Ranging patterns and resource use in samango monkeys

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Abstract

Loss and fragmentation of habitat can have significant negative consequences for forest-dwelling species. Understanding how a species uses space in an increasingly fragmented and human-dominated landscape is important to determine the extent to which they can persist in such landscapes. How animals use space is largely determined by the availability of resources and the risk of predation both across time and space and is highly scale-dependent. The aim of this study was to investigate the factors that influence space use at the species level using resource selection functions, at the group level by exploring ranging patterns, and at the individual level by exploring the role of predation risk on the spatial variation in behaviour.

Focal observations were collected from two well-habituated groups of samango monkey (*Cercopithecus albogularis schwarzi*) at the Primate and Predator Project (PPP), as part of the Lajuma Research Centre, South Africa. In addition, instantaneous scan observations from PPP's historic dataset were used to explore the ranging patterns and resource use of samango monkeys.

Space use at both the species and group levels was largely determined by access to highly productive habitat, particularly tall-canopy, indigenous mistbelt forest. At the individual level, perceived predation risk strongly influenced the spatial variation in behaviour, whilst other measures of risk such as habitat visibility, canopy height and distance from sleep site were also important. Distance from sleep site was also associated with an increase in anxiety,

indicated by self-directed scratching, in samangos. However, samangos appeared to manage risk across their home range by varying the number of nearby neighbours, thereby sharing the vigilance load between individuals.

The findings of this study highlight that space use is highly scale-dependent, and that the spatial and temporal distribution of resources and predation risk largely determines how animals use space at these different scales. Prioritising resources at different scales is therefore central to the development of efficient management plans to ensure the persistence of species in increasingly fragmented and human-dominated landscapes.

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Chapter 1

Introduction

1.1 Space use

Habitat loss and fragmentation are the most significant causes of global biodiversity loss (Fahrig, 2003; Lindenmayer and Fischer, 2006). Due to the anthropogenic conversion of land for agriculture and urbanisation, loss and fragmentation of forest habitat has accelerated at an unprecedented rate (Haddad et al., 2015). Forest-dwelling species rely on continuous patches of natural forest for foraging, reproduction and shelter. Fragmentation of these patches can lead to local population extinction through microclimate change (Haddad et al., 2015), genetic isolation (Fahrig and Merriam, 1985; Lawes et al., 2000; Pardini et al., 2009; Goossens et al., 2016), decreased availability of resources (Saunders et al., 1991; Ims et al., 1993; Mcloughlin et al., 2000; Emerson and Brown, 2013), increased predation risk (Irwin et al., 2009) and increased competition (Gabriel, 2013). As a result of this ongoing and rapid fragmentation, studies on space use are becoming increasingly important in order to determine the extent to which a species can persist in an increasingly fragmented and human-dominated landscape (Fahrig, 2007; Wilson et al., 2016).

The process of fragmentation leads to small, isolated patches of low-quality habitat (Hall et al., 1997), which differ in the availability and predictability of resources in time and space (Mcloughlin et al., 2000; Emerson and Brown, 2013). The ability of a population to survive in fragmented habitats therefore largely depends on the ability of individuals to access essential resources both within patches and within the surrounding matrix habitat (Ims et al., 1993). Understanding the resources that govern a species' distribution and use of space across a landscape is central to identifying key habitat and connectivity between populations, which in turn is essential for planning effective conservation and preventing biodiversity loss (Kopp et al., 1998; Mayor et al., 2009). The topic of resource selection is explored in Chapter 3. Within populations, understanding the factors which influence space use at the group level is fundamental to assessing the ability of a species to acquire essential resources in order to persist in fragmented habitats (Ims et al., 1993). Variation in ranging patterns is the focus of Chapter 4. Finally, understanding how individuals balance resource acquisition whilst minimising predation risk can provide important information on how individuals use space within their home range, which is important for the allocation of resources for wildlife management and conservation (Zeller et al., 2012). Spatial variation in behaviour is explored in Chapter 5, whilst Chapter 6 takes this further and explores the relationship between perceived predation risk and anxiety-related behaviours.

1.2 Resource selection

The relative importance of a resource to a species varies with the scale of interest (Boyce, 2006), and so identifying important habitat to a species is thus highly scale-dependent (Mayor et al., 2009). This scale-dependent selection ranges from coarse to fine scale, and has been described as the four orders of resource selection by Johnson (1980): first-order, selection at the geographic range by a species; second-order, selection within geographic range (e.g. home or subpopulation range); third-order selection, selection within home range; and fourth-order, selection of a specific resource (e.g. food source, sleep site).

Resource Selection Functions (RSFs; Manly et al., 2002) are increasingly being used as a tool to identify important resources required by a species at multiple scales (Boyce, 2006; DeCesare et al., 2012). RSFs are statistical models used to estimate the relative probability of use of a particular resource unit by an individual or group (Manly et al., 2002) and can be used to identify important habitat and connectivity across the landscape. These models compare the amount of used habitat or resources with the amount of available habitat or resources (Manly et al., 2002). For example, if a habitat type such as riverine habitat is used by an individual or group more than expected relative to the amount of this habitat available across the landscape, then this habitat type is assumed to be selected. In contrast, if this habitat type is used less than expected given the available habitat across the landscape it is assumed to be avoided (Koper and Manseau, 2012). Whilst alternative species distribution models also exist, such as ecological niche models/maximum entropy (MaxEnt) models (Phillips et al., 2006), they are essentially mathematically identical (Lele et al., 2013). One notable yet subtle difference, however, lies in the specification of the animal location points. MaxEnt models specify that locations have been used at least once over the study period, whereas RSF models account for locations being used multiple times across the study period (Lele et al., 2013).

RSFs are usually developed using satellite or telemetry datasets, with fixes from animal locations indicating “used” locations. Using a geographic information system (GIS), these “used” points are then compared to randomly generated “available” points by deriving the attributes for the landscape or resource variables of interest for each point (Koper and Manseau, 2012). Availability is typically quantified within the individual’s or group’s home range, or within an ecologically relevant buffer distance of the used locations. The number of available points varies with each study, but are usually generated at a 1:1 ratio of used to available points in large datasets (Koper and Manseau, 2012; Northrup et al., 2013).

Due to the accessibility of radio telemetry and remotely sensed environmental data, the majority of RSF studies have focussed on wide-ranging species, particularly ungulates (Johnson et al., 2004; Koper and Manseau, 2009; DeCesare et al., 2012) and large carnivores (Simcharoen et al., 2008; Davidson et al., 2012; Dellinger et al., 2013; Fattebert et al., 2015; Pitman et al., 2017). However, the value of using RSFs to explore resource selection in small-ranging and patchily distributed species living in fragmented habitats remains largely underutilised, yet the potential conservation benefits in terms of identifying critical habitat both within and between fragments are vast (Harris et al., 2008). Despite the imperilled conservation status of many of the world’s primates (Estrada et al., 2017), and the resolution of data gained through habituation and follows, RSF studies on primates are almost entirely lacking (Sawyer and Brashares, 2013). Whilst RSFs can identify important resources and habitat features for a species at different spatial scales, exploring how an individual or group responds to the spatial and temporal distribution of these resources is central to an understanding of the susceptibility of a species to fragmentation.

1.3 Ranging patterns

Understanding the variation in how an individual or group uses space is fundamental to the effective conservation and management of a species (Burt, 1943; Woodroffe and Ginsberg, 2000; Börger et al., 2008). Identifying the causes of this variation is important for the allocation of appropriate resources (Woodroffe and Ginsberg, 2000), producing population estimates (Gros et al., 1996), and determining how much space is needed when estimating carrying capacities for recovery areas (Herfindal et al., 2005). In addition, understanding how a species responds to habitat boundaries and matrix quality is essential for determining the extent to which they can persist in an increasingly fragmented and human-dominated landscape (Fahrig, 2007; Wilson et al., 2016).

Movement in fragmented habitats may be restricted by the availability of suitable habitat and surrounding matrix habitat (Eycott et al., 2012). The ability of individuals to exploit this matrix habitat largely determines their susceptibility to fragmentation and their ability to persist in such landscapes (Fahrig, 2007). How animals use space is typically explored using (i) the day journey length (DJL), the cumulative distance travelled per day by a group or individual, and/or (ii) the home range, the cumulative area covered over a certain period of time by a group or individual (Burt, 1943). These characteristics are governed by a species' requirements in terms of survival and reproduction (Clutton-Brock and Harvey, 1977). Animals should optimise their ranging patterns in order to maximise energy intake (Ricklefs, 1990; Barrett, 2009) whilst minimising costs (e.g. travel, predation risk). This results in two frequently adopted strategies when ranging: reducing ranging distances when food is abundant (the energy-maximising strategy; Hall, 1962), or ranging further when food is abundant (the energy-minimising strategy; Wrangham, 1977; Raemaekers, 1980). The latter of these is typical where resources are patchily distributed across the home range, such as fruiting trees or watering holes, in accordance with the resource dispersion hypothesis (MacDonald, 1983; Johnson et al., 2002).

Due to recent technological and analytical advances, studies on ranging patterns have vastly improved (Hebblewhite and Haydon, 2010). Developments in tracking devices, such as radio telemetry and handheld global positioning systems (GPS) (Cagnacci et al., 2010; Tomkiewicz et al., 2010), and geographic information systems (GIS) software has resulted in more frequent, accurate, and efficient data collection for movement ecology studies (Kie et al., 2010). These advances, coupled with advances in home range estimation methods that explicitly account for autocorrelation between temporally dependent data points (Getz et al., 2007; Lyons et al., 2013), has allowed for unprecedented accuracy when exploring the spatiotemporal dynamics in home range variation.

In addition to advances in animal tracking, monitoring changes in habitat productivity has also become a more accurate and efficient process with the application of remotely sensed data to ecological studies (Kerr and Ostrovsky, 2003; Turner et al., 2003; Pettorelli et al., 2011; Neumann et al., 2015). The NDVI (Normalised Difference Vegetation Index) and EVI (Enhanced Vegetation Index) in particular are frequently used for monitoring primary productivity over vast geographical scales at regular time intervals (Huete et al., 2006; Lu et al., 2015). However, due to these characteristics, the vast majority of studies using remote sensing in animal ecology have been biased towards wide-ranging species (birds: Evans et al., 2006, carnivores: Nilsen et al., 2005, ungulates: Ito et al., 2006; Kaczensky et al., 2014; Leimgruber et al., 2001), whilst finer scale studies on smaller-ranging species are lacking (McClintic et al., 2014; Chynoweth et al., 2015). Using remote sensing to monitor productivity leads to obvious comparisons with more commonly used techniques, such as field sampled estimates, with comparative studies currently spanning a range of taxa (birds: Gordo, 2007; ungulates: Villamuelas et al., 2016; primates: Willems et al., 2009). Furthermore, despite the imperilled conservation status of many of the world’s primates, studies using remotely sensed productivity to monitor ranging patterns, particularly in species which consume large amounts of leaves, are almost entirely lacking (Zinner et al., 2002; Willems et al., 2009).

