, suggest a correlation between damage occurrence and pruning activities in pine plantations. Pruning, defined as the removal of live lower branches, is a common silvicultural practice employed by foresters to enhance tree growth, quality and timber yield by promoting desirable stem forms and reducing competition among branches. This practice alters the tree's photosynthetic dynamics, potentially leading to changes in sap flow composition and nutrient concentrations that may be more appealing to baboons. However, findings from Ndagurwa (2007) indicated that live pruning of *Pinus patula* did not significantly influence the nutrient concentration of inner bark tissues over time post-pruning. Consequently, it seems unlikely that baboons specifically target freshly pruned areas for nutrients. Alternative triggers may include olfactory stimuli attracting baboons to freshly pruned compartments, easier access to the inner cambium through pruning wounds, increased accessibility into compartments due to less lateral branching, or a visibility bias, where damage becomes more apparent after pruning operations.

Despite efforts to understand the causes, the perception that damage escalates within compartments following pruning operations remains a concern for foresters, necessitating further investigation. However, constraints related to GPS technology limited the ability to spatially link bark-stripping events with compartment attributes during this study, as the 10-day period did not coincide with pruning activities. Nevertheless, given the demonstrated accuracy of predicting bark-stripping events using accelerometer collars, future research could explore whether such events increase in freshly pruned compartments. To address the challenge of GPS limitations under plantation canopies, future investigations should consider employing alternative GPS technologies capable of functioning in such environments, adjusting the frequency of GPS data recording (e.g., per minute vs. per second), or establishing virtual perimeters around pruned compartments that trigger signals when collared troops enter freshly pruned areas. These methodological refinements are essential for advancing our understanding of the relationship between pruning activities and baboon bark-stripping behaviour in plantation ecosystems.

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APPENDIX A.

Table A.1. Summary of the number of captures of the 19 species detected for 1-day occasion periods (i.e., before pooling) and included in our multi-species occurrence analysis across the two study sites: heavily (Site 1) and moderately (Site 2) transformed (*see* Figure 2.1) in Mpumalanga, South Africa.

Common name	**Scientific name**	**Heavy**	**Moderate**
African civet	*Civettictis civetta*	17	115
Black-backed jackal	*Canis mesomelas*	11	18
Bush buck	*Tragelaphus sylvaticus*	60	412
Bushpig	*Potamochoerus porcus*	54	93
Cape porcupine	*Hystrix africaeaustralis*	87	160
Chacma baboon	*Papio ursinus*	101	348
Common duiker	*Sylvicapra grimmia*	558	790
Genet species		68	145
Grey rhebuck	*Pelea capreolus*	0	54
Honey badger	*Mellivora capensis*	6	36
Klipspringer	*Oreatragus oreotragus*	0	14
Mongoose species		27	123
Mountain reedbuck	*Redunca fulvorufola*	3	60
Red duiker	*Cephalophus natalensis*	56	148
Samango monkey	*Cercopithecus albogularis*	22	39
Serval	*Felis serval*	14	18
Side-striped jackal	*Canis adustus*	31	91
Vervet monkey	*Cercopithecus pygerythus*	27	61

Table A.2. Summary of the number of captures of detected groups (i.e., before pooling) across the two study sites: heavily (Site 1) and moderately (Site 2) transformed (*see* Figure 2.1) that were not included in our multi-species occurrence analyses, as they were either not the target species or detections were less than 10 after pooling.

Common name	**Scientific name**	**Heavy**	**Moderate**
Aardwolf	*Proteles cristata*	0	6
African wild cat	*Felis lybica*	9	9
Birds		240	263
Bush baby species		0	3
Cape clawless otter	*Aonyx capensis*	0	2
Caracal	*Caracal caracal*	1	5
Eland	*Taurotragus oryx*	0	6
Hippo	*Hippopotamus amphibious*	0	7
Human activities and domestic animals (humans, cars, cows, dogs etc.)		107	214
Kudu	*Tragelaphus strepsiceros*	0	9
Leopard	*Panthera pardus*	0	1
Small mammals (incl. bats)		11	64
Oribi	*Ourebia ourebi*	0	1
Stocked wild animals		0	4
Unidentifiable species			

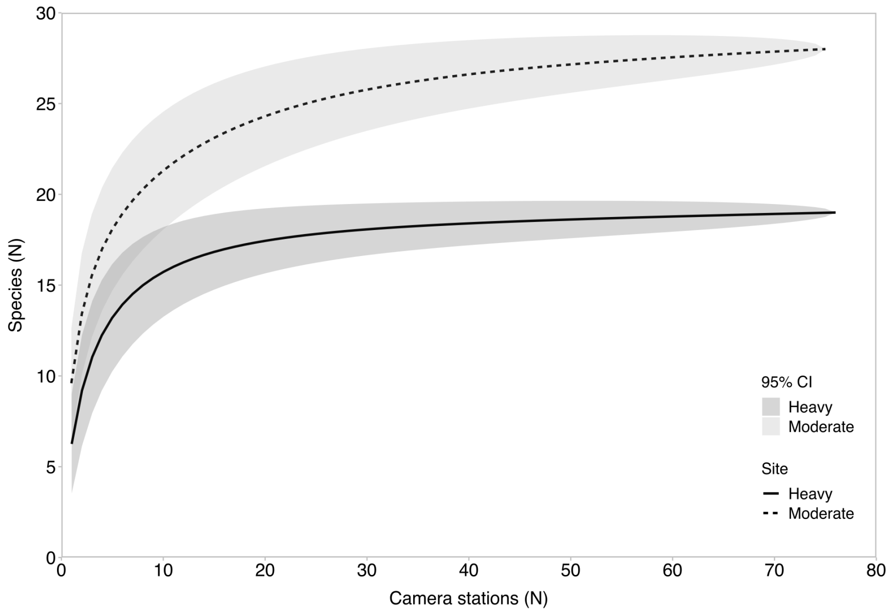

Figure A.1. Species rarefaction curves across the two study sites: heavily (Site 1) and moderately (Site 2) transformed (*see* Figure 2.1) in the Mpumalanga region of South Africa.

APPENDIX B.