Whilst the distribution of resources has an important influence on how animals use space, perhaps of more significance is the presence of predators due to the obvious costs of successful predation to an individual's fitness (Schoener, 1971; Mangel and Clark, 1986). Understanding how individuals gather sufficient resources in order to survive whilst minimising predation risk is a central theme in behavioural ecology (Lima and Dill, 1990), and is fundamental in the allocation of resources for wildlife management and conservation (Zeller et al., 2012).

1.4 Predation risk

The presence of predators can affect almost every aspect of prey behaviour (Lima, 1998; Caro, 2005). A common strategy adopted by many prey species is to disproportionately use areas of lower perceived risk from predation within their home range (Suhonen, 1993; Heithaus and Dill, 2002; Tolon et al., 2009; Valeix et al., 2009), a strategy also observed in primates. Vervet monkeys (*Chlorocebus pygerythrus*) in a multi-predator environment actively avoided areas of high perceived risk from leopards (*Panthera leo*) and baboons (*Papio ursinus*), despite these areas having potentially important resources (Willems and Hill, 2009). Similarly, samango monkeys (*Cercopithecus albogularis schwarzi*) at the same field site similarly avoided areas where perceived risk from crowned eagles (*Stephanoaetus coronatus*) was greatest (Coleman and Hill, 2014). However, areas where perceived risk from predation is high may also contain potentially important resources. Thus, prey species often face a trade-off between resource acquisition and predator avoidance (Lima and Dill, 1990). In a classic example in Yellowstone National Park, USA, bison (*Bison bison*) increased time spent foraging in food-poor forests after the reintroduction of wolves (*Canis lupus*), whilst avoiding the food-rich but 'riskier' open meadows (Hernández and Laundré, 2005). Off the coast of Western Australia, bottlenose dolphins (*Tursiops aduncus*) avoided foraging in the productive but 'risky' shallow habitats when tiger shark (*Galeocerdo cuvier*) density was high (Heithaus and Dill, 2002). Similarly, desert baboons (*Papio cynocephalus ursinus*) in Namibia avoided feeding in food-rich woodlands where risk of predation from leopards and lions (*Panthera leo*) was greater, instead preferring to feed in the food-poor but 'safer' open habitats (Cowlishaw, 1997a).

In some cases, however, the benefit of food acquisition (such as higher quality or temporally available food items) outweighs the potential costs of predation. Despite foraging in areas of higher risk from tiger shark predation, dugongs (*Dugong dugon*) minimised risk by foraging in the high quality interior seagrass beds when tiger shark abundance was lowest, despite the increased risk resulting from fewer escape options (Wirsing et al., 2007). Similarly, squirrel monkeys (*Saimiri sciureus*) spent more time feeding on artificial platforms in high-risk areas during the dry season when the availability of natural fruits was low (Stone, 2007).

As feeding is fundamental to survival (Schoener, 1971; Pyke, 1984), the foraging/risk trade-off is of primary concern to individuals concerning space use. However, the behavioural trade-off with risk has largely been unexplored in other behaviours. Cowlishaw (1997a) found that desert baboons not only avoided high-risk areas for feeding, but also avoided these areas for other activities such as resting and grooming. However, more studies are needed to validate the observed relationships, as such information can greatly increase our understanding of how animals use space. Further to this, whilst the indirect effects of predation on antipredator behaviour and foraging have received considerable attention in the literature, the physiological responses in terms of anxiety in wild animals remain largely unexplored.

1.5 Predator-induced anxiety

The fear of being eaten can affect all aspects of prey behaviour (Lima, 1998) and, as a result, prey species may experience anxiety in response to predators (Brown, 1999). Due to the fitness costs of mortality from successful predation, prey should maintain a baseline level of anxiety even in the absence of predators, as the possibility of predation is always present (Brown, 1999). However, this baseline may vary depending on the risk of predation in time and space, such as in risky versus safe habitats, or depending on time of day (Brown, 1992, 1999; Brown and Kotler, 2004).

Whilst faecal glucocorticoids are commonly used to explore anxiety and stress in old world monkeys (Rangel-Negrín et al., 2009; Foerster and Monfort, 2010; Crespi et al., 2013), recent evidence suggests elevated levels of glucocorticoids do not necessarily mean an individual is anxious or stressed (Beehner and Bergman, 2017). Therefore, displacement or self-directed behaviours (SDBs), such as self-grooming, scratching, body-shaking and yawning (Maestripieri et al., 1992), may be a more accurate measure of anxiety. In captive chimpanzees, self-scratching in particular was found to be the most reliable indicator of anxiety (Baker and Aureli, 1997). The relationship between self-scratching and anxiety has also been validated pharmacologically with the use anxiolytics (Schino et al., 1996). In contrast, whilst an increase in vigilance is often considered a response to anxiety (Barros et al., 2000; Coleman and Pierre, 2014), studies exploring this relationship with anxiolytics appear less conclusive (Schino et al., 1991, 1996; Barros and Tomaz, 2002; Barros et al., 2007). As such, SDBs such as self-scratching may be a more reliable indicator of anxiety.

Whilst the majority of work exploring predator-induced anxiety has been in captive primates, particularly marmosets (*Callithrix penicillate*) (Barros et al., 2000, 2004; Barros and Tomaz, 2002), studies on wild primates are lacking (Mineka et al., 1980; Nelson et al., 2003). Furthermore, studies exploring the indirect effects of predation are almost entirely absent. In a novel approach, Tkaczynski et al. (2014) found that olive baboons (*Papio anubis*) at the periphery of their group experienced more anxiety (indicated by increased rates of scratching), potentially as a result of the increased predation risk associated with being at the group's edge.

No studies have yet assessed how habitat structure, which can be an indirect measure of predation risk (Cowlishaw, 1998; Valeix et al., 2009), influences anxiety in wild primates. Habitat visibility can affect the ease of escape of prey species (Lima, 1992), whilst also affording predators camouflage and ambush opportunities (Hopcraft et al., 2005). In arboreal species, canopy height may also influence perceived predation risk as areas lower to the ground are viewed as 'riskier' habitats (Emerson et al., 2011). As a result, prey species may experience greater anxiety being in these 'riskier' habitats. Understanding this predator-induced anxiety can improve our understanding on the environmental factors that influence anxiety.

1.6 Samango monkeys

Samango monkeys belong to the larger polytypic group of arboreal guenons, *Cercopithecus nictitans*, which is often divided into two species; *C. albogularis* and *C. mitis* (Groves, 2005), usually referred to as Sykes', blue or white-throated monkeys. *C. albogularis* ranges from central and eastern to southern Africa (Dalton et al., 2015), whilst the samango monkey (*C. a. subspp.*) is largely endemic to South Africa where it is threatened. Only one of the subspecies exists outside of South Africa in neighbouring countries such as Zimbabwe, Mozambique and further north to Malawi. Across Africa, they occur in a range of tall-canopy evergreen indigenous forest types, such as Afromontane, riparian, swamp and coastal forests (Skinner and Chimimba, 2005).

The samango monkey subspecies living in the Soutpansberg Mountains, South Africa (*C. a. schwarzi*) is listed as endangered on the national Red-List (Linden et al., 2016), and inhabits a fragmented, highly seasonal and multipredator environment. As such, this population represents an ideal opportunity to study the ranging patterns and resource use at both the species and group level. In addition, variation in predation risk and substantial variation in habitat structure represent an ideal opportunity to explore the spatial variation in behaviour, and the behavioural responses to living in a multipredator environment.

1.7 Conservation

Samango monkeys are threatened across South Africa due to ongoing habitat loss of indigenous forest habitats and a decline in habitat quality as a result of commercial forestry plantations (Linden et al., 2016). Populations are undergoing further declines due to the loss of mature individuals from road collisions, electrocutions on power lines, and snaring and hunting for use in traditional medicine (Linden et al., 2016). However, the effects of hunting are assumed to be minimal as they are not a targeted species. Conservation management plans should be separated for each subspecies to prevent the loss of genetic diversity, with protected area expansion and proper management of indigenous forest habitats a key intervention strategy (Linden et al., 2016). Additionally, reclaiming and restoring areas of non-viable habitat or areas where indigenous forest previously existed is also important in order to increase connectivity between subpopulations, and to ensure the long term-persistence of this species.

1.8 Thesis structure

This thesis represents a series of observational studies investigating the ranging patterns and resource use in the samango monkey. Chapter 1 provides an overview of the problems faced by species in fragmented, seasonal and multipredator environments. In Chapter 2, I describe the study species and study site, before outlining the methodology used for the behavioural and environmental sampling undertaken throughout the thesis. Chapter 3 develops resource selection functions in samango monkeys and describes how these can be used to identify critical habitat across their range. Chapter 4 explores the effect of resource availability and habitat availability on samango ranging patterns. In Chapter 5, I explore the spatial variation in behaviour in response to perceived predation risk, habitat features associated with risk, and resource availability. Chapter 6 investigates the effect of perceived predation risk on anxiety-related behaviours. Finally, in Chapter 7 I summarise the results from the previous data chapters and present a general discussion on their importance for samango monkey behavioural ecology and conservation. This body of work is my own and builds upon other research on primate behavioural ecology which is referenced throughout the thesis.

1.8.1 Aims of thesis

i. To identify the habitat features and resources that influence samango monkey habitat selection at different spatial scales (Chapter 3).
    a. Where do samango monkeys establish their home range?
    b. Where do samango monkeys disproportionately use space within their home range?
    c. Where do samango monkeys disproportionately spend time feeding?
    d. What is the critical samango monkey habitat across their range in Limpopo Province, South Africa, and are populations isolated?
ii. To identify the habitat features and resources that influence samango monkey ranging patterns (Chapter 4).
    a. Does the availability of specific resources determine ranging patterns, or is this more broadly linked to productivity across the home range?
    b. Does the availability of suitable habitat influence ranging patterns, due to the arboreal nature of the samango monkey?
iii. To identify the habitat features and resources that influence the spatial variation in samango monkey behaviour across the home range (Chapter 5).
    a. Does perceived predation risk influence where certain behaviours occur?
    b. Does habitat visibility, canopy height and distance from sleep site, all indirect measure of predation risk, influence where certain behaviours occur?
    c. Does resource availability influence where certain behaviours occur?
iv. To determine the effect of perceived predation risk on anxiety-related behaviours (Chapter 6).

a. Do areas associated with increased predation risk increase anxiety-related behavious in samango monkeys?

Specific hypotheses and predictions can be found in the introduction of each chapter.

Chapter 2

General methods

Ethical statement

All behavioural data collection was covered by Liverpool John Moores University's (LJMU) use of Live Animals in Unregulated Research Protocol (NK_EP/2016-10), and followed the Association for the Study of Animal Behaviour (ASAB) Guidelines for the Treatment of Animals in Behavioural Research and Teaching (ASAB, 2012). All fieldwork was approved by LJMU's Life Sciences Ethical Review Process Committee and the Department of Anthropology Ethics Committee at Durham University, and was approved with permits by the Limpopo Province Department of Economic Development and Tourism (LEDET).

2.1 Study species

Samango monkeys (*Cercopithecus albogularis, subspp.*: *labiatus*, *erythrarchus*, and *schwarzi*, Dalton et al., 2015) are predominantly arboreal, medium-sized (males ~ 7.6 kg, females ~4.4 kg; Harvey et al., 1987), diurnal guenons, with an average life-span of around 27 years (Cords and Chowdhury, 2010). They exist in large single-male, multi-female groups (Henzi and Lawes, 1987) of around 40 individuals (Skinner and Chimimba, 2005). Females are philopatric, whereas males leave the group just before sexual maturity (6 – 8 years old) (Henzi and Lawes, 1987, 1988), where they either remain alone or join bachelor groups before taking over another group once sexual maturity is reached (Henzi and Lawes, 1987, 1988). The breeding season usually takes place between May and July (depending on subspecies), when groups may experience an influx of males (Henzi and Lawes, 1987, 1988). Females give birth to a single offspring after a gestation period of around 176 days (Pazol et al., 2002), with birthing periods depending on locality and subspecies (Linden et al., 2016). They are heavily reliant on areas of tall indigenous forest which they use for food, shelter and reproduction (Linden et al., 2016; Wimberger et al., 2017). Like many arboreal primates, samangos use the tallest trees in these forests as sleep sites due to the reduced risk of predation, particularly from terrestrial predators, associated with these trees (Smith et al., 2008; Albert et al., 2011). Sleeping sites are used regularly, with some groups consistently returning to the same area (Figure 2.1).

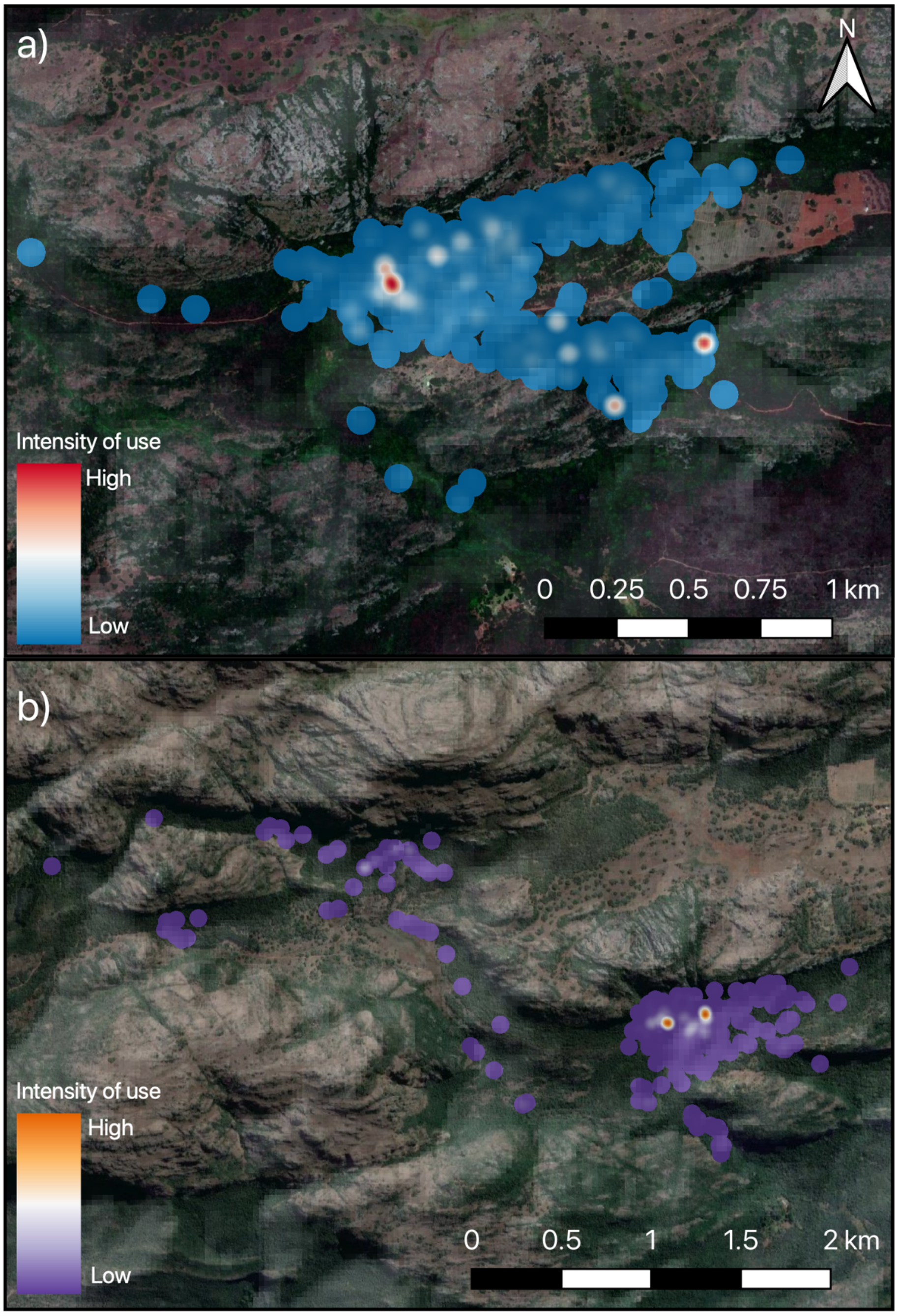

Figure 2.1. Sleep site locations and intensity of use for 'Barn' (a) and 'House' (b) groups at Lajuma Research Centre, South Africa.

2.1.1 Diet

Samango monkeys are predominantly frugivorous, with 52 - 91% of their diet comprising fruits (Lawes et al., 1990; Coleman and Hill, 2015; Linden et al., 2015). However, samangos show a considerable amount of dietary flexibility compared to other forest guenons. The gut morphology of samango monkeys, which includes having a longer caecum and more cellulose-digesting bacteria than other guenons (Bruorton and Perrin, 1991), allows them to considerably increase their leaf consumption, particularly in periods of fruit scarcity (Fairgrieve, 1995; Beeson et al., 1996). In some populations, leaves can make up as much as 44% of the diet, whilst other items such as insects, flowers, seeds and fungi are also consumed in smaller amounts (Coleman and Hill, 2015; Linden et al., 2015). They are also capable of eating the fruits and seeds of exotic species which may be found in commercial plantations and residential gardens (Wimberger et al., 2017).

2.1.2 Distribution

Samango monkeys represent Africa's southernmost arboreal guenon and are South Africa's only exclusively forest-dwelling primate. *C. a. schwarzi* is assumed to be endemic to South Africa and is the most endangered of the three subspecies (Linden et al., 2016). Its distribution ranges from the Soutpansberg Mountains in Limpopo Province in the north of South Africa, down to Mariepskop and Magoebaskloof in Mpumalanga Province (Dalton et al., 2015). The Soutpansberg populations are likely completely isolated from neighbouring populations due to lack of suitable connecting habitat (Linden et al., 2016). *C. a. erythrarchus* is near threatened and occurs in South Africa, Zimbabwe, Mozambique and up to Malawi. Within South Africa it occurs from southern Mpumalanga Province to northern KwaZulu-Natal Province (Dalton et al., 2015). Finally, *C. a. labiatus* is vulnerable and endemic to South Africa, where it is found from KwaZulu-Natal Province to the Eastern Cape (Dalton et al., 2015) (Figure 2.2).

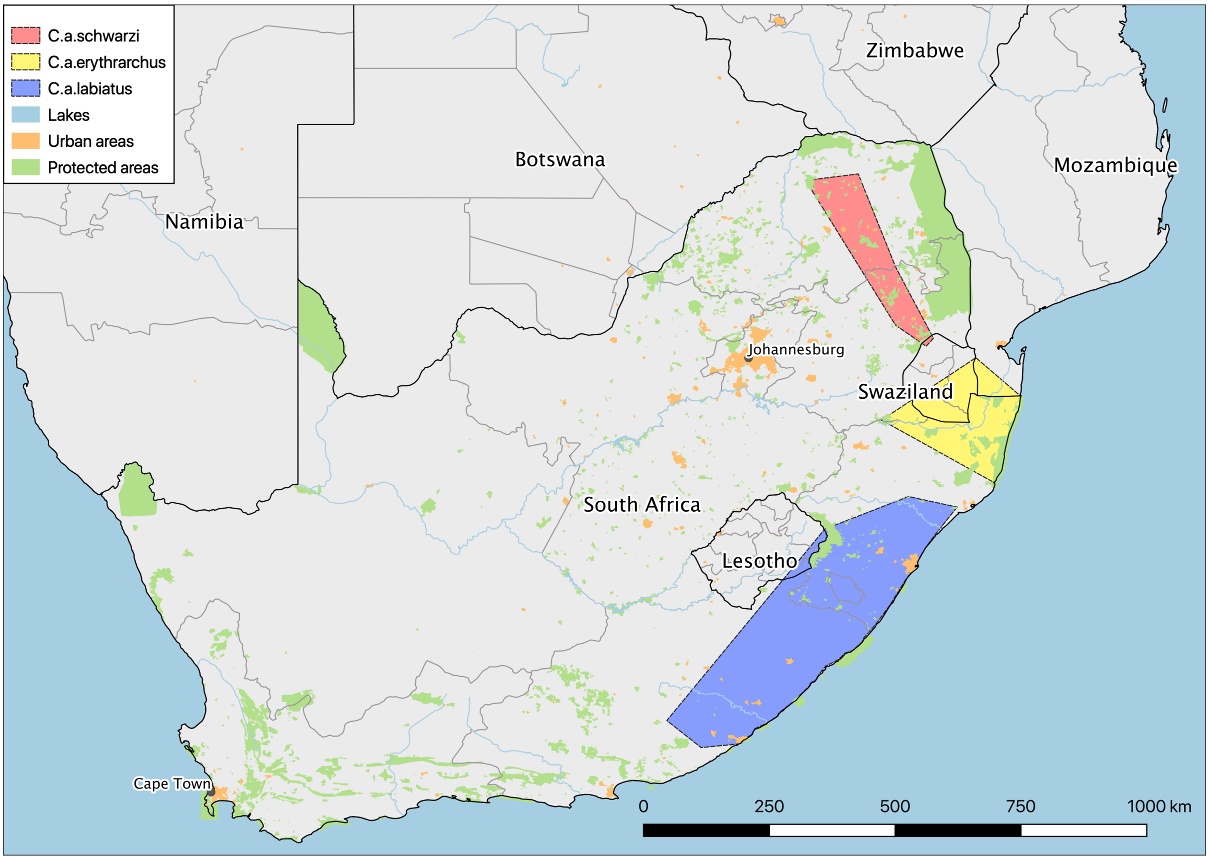

Figure 2.2. Approximate distribution of the three samango monkey subspecies (*Cercopithecus albogularis spp*.) across South Africa, Lesotho and Swaziland according to (Dalton et al., 2015).