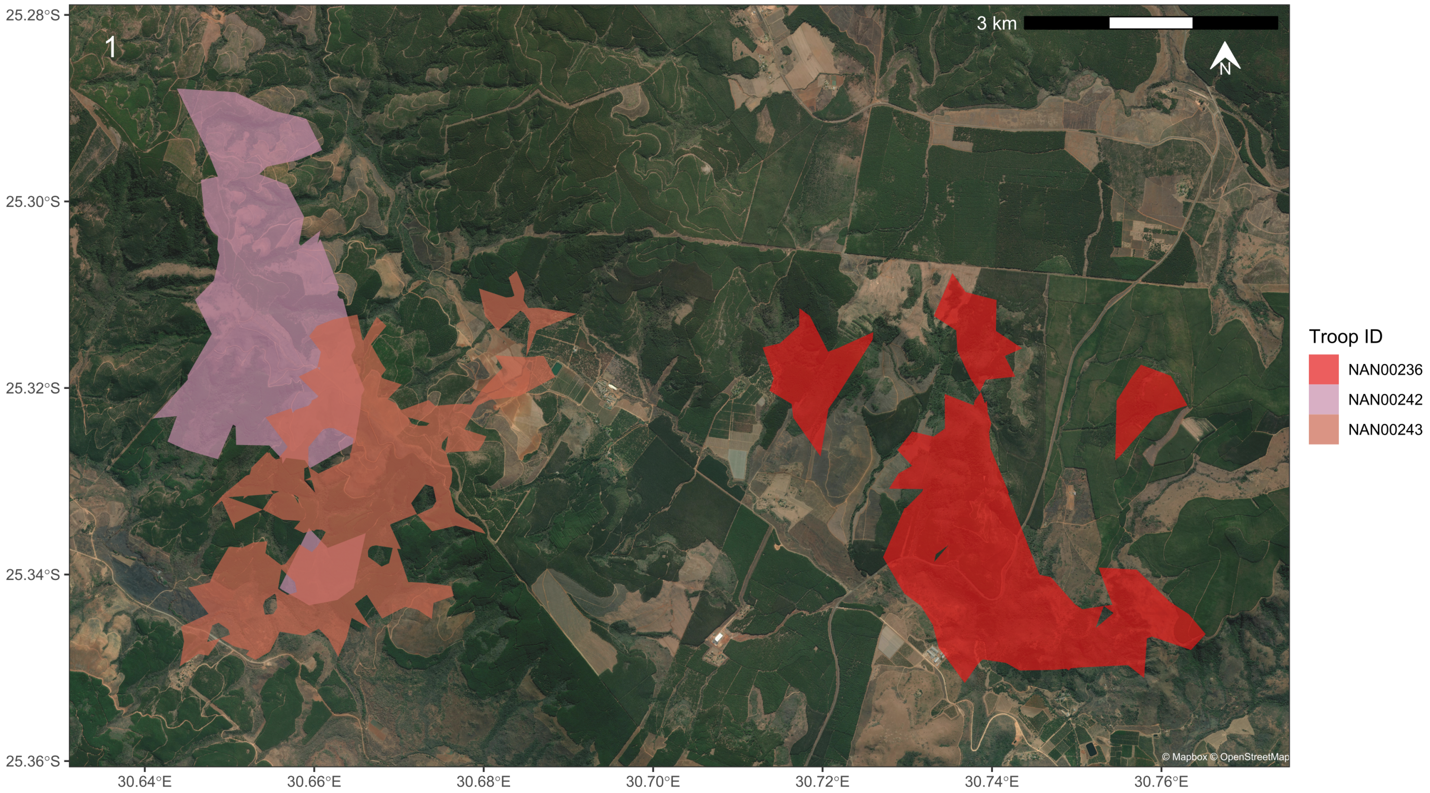

Figure B.1. Home ranges (95% T-LoCoH utilisation distribution) for chacma baboon troops (n = 3) located within region 1 (*see* Figure 3.1). Each troop is represented by a different colour.

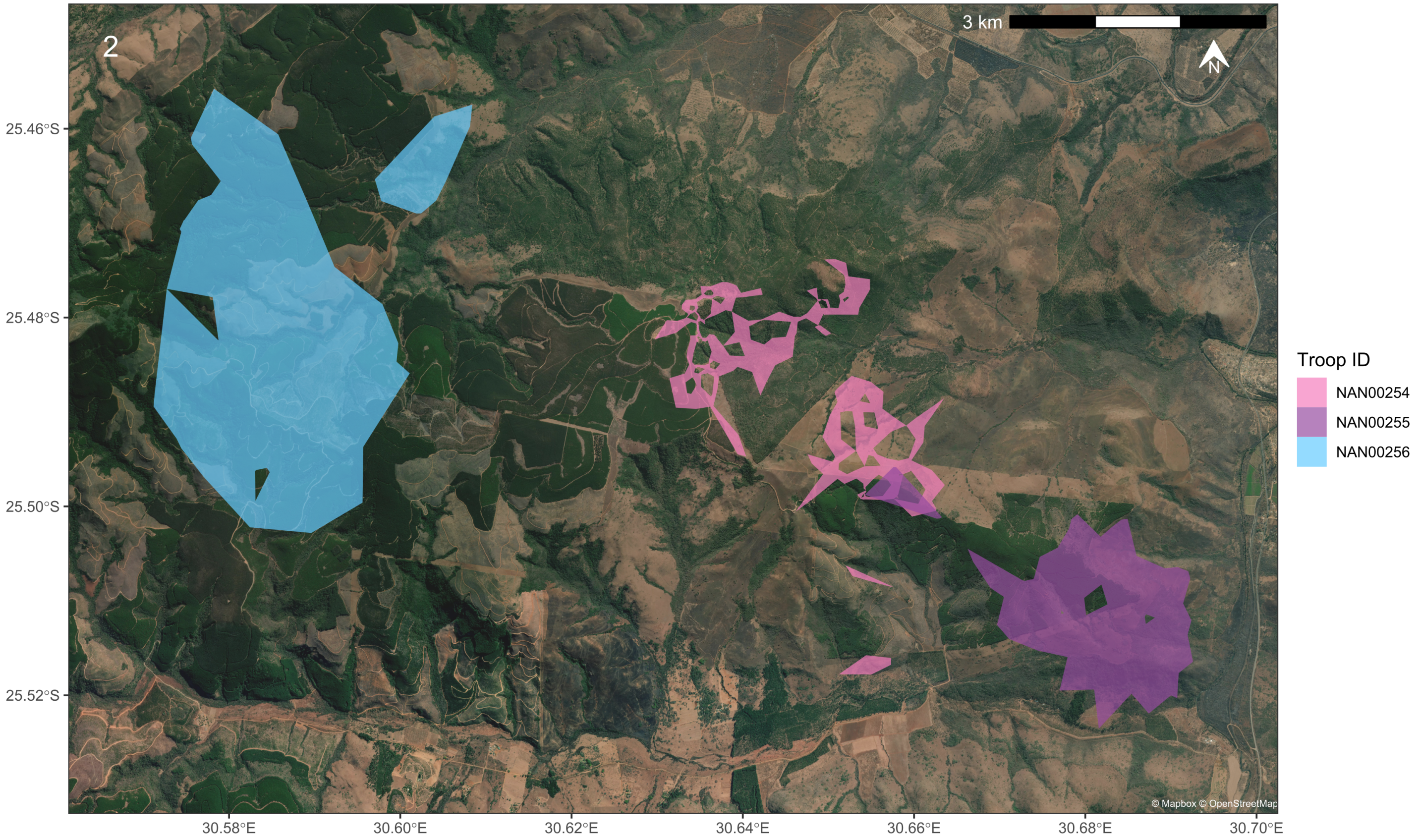

Figure B.2. Home ranges (95% T-LoCoH utilisation distribution) for chacma baboon troops (n = 3) located within region 2 (*see* Figure 3.1). Each troop is represented by a different colour.

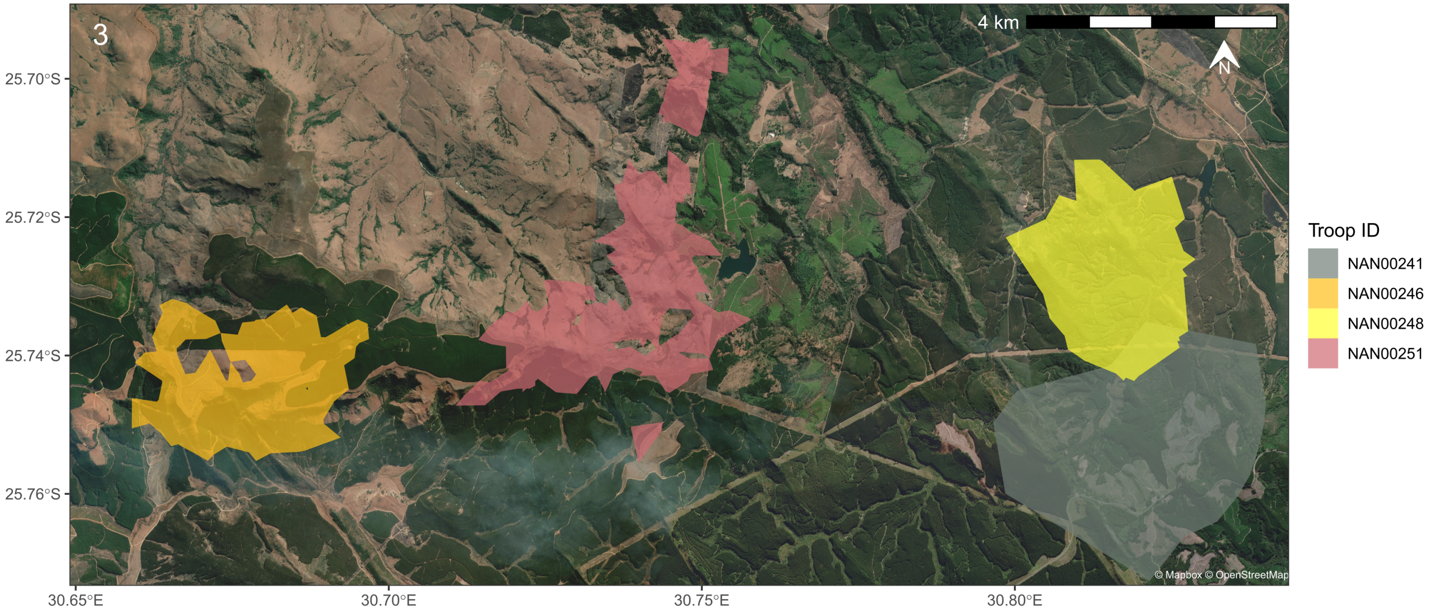

Figure B.3. Home ranges (95% T-LoCoH utilisation distribution) for chacma baboon troops (n = 4) located within region 3 (*see* Figure 3.1). Each troop is represented by a different colour.

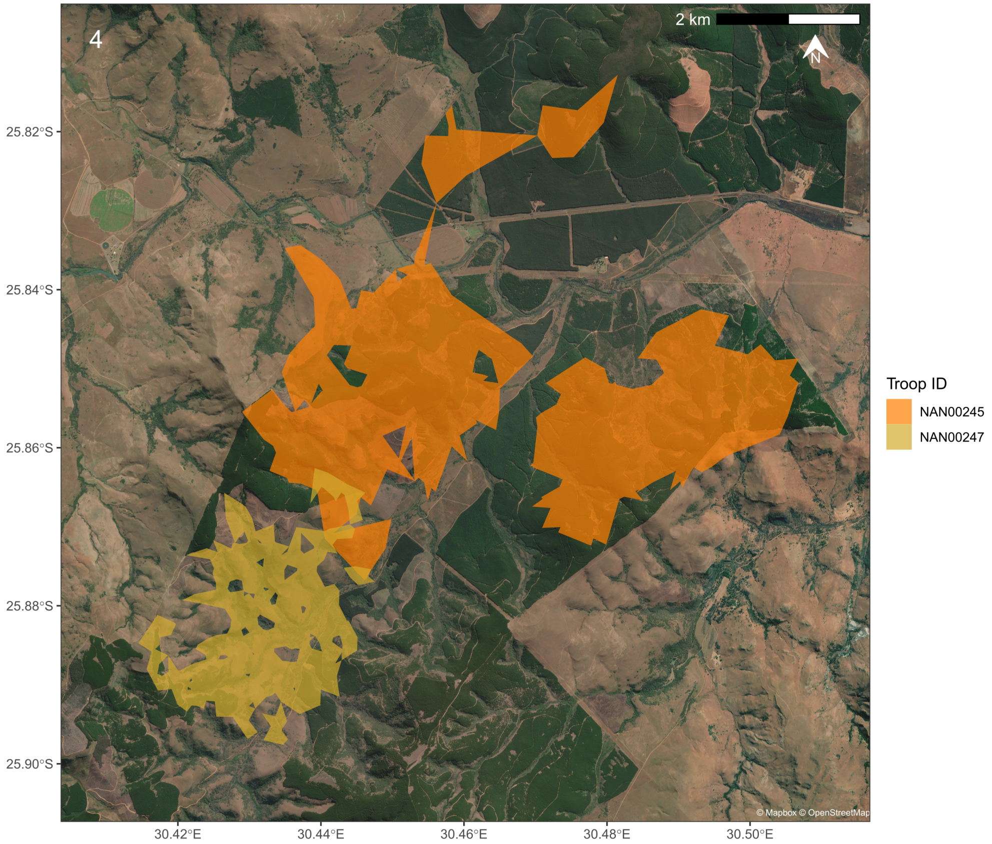

Figure B.4. Home ranges (95% T-LoCoH utilisation distribution) for chacma baboon troops (n = 2) located within region 4 (*see* Figure 3.1). Each troop is represented by a different colour.

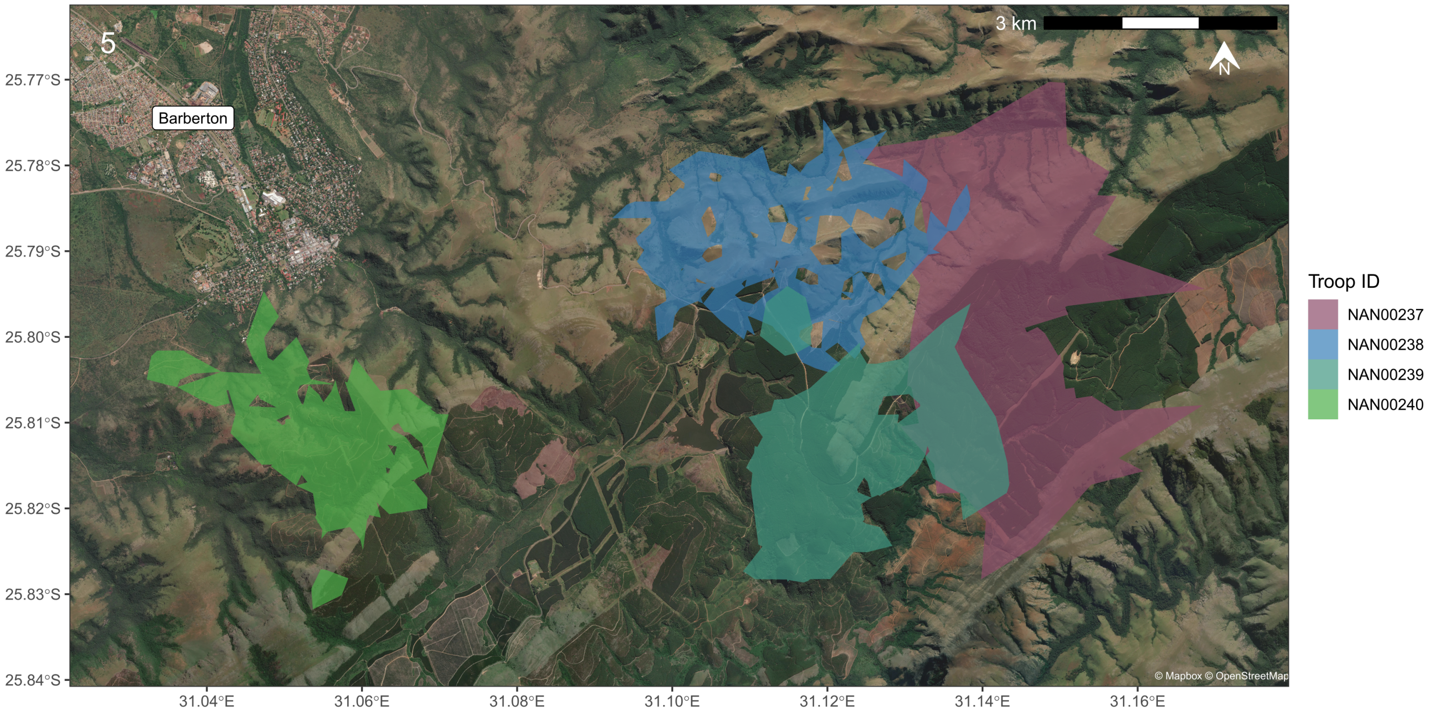

Figure B.5. Home ranges (95% T-LoCoH utilisation distribution) for chacma baboon troops (n = 4) located within region 5 (*see* Figure 3.1). Each troop is represented by a different colour.