Across South Africa, samango monkey distribution is closely linked to that of tall-canopy indigenous forests such as Afromontane/mistbelt, scarp and coastal belt forests (Lawes, 1990a; Hayward et al., 2005). However, samangos are also capable of utilising matrix habitat such as acacia woodland and forest thicket (Lawes and Piper, 1992; Heikamp, 2008; Emerson and Brown, 2013), in addition to various human-modified habitats, although samangos view these areas as "riskier" habitats and have been shown to preferentially forage in indigenous forests if given the opportunity (Nowak et al., 2017). Samangos heavily rely on indigenous forests for successful foraging, reproduction and recruitment (Linden et al., 2016) and, as with other arboreal primates, are highly susceptible to forest fragmentation and anthropogenic landscape change (Chapman et al., 2000). Due to the recent and rapid fragmentation of forest habitats in South Africa, resulting from the conversion of land for agriculture and urbanisation (Friedmann and Daly, 2004; Kingdon et al., 2008), samango monkeys are currently restricted to isolated or semi-isolated forest fragments with little or no connectivity between patches (Linden et al., 2016). Samangos are also poor dispersers and are generally reluctant to traverse open ground (Lawes, 1992, 2002; Lawes et al., 2000). As such, isolated samango populations are at risk of local extinction (Linden et al., 2016).

2.2 Study site

Field work was conducted over a six-year period at the Primate and Predator Project (hereafter PPP), as part of the Lajuma Research Centre, at the western edge of the Soutpansberg Mountains, Limpopo Province, South Africa (23°02’23”S, 29°26’05”E, Figure 2.3). Lajuma is part of the UNESCO Vhembe Biosphere Reserve, an area covering around 30,701 km^2, which stretches from the Botswana, Zimbabwe and Mozambique borders to the north and west, Kruger National Park to the east and south to the Blouberg and Soutpansberg Mountain ranges.

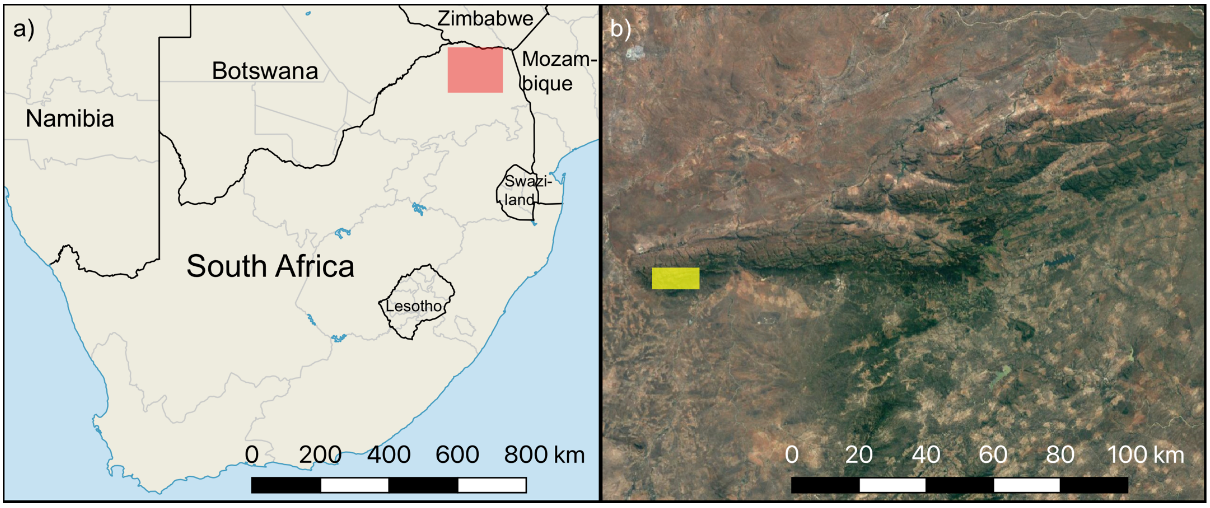

Figure 2.3. Location of Soutpansberg Mountain range within South Africa (red, a), and location of Greater Lajuma in the western Soutpansberg Mountains (yellow, b).

2.2.1 Habitat

The Soutpansberg Mountains covers an area of around 6800 km^2. The mountain range spans a distance of approximately 210 km, is about 60 km at its widest point and 15 km at its narrowest. Altitude ranges from 200 m to 1748 m at the peak of Mount Lajuma. Altitude at the field site ranges from 1150 m to 1748 m, whilst there is also substantial seasonal variation in rainfall and temperature which gives rise to a variety of vegetation types (Mostert, 2006). Montane grasslands occur on the flat plateaus at higher elevations, whilst the south-facing ridges are dominated by indigenous evergreen mistbelt forest (Mostert, 2006; Mucina and Rutherford, 2006) as a result of direct mist precipitation and the collection of groundwater from the base of the cliffs. The mistbelt forest exists in a matrix of semi-deciduous woodland, thicket and riverine forests (Hahn, 2006). These forest types are further fragmented by commercial plantations, farmlands and residential gardens, whilst urban settlements become more prevalent off the mountains.

2.2.2 Climate

Climate at Lajuma is described as temperate with hot, wet summers from October to March, and cool, dry winters from April to September (Willems, 2007) (Figure 2.4). Over the study period mean temperature during the summer was 20°C, with a mean total rainfall of 561 mm. In contrast, mean temperature during the winter was 16°C with a mean total rainfall of 16 mm.

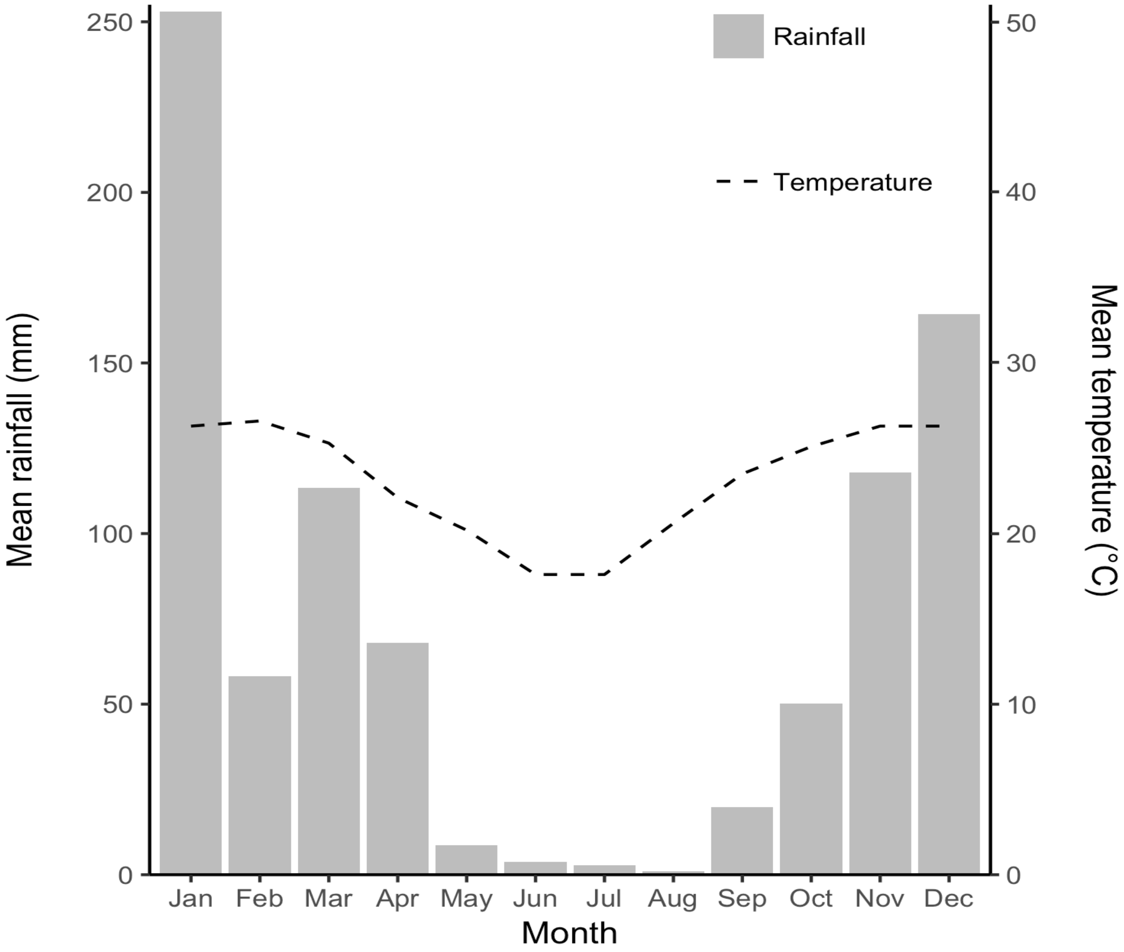

Figure 2.4. Mean total monthly rainfall and mean monthly temperature across the study period (2012 – 2016) at Lajuma Research Centre, South Africa.