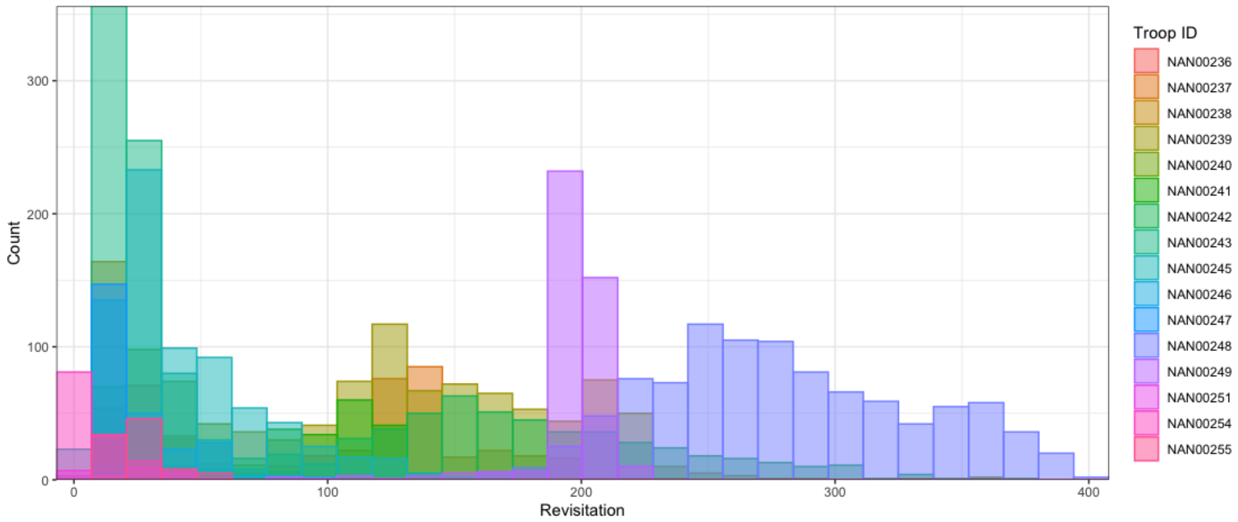

Figure B.6. Frequency distribution of the number of separate visits (NSV), or revisitation rate, with a intervisit gap period of 12 hours for each troop over the entire study period (*see* Table 3.1).

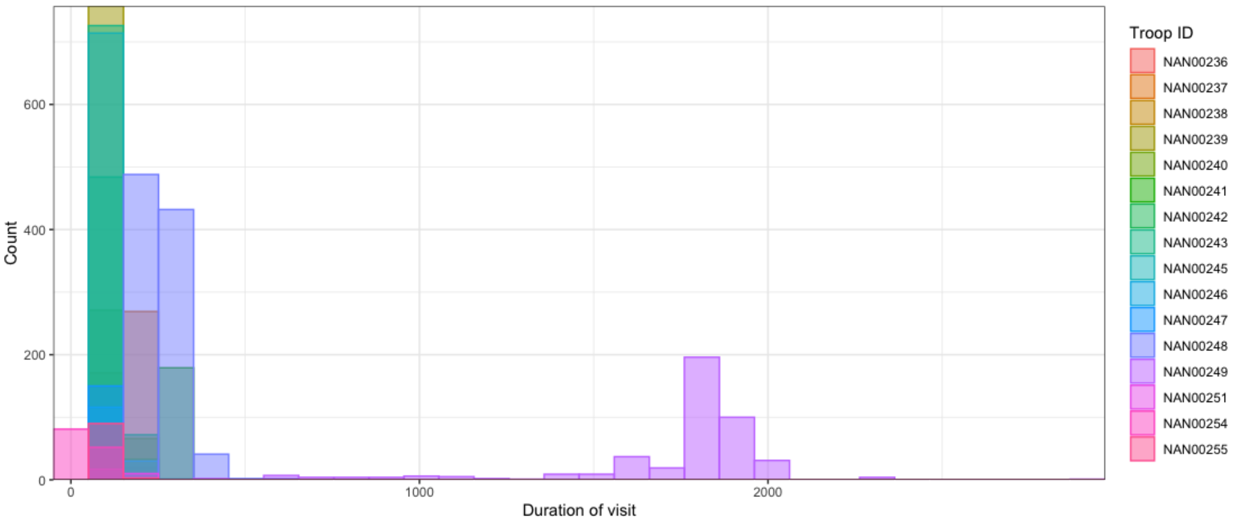

Figure B.7. Frequency distribution of the mean number locations per visit (MNLV), or duration of visit, with a intervisit gap period of 12 hours for each troop over the entire study period (*see* Table 3.1).

Table B.1. Breakdown of Plantation and Compartment overlap with individual baboon troop (Troop ID) home range (HR) areas. HR Areas were calculated using T-LoCoH at the 95% level

Troop ID	**Compartment**				**Plantation**	
	Tree Species	**Area in HR (km^2)**	**Percentage of HR Area (%)**	**Total Percentage in HR Area (%)**	**Area in HR Area (km^2)**	**Percentage of HR Area (%)**
NAN00236	*E. dun*	0.86	11.27	21.51	5.00	65.74
	E. gra	0.07	0.89			
	P. ech	0.50	6.63			
	P. ell	0.12	1.60			
	P. pat	0.09	1.13			
NAN00237	*E. gxn*	0.06	0.47	33.35	8.07	62.64
	P. pat	0.73	5.66			
	P. ptl	0.16	1.25			
	P. tae	3.35	25.98			
NAN00238	*E. gxn*	0.08	0.98	12.16	1.46	18.85
	P. pat	0.38	4.87			
	P. ptl	0.06	0.83			
	P. tae	0.42	5.48			
NAN00239	*E. gxn*	0.07	0.97	67.81	6.80	95.50
	P. ech	0.62	8.64			
	P. mix	0.02	0.22			
	P. pat	1.23	17.25			
	P. ptl	0.67	9.39			
	P. tae	2.23	31.34			
NAN00240	*P. ech*	1.00	20.38	36.03	4.58	93.59
	P. ell	0.44	9.00			
	P. pat	0.32	6.50			
	P. ptl	0.01	0.15			
NAN00241	*E. dun*	2.18	18.48	47.43	8.44	71.71
	E. gra	0.54	4.63			
	E. gxn	0.88	7.52			
	P. ech	1.45	12.28			
	P. pat	0.04	0.37			
	P. ptl	0.49	4.15			

continued . . .

Table B.1. Breakdown of Plantation and Compartment overlap with individual baboon troop (Troop ID) home range (HR) areas. HR Areas were calculated using T-LoCoH at the 95% level – *(continued).*

Troop ID	**Compartment**				**Plantation**	
	Tree Species	**Area in HR (km^2)**	**Percentage of HR Area (%)**	**Total Percentage in HR Area (%)**	**Area in HR Area (km^2)**	**Percentage of HR Area (%)**
NAN00242	*P. ech*	0.46	6.46	26.74	3.17	44.69
	P. poh	0.53	7.46			
	P. ptl	0.91	12.81			
NAN00243	*P. ech*	1.68	21.62	42.47	5.02	64.54
	P. ell	0.00	0.06			
	P. pat	0.40	5.10			
	P. poh	0.42	5.43			
	P. ptl	0.80	10.26			
NAN00245	*E. ben*	0.06	0.37	60.07	15.62	92.48
	E. dun	0.44	2.58			
	E. gxn	0.04	0.26			
	P. ech	0.93	5.52			
	P. ell	0.65	3.86			
	P. gre	2.24	13.23			
	P. kes	0.23	1.39			
	P. pat	4.40	26.05			
	P. ptl	1.15	6.81			
NAN00246	*E. dun*	0.36	5.35	58.20	6.08	91.41
	E. gxn	0.87	13.09			
	E. mac	0.12	1.78			
	P. ech	0.41	6.14			
	P. ell	0.27	4.07			
	P. pat	1.80	27.08			
	P. ptl	0.05	0.69			
NAN00247	*E. ben*	0.17	3.07	17.84	5.21	93.55
	E. dun	0.00	0.07			
	P. ech	0.12	2.19			
	P. pat	0.15	2.78			
	P. ptl	0.54	9.73			

continued . . .

Table B.1. Breakdown of Plantation and Compartment overlap with individual baboon troop (Troop ID) home range (HR) areas. HR Areas were calculated using T-LoCoH at the 95% level – *(continued).*

Troop ID	**Compartment**				**Plantation**	
	Tree Species	**Area in HR (km^2)**	**Percentage of HR Area (%)**	**Total Percentage in HR Area (%)**	**Area in HR Area (km^2)**	**Percentage of HR Area (%)**
NAN00248	*E. clo*	0.03	0.40	65.17	6.55	97.93
	E. dun	3.13	46.86			
	E. gra	0.24	3.64			
	E. gxn	0.02	0.37			
	E. gxu	0.21	3.17			
	P. ech	0.38	5.65			
	P. ell	0.34	5.08			
NAN00249	*A. rbo*	0.01	0.08	48.05	5.45	86.01
	E. gxn	0.27	4.24			
	P. ech	0.33	5.16			
	P. ell	0.17	2.71			
	P. pat	0.69	10.81			
	P. ptl	0.51	8.06			
	P. tae	1.08	16.99			
NAN00251	*E. gxn*	0.06	0.65	8.21	2.19	24.99
	P. pat	0.66	7.56			
NAN00254	*E. dun*	0.01	0.24	10.54	1.43	45.99
	E. gxn	0.01	0.28			
	P. ech	0.00	0.12			
	P. gre	0.12	3.74			
	P. pat	0.17	5.57			
	P. ptl	0.02	0.59			
NAN00255	*E. dun*	0.10	2.68	22.45	2.45	66.06
	E. gra	0.01	0.32			
	P. ech	0.27	7.27			
	P. gre	0.27	7.35			
	P. mix	0.18	4.84			
NAN00256	*E. dun*	0.04	0.41	67.95	9.42	92.65
	E. gxn	0.62	6.14			
	P. ell	0.60	5.94			
	P. pat	2.24	22.04			
	P. ptl	3.40	33.42			

Table B.2. Optimisation of the number of variables to be randomly selected at each node split (*mtry*), node size and the number of decision trees (*ntree*) using a grid search procedure for use in the Revisitation (NSV) mixed-effects random forest model (MixRF). The Out-of-Bag (OOB) root-mean-square deviation (RMSE) estimate was used to determine the error rate for the different combinations of parameters, where lower OOB RMSE values represent a better fit. Only the top 10 parameter combinations are shown.

mtry	Node size	ntree	OBB RMSE
14	2	1700	32.409
14	2	1300	32.410
14	2	1400	32.413
12	1	1400	32.415
14	2	1900	32.415
14	2	1800	32.419
14	2	1500	32.420
12	1	1600	32.420
14	2	1600	32.420
12	1	1300	32.421

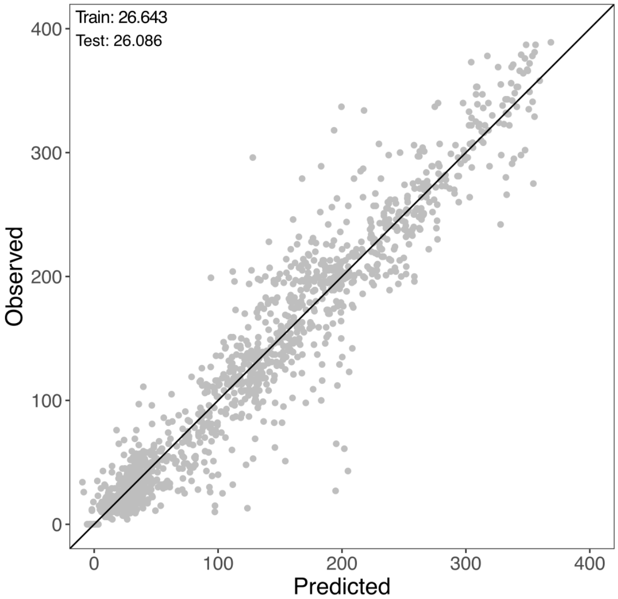

Figure B.8. Predicted (fit on 20% testing dataset) and observed (fit on 80% training dataset) values of the dependent variable (Revisitation: NSV) for our mixed-effects random forest model (MixRF). Root-mean-square deviation (RMSE) estimates between the training and testing data sets were similar: 26.643 and 26.086 respectively. The black line indicates the 1:1 line.

APPENDIX C.

Table C.1. Behavioural ethogram used for the classification of general baboon behaviours.

Category	Behaviour	Additional category	Definition
SOCIAL	Aggression (give)	+ Partner (sex, approximate age, rank)	Individual bites, grabs, scruffs, lunges, eye flashes, jaw chomps or slaps ground at conspecific
	Aggression (receive)	+ Partner	Individual receives bite(s), grab(s), scruff(s), lunges, eye flashes, jaw chomps or ground slaps from conspecific
	Groom (give)	+ Partner or Self	Individual manipulates or picks through hair or skin of a conspecific with hands or mouth
	Groom (receive)	+ Partner	Individual's hair or skin is manipulated or picked through by the hands or mouth of a conspecific
	Play		Individual engages in wrestling, non-aggressive chasing, non-aggressive biting, manipulation of non-food item, etc., alone or with conspecific(s)
	Other social		Any social behaviour that is not described above
FEED	Drink	River/Road/Human Source	Individual consumes water from any of these sources
	Feeding	Pine product (bark, needles, cones)/Natural (grass, fruit, bulbs)/Human food/Other/Unknown	Individual consumes food item from any of these sources. Standing or sitting still
	Foraging	Pine product/Natural/Human food/Other/Unknown	Individual is actively searching for food items amongst one of these sources. Moving.
REST	Rest		Individual is sitting motionless with eyes open or closed.
MOVE	Walking		
	Running		
	Climbing		
OTHER	Vigilance	Baboon/Human/Food source/Unknown/Other	Individual is actively maintaining visual contact with any of these sources.
	Other behaviour		Individual is engaged in any behaviour not listed above.
	Out of sight		Individual is out of line of sight of the observer.