2.2.3 Predators of samango monkeys

Due to their arboreal nature, the main predators of samango monkeys at Lajuma are the African crown eagle (*Stephanoaetus coronatus*) and the Verreaux's or black eagle (*Aquila verreauxii*). Other potential predators include the leopard (*Panthera pardus*), the African rock python (*Python sebae*) and to a lesser extent, brown hyaenas (*Hyaena brunnea*), servals (*Leptailurus serval*), caracals (*Felis caracal*), African wildcats (*Felis silvestris lybica*), honey badgers (*Mellivora capensis*) and Verreuax's eagle owl (*Bubo lacteus*). Whilst not being true predators of samangos, venomous snakes such as the black mamba (*Dendroaspis polylepis*), Mozambique spitting cobra (*Naja mossambica*) and puff adder (*Bitis arietans*) still pose significant mortality threats if encountered and would often elicit an antipredator response (jumping into trees and alarm calling). However, attacks by venomous snakes are rarely recorded in guenons (Foerster, 2008) and snakes are almost always discovered by individuals and avoided well before they actually become dangerous (Smith et al., 2008).

2.3 Study groups

The samango monkey subspecies at Lajuma, *C. a. schwarzi*, is listed as endangered on the national Red List (Linden et al., 2016). On site, there are two well-habituated samango groups: 'Barn' and 'House'. Estimates place 'Barn' at around 40 individuals, and 'House' at around 70 individuals, representing one of the largest reported groups of samango monkeys (Skinner and Chimimba, 2005). Samangos are notoriously difficult to identify, particularly in such large groups. Whilst the majority of data collected was primarily focussed on age-sex class, individuals were identified where possible. However, due to the large number of individuals in each group, and the difficulty of observing the whole group due to the nature of the environment, estimates of the number of each age-sex class were difficult to obtain.

Identification was possible either through ear tags (*n* = 12) or distinguishing features (*n* = 13), such as injuries or ear notches due to lost tags. This led to an identifiable total of five individuals in 'Barn' group and 20 individuals in 'House' group, with any additional males identified where possible during breeding season. The resident male of each group changed multiple times throughout the study period but was always identified (Table 2.1). The breeding season at Lajuma typically occurs between May to July when groups experience an influx of males, with birthing occurring during the wet season between October to March (Linden et al., 2016).

Table 2.1. Resident males, and periods as resident male, of both 'Barn' and 'House' samango monkey groups at Lajuma Research Centre, South Africa.

Barn		House	
Name	Resident male between	Name	Resident male between
Red-red	Sep 2012 - May 2014	Steve	May 2012 - Apr 2015 & May 2016 - Jul 2016
Scar	Jun 2014 - Jun 2015	Lost-red	May 2015 - Dec 2015
Chief	Jul 2015 - Apr 2016	Blue-green	Jan 2016 - Apr 2016
James	May 2016 - Dec 2016	Skeletor	Aug 2016 - Dec 2016

Despite samangos at other field sites being described as predominantly frugivorous, leaves made up the greatest proportion (40.1%) of the diet of both groups at Lajuma over the study period (Table 2.2). Fruit (37.7%) also contributed significantly to the diet, whilst items such as seeds (7.7%) and flowers (2.0%) were eaten much less regularly. Items such as moss, roots and shoots contributed such a small proportion of the diet of both groups that they are excluded from Table 2.2. Whilst samangos are capable of eating exotic fruits and seeds (Wimberger et al., 2017), the macadamia farm which was adjacent to Barn groups' home range was never entered by either group (Figure 2.5) due to the reluctance of samangos to traverse open ground (Lawes et al., 2000).

Table 2.2. Percentage of total time spent feeding on each food item by samango monkeys at Lajuma between 2012 – 2016.

Food item	% Total feeding time
Bark	3.6
Flowers	2.0
Fruit	37.7
Fungi	0.7
Grass	2.6
Tree sap	0.1
Herbs	5.3
Leaves	40.1
Seeds	7.7
Invertebrates	0.2

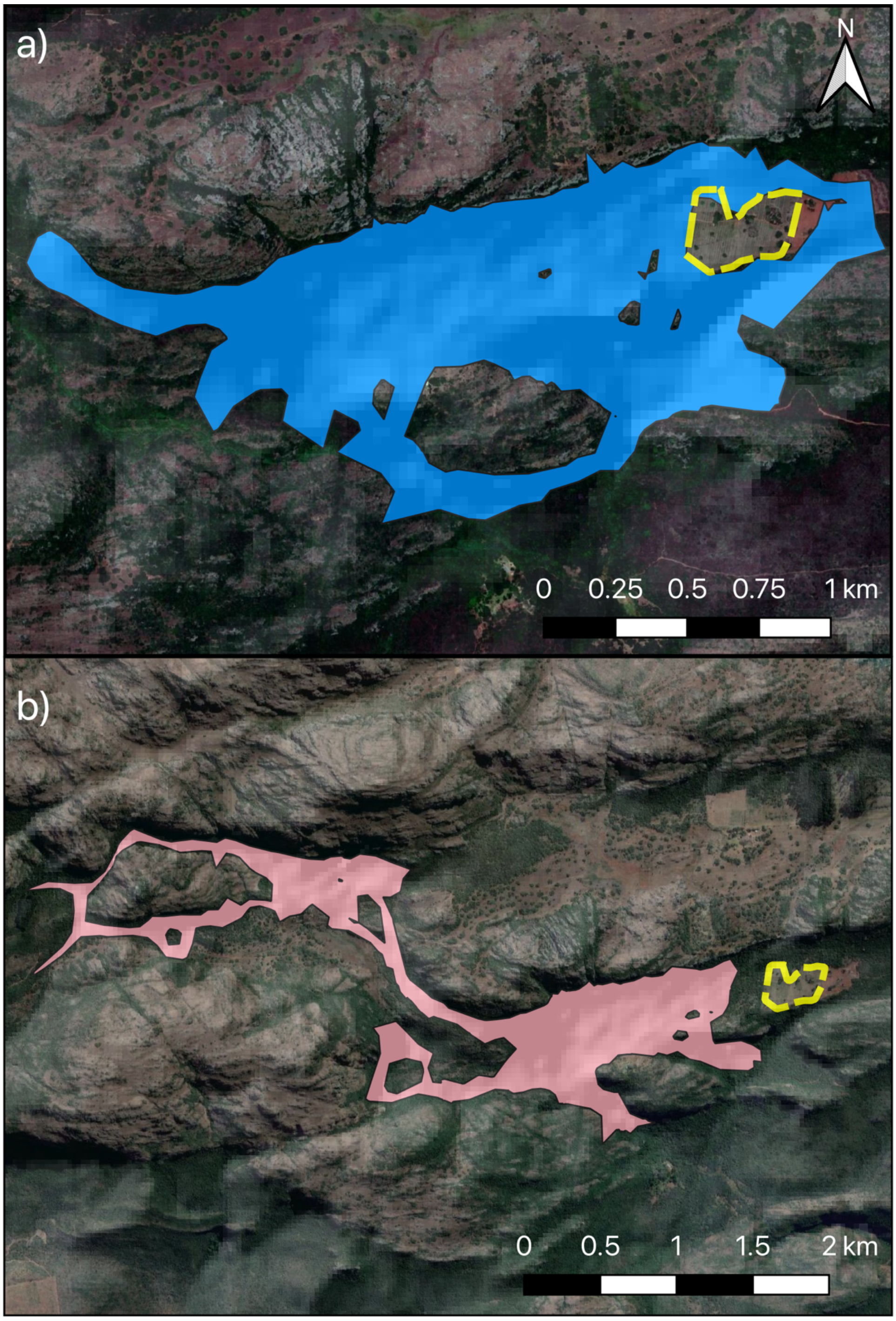

Figure 2.5. Combined annual home ranges of ‘Barn’ (a) and ‘House’ (b) groups at Lajuma Research Centre, South Africa, showing avoidance of macadamia farm (yellow outline).

2.4 Data collection

The PPP collects long-term data on the role of mountainous regions on biodiversity conservation, the behavioural ecology of predator-prey interactions and human-wildlife conflict across the Soutpansberg Mountains. Data was collected on the three diurnal primates on site (samango monkey; vervet monkey, *Chlorocebus pygerythrus*; and chacma baboon, *Papio ursinus*) in addition to the terrestrial predator, the African leopard (*Panthera pardus*). Data collection for the primate side of the project focussed on behavioural instantaneous scan sample observations on both samango monkey groups, in addition to a single group of both vervet monkeys and chacma baboons. Data collection began on February 2012 for 'Barn' group and May 2012 for 'House' group and continued until 2017 for this study. All primate groups were typically followed three to four days per week, resulting in an average of eight full follow days for each group per month over the six-year study period (2012 – 2017). Full days consisted of following the focal group from morning sleep site to evening sleep site without losing audio or visual contact for more than a total of 60 minutes. This totalled 105 sample months, with 72 months containing eight full days or more. Gaps in the data occurred between August – September 2013 ('Barn'), February – April 2012 and August – November 2013 ('House' group respectively). Day length over the study period ranged from 10 h 45 m in June to 13 h 31 m in December.

In addition to behavioural scan sampling, data collection as part of the project involved vegetation sampling of random 5 x 5 m^2 quadrats across Lajuma one day per week, and phenological sampling of individually marked trees over two days within the first two weeks of every month (section 2.4.2). All observers were trained and tested to a specific protocol and were regularly monitored across the study period. All data collection in the field was conducted by PPP assistants between 2012 – 2017, whilst I (EP) contributed to all data collection from May 2016 to August 2017. In addition to the above fieldwork, EP also collected focal samples alongside PPP data collection between August 2016 and August 2017.

2.4.1 Behavioural sampling

GPS recordings

A handheld navigator (Garmin GPSmap 64S) was used to record the location of the focal group or individual to within an accuracy of around 5 m. GPS points were recorded at the start of each instantaneous scan and focal sample, and therefore could later be coupled for analysis. All GPS data were imported into Garmin BaseCamp (v4.7, Garmin Ltd) and exported into files compatible with GIS.

Instantaneous scan sampling

During each full day, instantaneous scan samples (Altmann, 1974) on as many individuals as possible were collected by EP and PPP assistants within a five-minute window. Individuals were scanned from left to right whilst moving through the group where possible to remove any potential bias. Scan samples were collected at 20-minute intervals (e.g., 12:20, 12:40, 13:00) on a handheld PDA (Psion Teklogix Workabout Pro 3) using *Excel Mobile*. Information collected during each scan sample included: date, observer, group, time, age-sex class, general activity, qualifying activity, plant species and food item (during feeding behaviours), vigilance and the number of neighbours within 5 m (Table 2.3). Vigilance behaviours recorded included: not vigilant (e.g. during grooming), looking upwards, looking downwards, scanning (in a horizontal plane), social looking at another monkey and unknown.