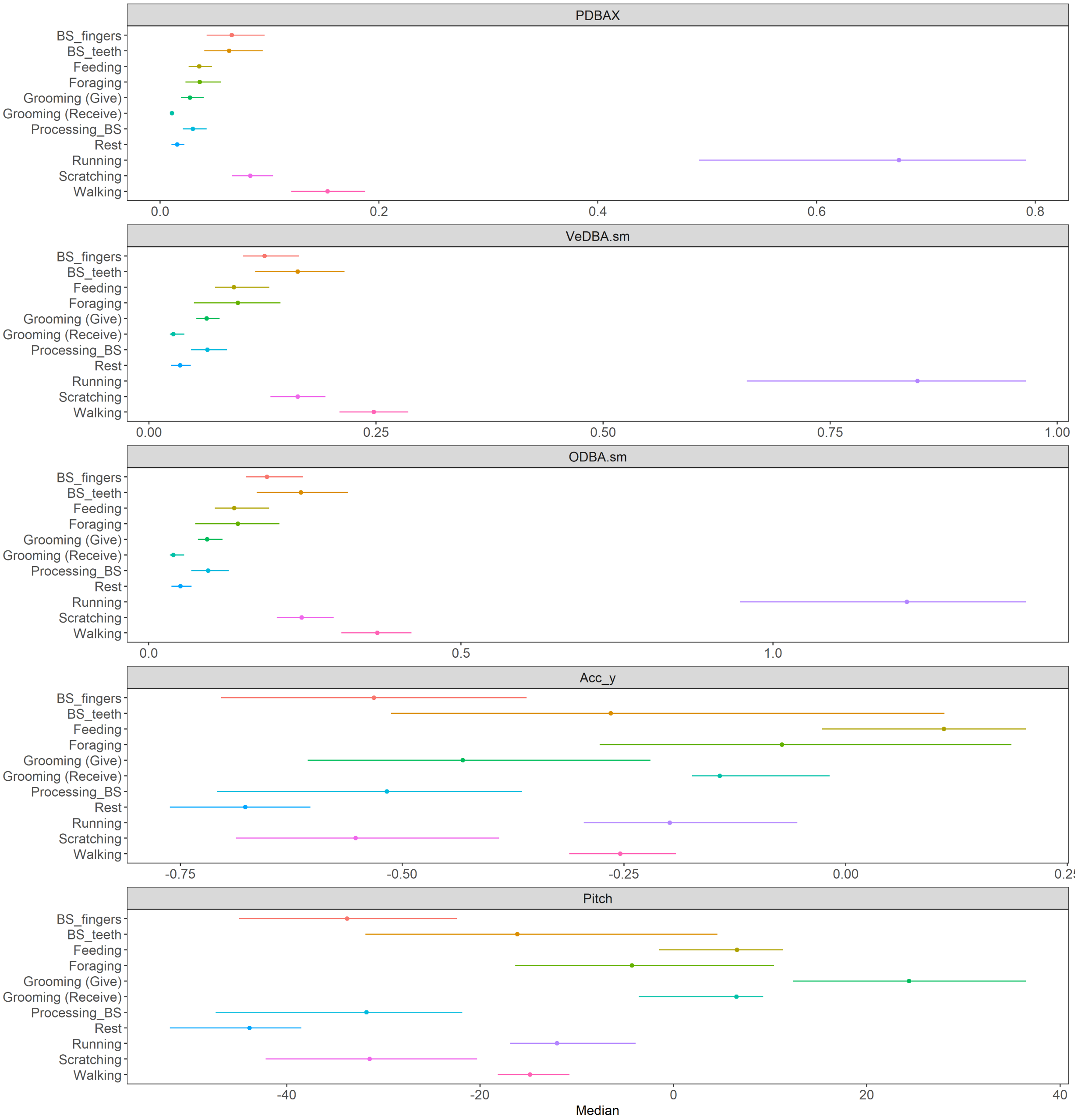

Figure C.1. Interquartile ranges (25% and 75%) for the 5 most important variables from the Random Forest model, with the median value represented as a point.

Table C.2. Percentage of time (mean ± SD) each individual was engaged in the identified behaviours based on acceleration data restricted for daylight hours. Individuals are coded by Age-Sex, including adult males (AdM), adult females (AdF), and sub-adult males (SubAdM), followed by their collar numbers.

	AdM2	**AdM6**	**AdF7**	**AdF8**	**AdF10**	**AdF11**	**SubAdM12**	**SubAdM13**	**SubAdM14**	**AdF15**	**AdF17**	**Mean**
BS_fingers	0.136 ± 0.060	0.054 ± 0.064	0.339 ± 0.260	0.015 ± 0.009	NA	0.057 ± 0.113	0.069 ± 0.035	0.154 ± 0.202	1.093 ± 0.419	0.007 ± 0.006	0.009 ± 0.013	**0.356 ± 0.495**
BS_teeth	0.731 ± 0.509	6.660 ± 2.511	1.906 ± 0.586	1.199 ± 0.398	0.083 ± 0.035	4.311 ± 1.436	2.462 ± 0.654	5.527 ± 0.982	4.898 ± 1.671	3.545 ± 0.965	0.625 ± 0.272	**2.961 ± 2.218**
Feeding	1.018 ± 1.050	25.211 ± 5.487	2.818 ± 1.039	1.748 ± 0.690	0.036 ± 0.142	0.071 ± 0.112	2.015 ± 1.038	1.053 ± 0.961	1.110 ± 0.771	0.142 ± 0.121	5.809 ± 2.755	**3.318 ± 6.188**
Foraging	54.210 ± 5.070	38.945 ± 5.048	13.192 ± 2.213	27.230 ± 3.516	0.189 ± 0.084	1.415 ± 0.475	25.101 ± 4.876	28.970 ± 3.199	24.788 ± 6.930	11.955 ± 2.250	60.735 ± 6.697	**22.788 ± 15.467**
Grooming (Give)	2.797 ± 2.075	1.394 ± 0.773	0.030 ± 0.044	0.585 ± 0.358	40.202 ± 6.441	0.003 ± 0.002	0.018 ± 0.022	0.061 ± 0.108	12.180 ± 18.362	NA	1.030 ± 0.539	**9.531 ± 16.828**
Grooming (Receive)	0.598 ± 0.631	8.928 ± 2.659	9.073 ± 4.037	11.044 ± 5.424	2.787 ± 1.661	3.471 ± 2.366	6.533 ± 3.331	5.505 ± 2.669	23.112 ± 24.174	3.048 ± 2.588	0.361 ± 0.515	**10.257 ± 14.627**
Processing_BS	1.981 ± 0.811	0.543 ± 0.783	13.369 ± 2.149	4.844 ± 2.036	0.006 ± 0.006	0.581 ± 0.377	3.434 ± 0.952	10.266 ± 4.531	12.885 ± 13.184	3.400 ± 1.144	0.129 ± 0.278	**6.807 ± 8.320**
Rest	15.500 ± 3.201	4.259 ± 2.506	32.749 ± 6.171	18.502 ± 4.881	17.451 ± 4.254	52.120 ± 10.266	26.297 ± 5.046	23.683 ± 5.151	27.926 ± 20.335	44.246 ± 6.670	6.393 ± 3.743	**25.708 ± 15.562**
Running	1.013 ± 0.383	1.436 ± 0.832	0.568 ± 0.209	1.675 ± 0.666	1.255 ± 0.425	1.034 ± 0.393	2.797 ± 1.010	4.181 ± 1.226	1.810 ± 0.791	0.892 ± 0.324	0.691 ± 0.273	**1.656 ± 1.134**
Scratching	0.316 ± 0.092	0.003 ± 0.003	0.943 ± 0.320	0.669 ± 0.313	2.159 ± 0.744	0.466 ± 0.127	1.132 ± 0.249	0.803 ± 0.163	0.039 ± 0.021	0.359 ± 0.119	0.242 ± 0.108	**0.745 ± 0.693**
Walking	21.671 ± 2.403	11.105 ± 2.897	23.470 ± 3.828	32.200 ± 3.727	34.625 ± 6.690	34.297 ± 8.551	29.909 ± 5.342	19.814 ± 2.857	19.226 ± 6.024	30.926 ± 6.271	23.014 ± 3.875	**25.806 ± 8.530**