Table 2.3. Activity types and definitions recorded as part of instantaneous scan sampling. General activity was recorded first followed by a qualifying activity.

General activity	**Definition**	**Qualifying activity**	**Definition**
Feeding	Searching for, processing or ingesting food	Feeding	Chewing or ingesting food, or mouth in contact with food
		Foraging	Searching for food or picking/handling food
Moving	Moving without any obvious sign they are searching for food	Walking	Always 3 limbs touching the ground, also applies to slow climbing
		Running	Less than 3 limbs always touching the ground, also applies to fast climbing
Socialising	Any social activity, e.g. fighting, playing, grooming	Grooming given	Grooming another individual
		Grooming received	Bring groomed by another individual
Resting	Sitting, lying or standing, without engaging in any specific behaviour	Resting sitting	Sitting
		Resting standing	Standing
		Resting lying	Lying down
		Resting huddled	Huddling with other individuals
		Self-grooming	Grooming itself. Also referred to as autogrooming

Focal sampling

Focal samples were collected by EP between August 2016 and August 2017. Focals were collected to provide additional information on identifiable individuals (Altmann, 1974). Focal samples were collected within a five-minute window using *Prim8*, a behavioural data collection application (McDonald and Johnson, 2014) on a mobile smart phone (Samsung Galaxy S5). A total of 25 identifiable individuals (Barn: 5, House: 20) were sampled over the study period. A maximum of two focal samples were collected on the same individual per day, one in the morning session (before 13:00), and one in the afternoon session (after 13:00).

Information collected during each five-minute focal sample included: date, time, individual ID, group ID, number of nearest neighbours within 5 m (continuously recorded throughout the focal), and the frequency of scratching events. The total number of focal observations over the study period was 468. Focal samples were compared to scan samples from the same period and were shown to be representative.

Ad libitum sampling

During every follow day, adult male and group-wide alarm calls were recorded by EP and PPP assistants on an all-occurrence basis. Samango monkeys show a range of acoustically distinct vocalisations, some of which are associated with predator alarm calls. Juveniles and adult females regularly “grunt” as a means of maintaining group cohesion, and use “hacks” and “chirps” as alarm calls (Coleman, 2013). In contrast, males have six acoustically distinct alarm calls: *ant*, *boom*, *ka*, *katrain*, *nasal scream* and *pyow* (Fuller, 2013). *Booms* are low frequency, tonal calls and may be heard by other samangos up to 1 km away. *Booms* are the most common male call and likely function in group cohesion due to their interaction with females and juveniles which often “ask” and “respond” to *booms* (Fuller, 2013). *Nasal screams* are rasping vocalisations and are associated with aggression between males. *Pyows* are loud, tonal calls that can be heard up to 1 km away and can be used in combination with *ants*, *booms* or *katrains.* Whilst males have been shown to *pyow* in response to some terrestrial predators they also occur in a range of other contexts, with their most likely function being to maintain group boundaries (Fuller, 2013). *Ants* frequently occur with *pyows* and are possibly just exhausted *pyows* due to their acoustic similarity, but may also have an association with terrestrial predators such as snakes or dogs (Fuller, 2013). Despite some association of *ants* and *pyows* with terrestrial predators, their categorisation as “alarm calls” seems inappropriate as unlike some primates, the avoidance strategy of arboreal primates (climbing up trees and keeping predator in view) may not have warranted the evolution of specific alarm calls for these predator guilds. *Kas* are short, loud, abrupt calls and form a *katrain* when multiple *kas* are strung together in pulsed units. Both *kas* and *katrains* have a strong association with aerial predators. In a study on adult male blue monkeys (*Cercopithecus mitis stulmanni*) in Kenya, 59% of all *katrain* calls recorded were associated with the presence of raptors, with a further 22% of calls consistent with antipredator behaviour associated with this predator guild (looking up, dropping down into the canopy etc.) (Fuller, 2013). The time and a description of all adult male *ka* and *katrain* vocalisations, regardless of whether the male was visible, were recorded along with a GPS point of the calls' location across the six-year study period. Group-wide alarm calls were also recorded and used as part of the analysis.

2.4.2 Vegetation sampling

Vegetation sampling was carried out by EP and PPP assistants to give measures of habitat structure and species composition across the study area. Phenological sampling was also carried out on 24 important species to the samango monkey (Heikamp, 2008; Coleman, 2013) to give estimates of food availability. Table 2.4 shows these species along with the combined percentage contribution (of leaves, fruits and seed pods) of each species to the samango diet over the study period. These species accounted for 94% of all species eaten by samango monkeys over the study period.

Table 2.4. List of 24 plant species sampled in phenology data over the study period with percentage contribution to overall diet.

Common name	Scientific name	% Time spent feeding
Flame thorn	*Acacia ataxacantha*	14.4
Sweet thorn	*Acacia karoo*	5.8
Paperbark thorn	*Acacia sieberiana*	1.7
White stinkwood	*Celtis africanus*	3.2
Rock alder	*Canthium mundianum*	0.5
Apricot sourberry	*Dovyalis zeyheri*	0.4
Cape ash	*Ekebergia capensis*	2.9
Sacred coral tree	*Erythrina lysistemon*	1.5
Stem fruit	*Englerophytum magalismontanum*	0.7
Twin red-berry	*Erythroccoca trichogyne*	3.7
Common wild fig	*Ficus burkei*	6.6
Forest Fig	*Ficus craterostoma*	9.2
Broom-cluster fig	*Ficus sur*	6.1
Thorny Gardenia	*Hypercanthus amoenus*	1.4
Transvaal red milkwood	*Mimusops zeyheri*	1.9
Wild olive	*Olea europaea*	2.0
Quinine tree	*Raulvolfia caffra*	2.6
Forest grape	*Rhoicisuss tomentosa*	4.1
Red currant	*Searsia chirindensis*	9.9
Common waterberry	*Sygium cordatum*	2.3
Mountain waterberry	*Sygium legatii*	1.3
Crowberry	*Searsia pentheri*	8.4
Forest mahogany	*Trichilia dregeana*	2.2
Buffalo thorn	*Ziziphus mucronata*	1.2
% Total of overall diet		94

Phenological sampling

Monthly estimates of food availability were collected by EP and PPP assistants for 20 individually marked mature trees of various sizes of 24 species (480 trees in total) (Table 2.4) between 2012 – 2017 (Figure 2.6). Tree species were selected based on the relative importance to the diet of the samango monkey, whilst also giving a representation of the various vegetation types across Lajuma. The height, diameter at breast height (DBH), crown diameter and perpendicular diameter were measured for each tree, along with an estimate for the number of branches for the whole tree. A branch was marked for each tree and the number of leaves, fruit, flowers and seeds, % mature leaves and % ripe fruit (underripe, ripe and overripe) were estimated for the marked branch every month. This was then scaled up using the branch estimate for the whole tree to give an estimate per food item for the whole tree. Visual estimates were made for the whole tree where no items were present on the marked branch but were on the tree.

Vegetation plots

Vegetation plots were used to estimate different measures of habitat structure and to calculate food availability across Lajuma. Plots were generated in Garmin BaseCamp (v4.7, Garmin Ltd), and were randomly generated in order to remove any statistical bias from non-random design (Diekmann et al., 2007). As many plots as possible were sampled each month, with the GPS points of each plot downloaded to a handheld navigator (Garmin GPSmap 64S) and located in the field. Due to the difficulty of the terrain not all plots could be sampled. Where plots could be sampled, a 5 m^2 quadrat was established using the GPS point as the northwest corner of the quadrat. This resulted in 702 quadrats over the study period (Figure 2.6). Data recorded by EP and PPP assistants in each quadrat included the slope and aspect (from the northwest corner), percentage ground cover (rock, bare ground, herb, vine, grass, leaf litter, moss, manmade, roots and water) and the number of saplings. Where trees with a diameter > 10 cm at a height of 1 m were present, they were identified where possible and the following measurements were taken: height (in m), DBH (in cm), crown diameter at widest point and perpendicular crown diameter (in m). The first of these measurements was estimated visually to the nearest 0.5 m, with the latter two measured using a tape measure. From this information, mean crown diameter (in m) for each tree was calculated by averaging the latter two measurements which, along with DBH, was then used to calculate subsequent estimates of food availability. In addition, mean canopy height (in m) was calculated from the average height of all trees within the quadrat and also used in subsequent analyses. Finally, measures of understory visibility were estimated by counting the number of squares on a 0.8 m^2 chequerboard with 0.1 m^2 cells at each of the four cardinal point directions from the northwest corner of each quadrat. Chequerboard squares were counted at a height of 0 m and 1.25 m and at a distance of 5 m and 10 m in each direction, giving a total of 16 chequerboard measurements per plot. The number of squares counted were then averaged across all 16 measurements to give a mean understory visibility measurement for each quadrat. Despite many plots occurring outside the range of both samango groups (Figure 2.6), these quadrats were kept in subsequent analyses in order to increase sample size and reliability when creating habitat maps, and also as the range area was similar to the wider area in many instances.