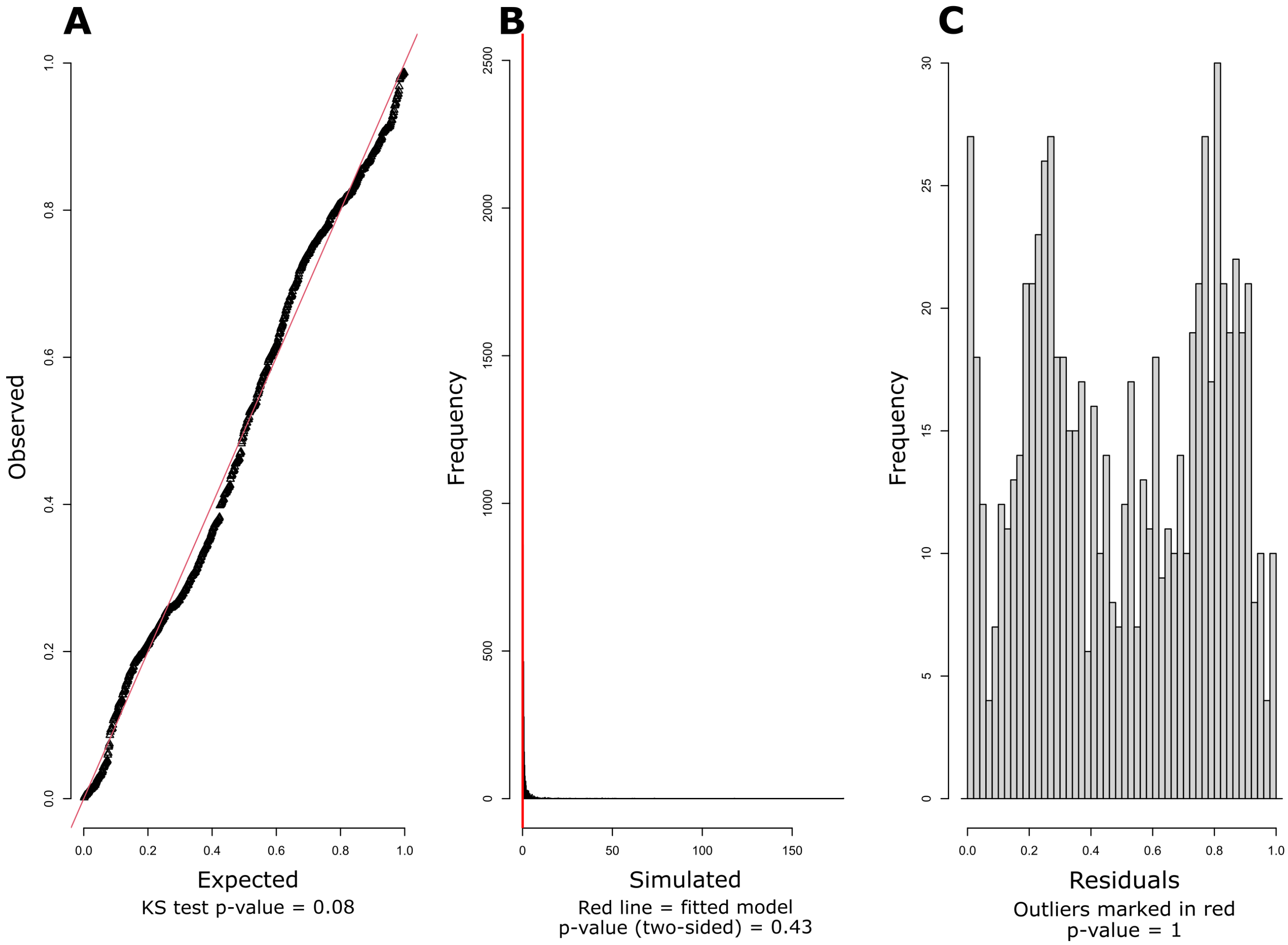

Figure C.2. Model fitting diagnostics for GLMM 1 of bout frequency vs. climatic variables (*see* Table 4.4). (**A**) Residual normal probability QQ-plot, (**B**) Non-parametric dispersion test via standard deviation of residuals fitted vs. simulated and (**C**) Residual outlier distribution.

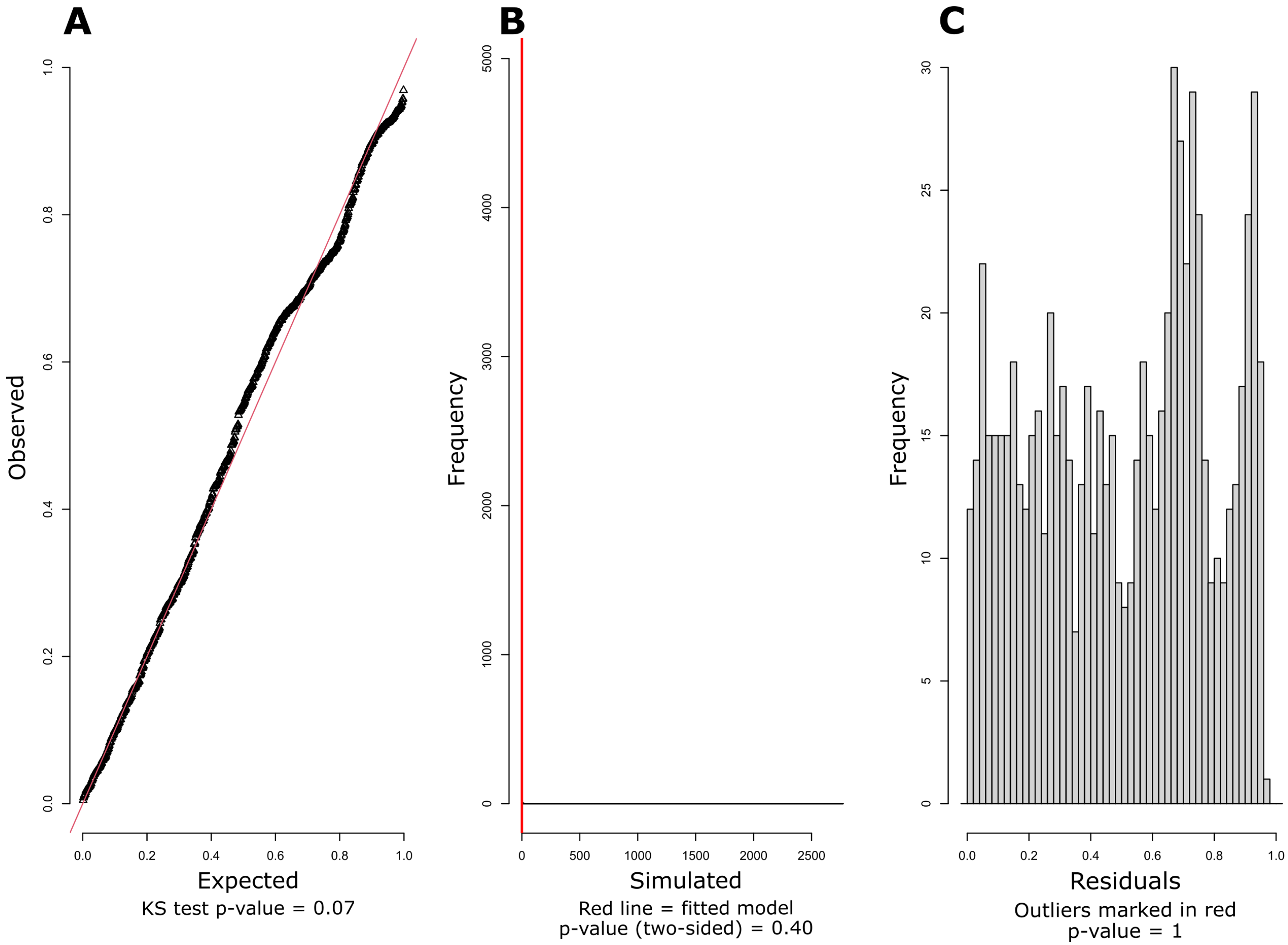

Figure C.3. Model fitting diagnostics for GLMM 2 of bout duration vs. climatic variables (*see* Table 4.4). (**A**) Residual normal probability QQ-plot, (**B**) Non-parametric dispersion test via standard deviation of residuals fitted vs. simulated and (**C**) Residual outlier distribution.

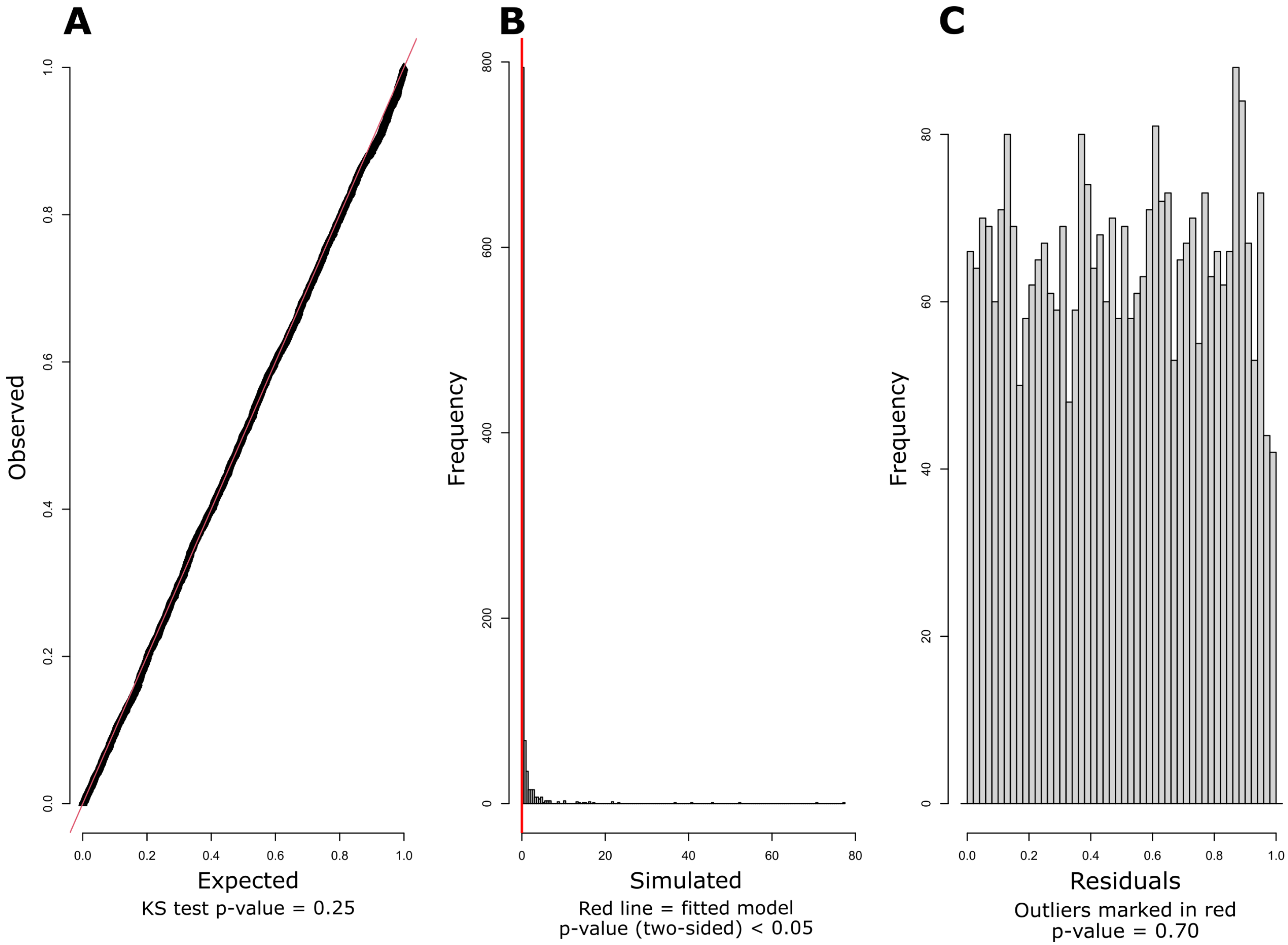

Figure C.4. Model fitting diagnostics for GLMM 3 of bout frequency vs. plantation variables (*see* Table 4.4). (**A**) Residual normal probability QQ-plot, (**B**) Non-parametric dispersion test via standard deviation of residuals fitted vs. simulated and (**C**) Residual outlier distribution.

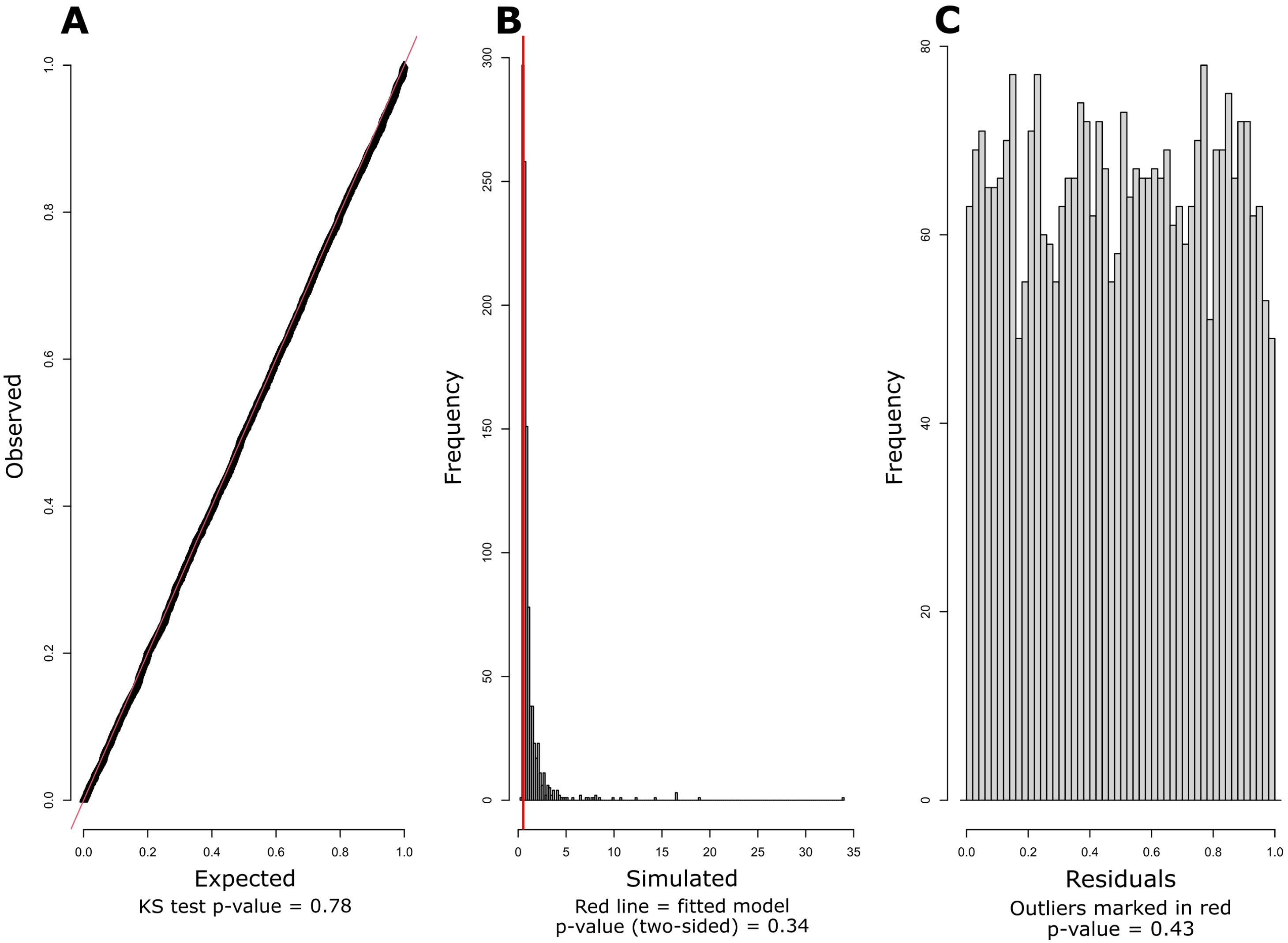

Figure C.5. Model fitting diagnostics for GLMM 4 of bout duration vs. plantation variables (*see* Table 4.4). (**A**) Residual normal probability QQ-plot, (**B**) Non-parametric dispersion test via standard deviation of residuals fitted vs. simulated and (**C**) Residual outlier distribution.