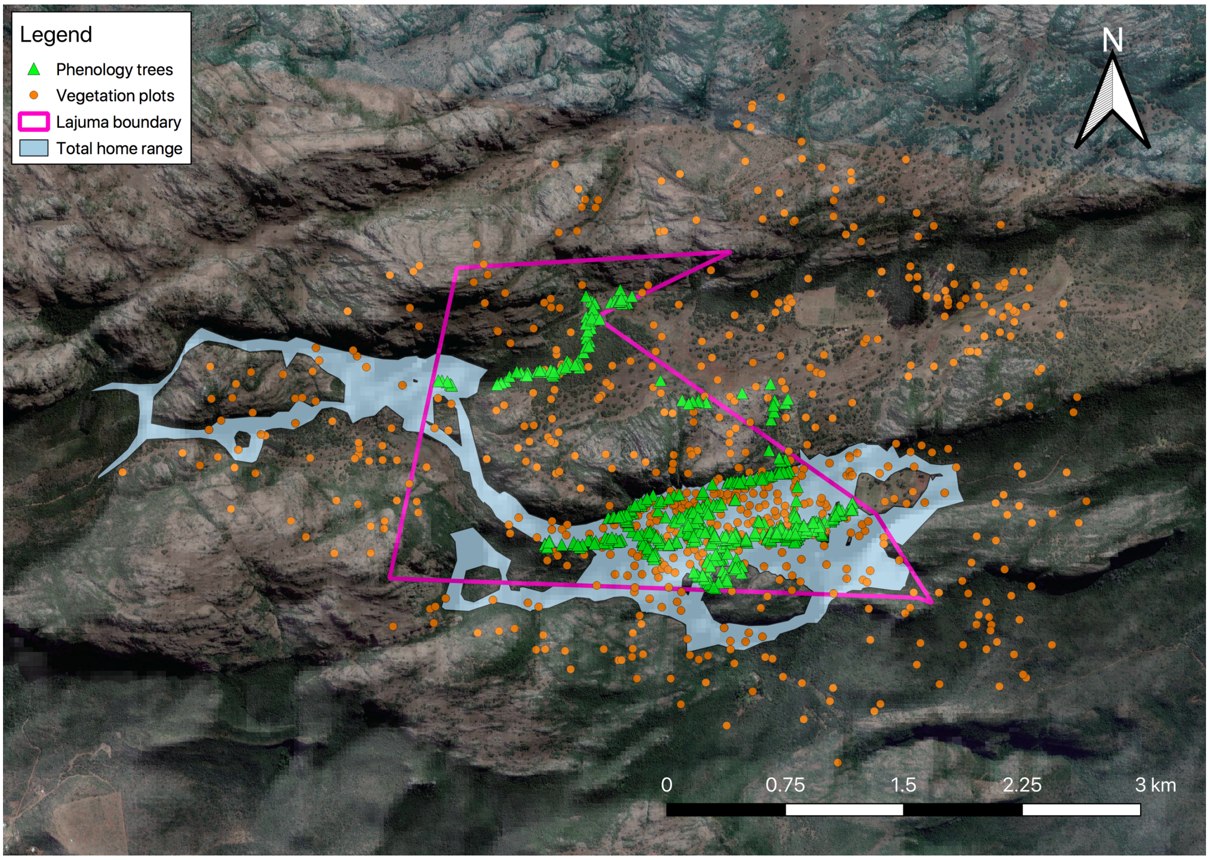

Figure 2.6. Map of study area showing Lajuma boundary, location of phenology trees (n = 480) and vegetation plots (n = 702), and combined outline of both groups' home ranges across the study period (2012 – 2016) at Lajuma Research Centre, South Africa.

2.4.3 Remote sensing

Remotely sensed information on primary productivity was collected by EP, using the enhanced vegetation index (EVI) from the Landsat 7 and Landsat 8 databases (Huete et al., 2002). Annual composites were downloaded for analysis in Chapter 3 for comparability with other studies (Sawyer and Brashares, 2013), whereas monthly composites were used in Chapter 4 for comparability with monthly estimates of food availability used in this chapter. EVI uses the red-infrared parts of the electromagnetic spectrum, whilst accounting for the reflectance of the blue band, to calculate the difference in Earth surface reflectance patterns (Eidenshink and Faundeen, 1994). This makes it less sensitive to atmospheric conditions whilst increasing sensitivity to changes in areas of high biomass, canopy differences, canopy structure and plant phenology when compared to other vegetation indices such as the normalised difference vegetation index (NDVI) (Huete et al., 2002). EVI values range from -1.0 (indicating non-vegetated areas) to + 1.0 (densely vegetated areas) (Huete et al., 2002). In addition, elevation and water flow layers were also downloaded by EP from NASA's Shuttle Radar Topography Mission and WWF HydroSHEDS Flow Accumulation datasets respectively.

All remote sensing composites were downloaded from Google Earth Engine (https://earthengine.google.com) for the entire Soutpansberg Mountains at a resolution of 30 m^2 and were imported into QGIS 2.18 – 3.0 (QGIS Development Team, 2018) for visualisation and analysis. QGIS is an open-source geospatial modelling software which is used for viewing, editing and analysing geospatial data. Terrain ruggedness was calculated by EP from the elevation layer using the 'Terrain Analysis' toolbox in QGIS, and a 'distance to rivers' layer was created by converting the flow accumulation layer into a presence/absence raster and applying the 'Proximity' function in the 'Analysis' toolbox in QGIS (Figure 2.7). Finally, an orthorectified satellite image of the study area was downloaded by EP from the Digitalglobe Satellite (Google Maps, 2018) using the 'QuickMapServices' menu in QGIS, which represented the base map for all visualisation. The cell size of the base map was set to 30 m^2 due to the resolution of rasters downloaded for all analyses carried out in this thesis. All locational and satellite data were projected into the Universal Transverse Mercator coordinate reference system (WGS 1984, zone 35S).

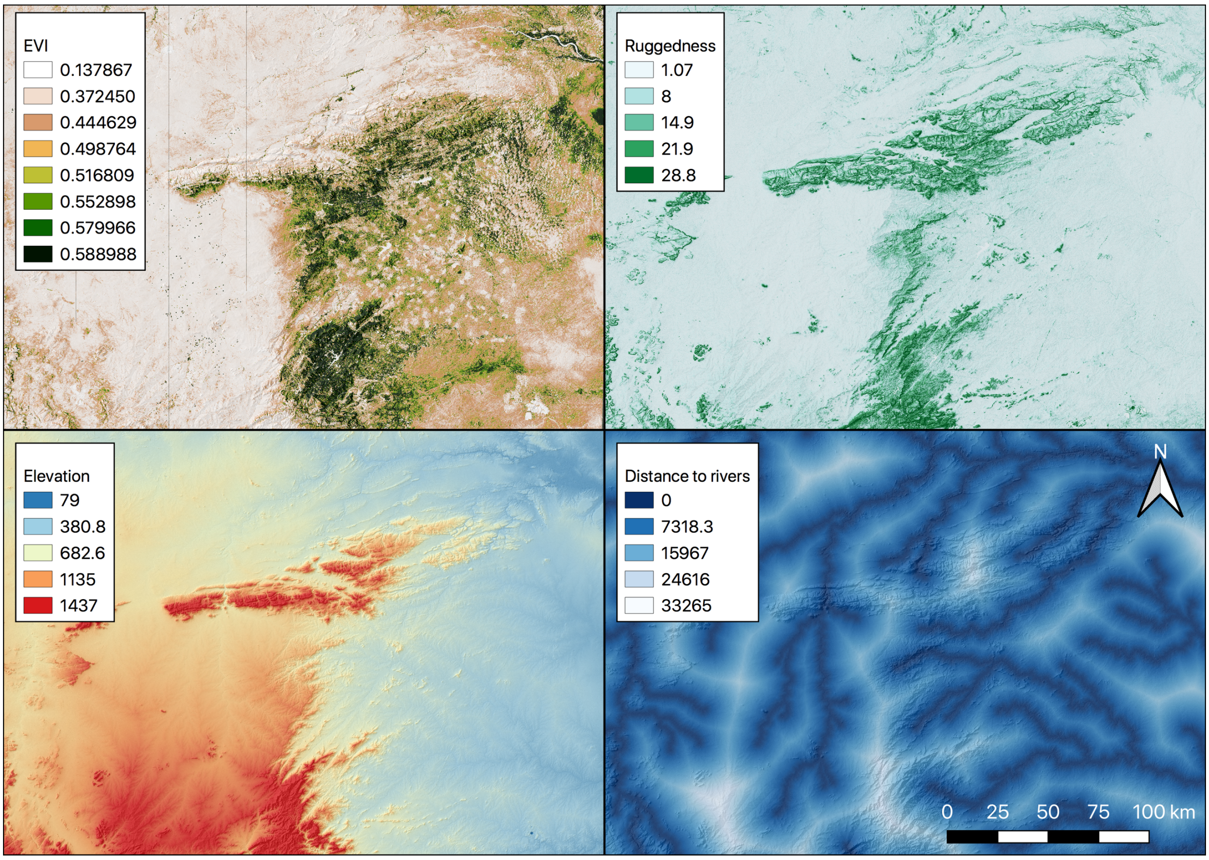

Figure 2.7. Remotely sensed composites of EVI (Enhanced Vegetation Index, 2016 composite), terrain ruggedness, elevation (m) and distance to rivers (m), across the Soutpansberg Mountains, South Africa.

2.5 Data processing and analysis

All data processing and analysis described from below was carried out by myself (EP), unless stated otherwise.

2.5.1 Food availability

Analyses in both Chapter 4 and Chapter 5 required estimates of food availability. A simple monthly food availability estimate was calculated for Chapter 4 due to the difficulty in estimating food availability accurately in this highly seasonal environment (Coleman, 2013), which comprises various microhabitats (Mostert, 2006). In addition, a monthly food availability estimate was the appropriate scale for the question being asked in this study. In

Chapter 5 which explores spatial variation in behaviour, a seasonal fruit availability estimate was calculated due to the scale of other variables explored in this analysis, and as this was the finest scale at which fruit availability could be estimated accurately (Coleman, 2013). Fruit availability was the only measure of food availability considered in this analysis owing to the samangos' mainly frugivorous diet (Coleman and Hill, 2015; Linden et al., 2015) and for comparability with other studies (Coleman and Hill, 2014). Leaf maturity and fruit ripeness were not considered in any calculations of food availability, as samangos are known to eat leaves and fruits at various stages of maturity and ripeness respectively (Linden et al., 2015).

Monthly food availability

For the analysis in Chapter 4, simple monthly food availability estimates were calculated for fruit, leaves and seed pods as these items make up a significant proportion of the samango monkey diet (Coleman, 2013; Linden et al., 2015). Flowers were not included in this analysis as they contribute only a small proportion of the samango diet (Linden et al., 2015). Monthly food estimates were calculated for each food item of each tree species using the phenology data. The monthly estimates of fruit, leaves and seed pods were averaged across the 20 individual trees for each of the 24 species sampled in the phenology data, giving a monthly mean number of each food item per species. These estimates were then scaled up across each group's home range using estimates for the number of each tree species across each group's home range. The number of trees within each group's range was estimated by dividing the total combined area of each group's annual home range by the area of a vegetation plot (5 m^2), and then multiplying this figure by the mean number of trees per species sampled across all the vegetation plots (n = 702). The monthly mean number of each food item per species were then multiplied by the estimated number of each respective tree species to give a total monthly food availability estimate per food item per species. This resulted in a raw value for the total estimated availability of fruit, leaves and seeds for each tree species across each group's home range. These raw values were used to calculate two estimates of food availability.

Total food availability per food item was calculated by summing the total availability across all species, whilst the availability of food items for the five most commonly eaten species was calculated by summing the total availability of items across each of these species. The five most commonly eaten items per species were determined by counting the number of scan samples recorded feeding on a particular food item of each species, and then calculating this value as a proportion of the number of scans recorded as feeding across the study period. As only four species of seed are regularly eaten, only these species were included in monthly estimates. Five species was considered the cut-off point for this estimate as these species contributed over 60% of the samango diet for each food item. The percentage of time spent feeding on each food item of each species is shown in Table 2.5, which was used to determine the five most commonly eaten items per species.

Table 2.5. Percentage of time spent feeding by samango monkeys on leaves, fruit and seed pods of each species from 2012 – 2016. Values in bold represent the top five most commonly eaten species of that food item.

	% Total feeding time		
Common name	**Leaves**	**Fruit**	**Seed pods**
Flame thorn	**21.0**	n/a	**78.1**
Sweet thorn	**11.6**	n/a	**11.0**
Paperbark thorn	2.7	n/a	**7.7**
White stinkwood	2.3	4.9	n/a
Rock alder	0.8	0.4	n/a

Apricot sourberry	0.5	0.4	n/a
Cape ash	2.0	4.5	n/a
Sacred coral tree	3.1	n/a	**3.2**
Stem fruit	0.1	1.3	n/a
Twin red-berry	**10.7**	0.4	n/a
Common wild fig	1.4	**12.6**	n/a
Forest Fig	1.9	**17.5**	n/a
Broom-cluster fig	0.5	**12.3**	n/a
Thorny Gardenia	1.8	1.5	n/a
Transvaal red milkwood	0.7	2.5	n/a
Wild olive	2.5	2.0	n/a
Quinine tree	0.8	4.8	n/a
Forest grape	4.0	**5.4**	n/a
Red currant	**6.7**	**15.3**	n/a
Common waterberry	1.3	3.6	n/a
Mountain waterberry	1.2	1.9	n/a
Crowberry	**19.6**	3.6	n/a
Forest mahogany	1.1	3.7	n/a
Buffalo thorn	1.6	1.3	n/a
% contribution to diet of five most commonly eaten species	69.6	63.1	100

Seasonal food availability

For the analysis in Chapter 5, food availability was calculated on a seasonal (wet versus dry season) basis, and only for fruit given the samango's mainly frugivorous diet (Lawes, 1991; Coleman and Hill, 2015; Linden et al., 2015). Monthly estimates of fruit availability for each individual tree (*n* = 20) for each species (*n* = 24) were summed per season to give total seasonal fruit availability estimate for each of the 20 differently sized trees across 24 species. Using these estimates, the mean crown diameter or DBH of each of the 20 trees sampled was used to apply a linear regression to predict the total seasonal fruit availability for an individual tree of each species based on its mean crown diameter or DBH. Each linear regression was then applied to the vegetation plots to predict the seasonal fruit availability for each individual tree of each species based on its mean crown diameter or DBH, recorded as part of the quadrat sampling. Where no significant relationship could be found in the regression analyses, categorical differences in seasonal fruit availability based on mean crown diameter/DBH were used to assign a mean fruit number to each tree species based on these differences, similarly to Coleman (2013). Finally, the seasonal fruit availability estimates for each tree within a vegetation plot were summed to give a seasonal fruit availability estimate per plot. Spatial maps of seasonal fruit availability were then created using the 'Raster Calculator' in QGIS, and the 'Point Sampling Tool' was used to derive seasonal fruit availability estimates for each scan sample.

2.5.2 Home range and day journey length

One of the most recent home range estimation methods developed is the LoCoH (Localised Convex Hulls) method and includes three distinct methods: Fixed *k*-LoCoH, Fixed *r*-LoCoH, and Adaptive *a*-LoCoH (Getz et al., 2007). The Fixed *k* method calculates nearest neighbour convex hulls around a point using value *k*, the Fixed *r* method constructs hulls around a point based on a fixed radius *r*, and the Adaptive *a* method uses all points within a variable sphere around a point to construct hulls, enabling smaller convex hulls to arise in areas of higher use. The *a*-LoCoH method commonly uses the furthest distance between two locations as the *a* value to ensure correct formation of the 100% isopleth (Getz et al., 2007). Essentially, the LoCoH method is a non-parametric kernel density estimation and generalisation of the minimum convex polygon, constructing convex hulls around individual data points in order to determine the utilization distribution (UD) (Coleman, 2013). LoCoH has been shown to be much more superior at not only calculating home ranges more precisely, but also at dealing with more data. LoCoH is much more capable of dealing with hard boundaries such as cliffs, rivers/lakes or fences and better at coping with repeated data points (Getz and Wilmers, 2004; Ryan et al., 2006; Getz et al., 2007; Coleman, 2013). In addition, LoCoH also identifies areas in a range which aren't used (Ryan et al., 2006), which is particularly important in habitats separated by fragmentation.

The UD uses isopleths to delineate regions of varying probabilities where an individual might be found. A 10% isopleth contains 10% of the data points, whilst a 100% isopleth contains every point in the dataset. The boundary of a home range is typically delimited as the 95% isopleth (Silverman, 1986; Worton, 1989). Similarly, it is widely accepted that the 50% isopleth accurately represents the core areas of home range use (Börger et al., 2006; Getz et al., 2007). Total (95% isopleth) and core (50% isopleth) home ranges were created in 5% divisions using the '*t*-LoCoH' package (Lyons et al., 2013) in R 3.4 (R Core Team, 2017). Both the total and core home ranges were used in Chapter 3 and 4, whilst the total home range was used in Chapter 5 to create the landscapes of fear. Monthly mean day journey length (DJL) was also calculated in R for analysis in Chapter 4. This was done by summing the straight-line distance (in km) between sequential GPS points across a full day and averaging across DJLs for each month. Home ranges were imported into QGIS for further manipulation and presentation.

2.5.3 Habitat maps

Spatial maps of the seasonal (wet and dry season) availability of fruit across the home range were created for each year across the study period (Figure 2.8: example maps for 2016) for analysis in Chapter 5. To do this, the 'Point sampling tool' plugin in QGIS was used to sample remotely sensed estimates of EVI (averaged across the study period), terrain ruggedness, elevation and distance to rivers (see section 2.4.3, Figure 2.7) for each of the vegetation plots sampled (see section 2.4.2: *Vegetation sampling*). A linear regression was then used to predict the total seasonal fruit availability for each plot based on these measurements. The ‘Raster Calculator’ in QGIS was then used to spatially map the seasonal fruit availability for each year across the landscape using the estimates from each regression. A similar approach was used to create spatial maps of understory visibility and canopy height, using the landscape variables sampled for each vegetation plot to predict a mean value for each of these measurements per plot. Using the estimates from each regression, spatial maps of understory visibility and canopy height were created across the study area using the ‘Raster Calculator’ in QGIS (Figure 2.9, 2.10).

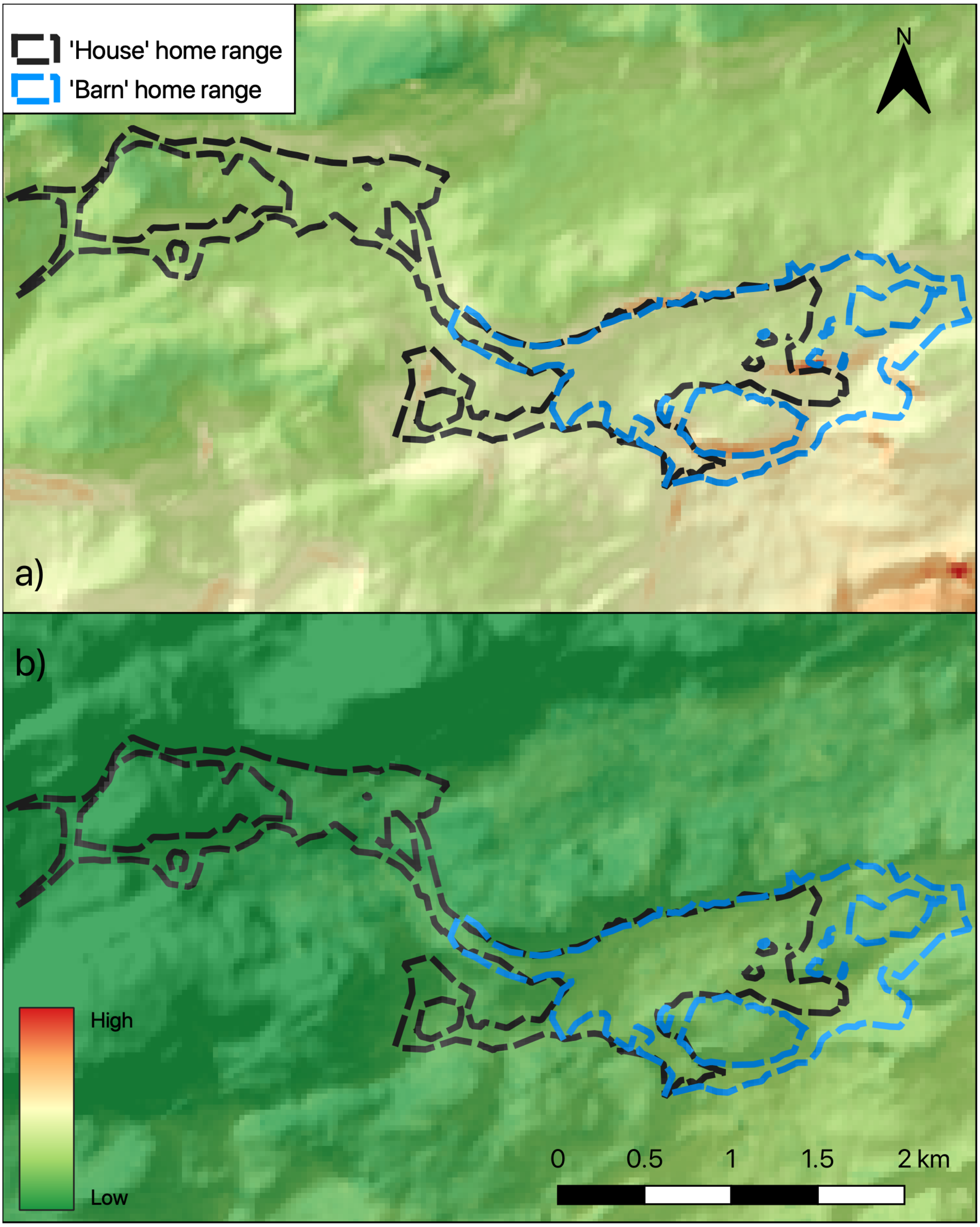

Figure 2.8. Example fruit availability maps for summer (a) and winter (b) 2016 across both samango groups' combined home range (2012 - 2016), at Lajuma Research Centre, Soutpansberg Mountains, South Africa.

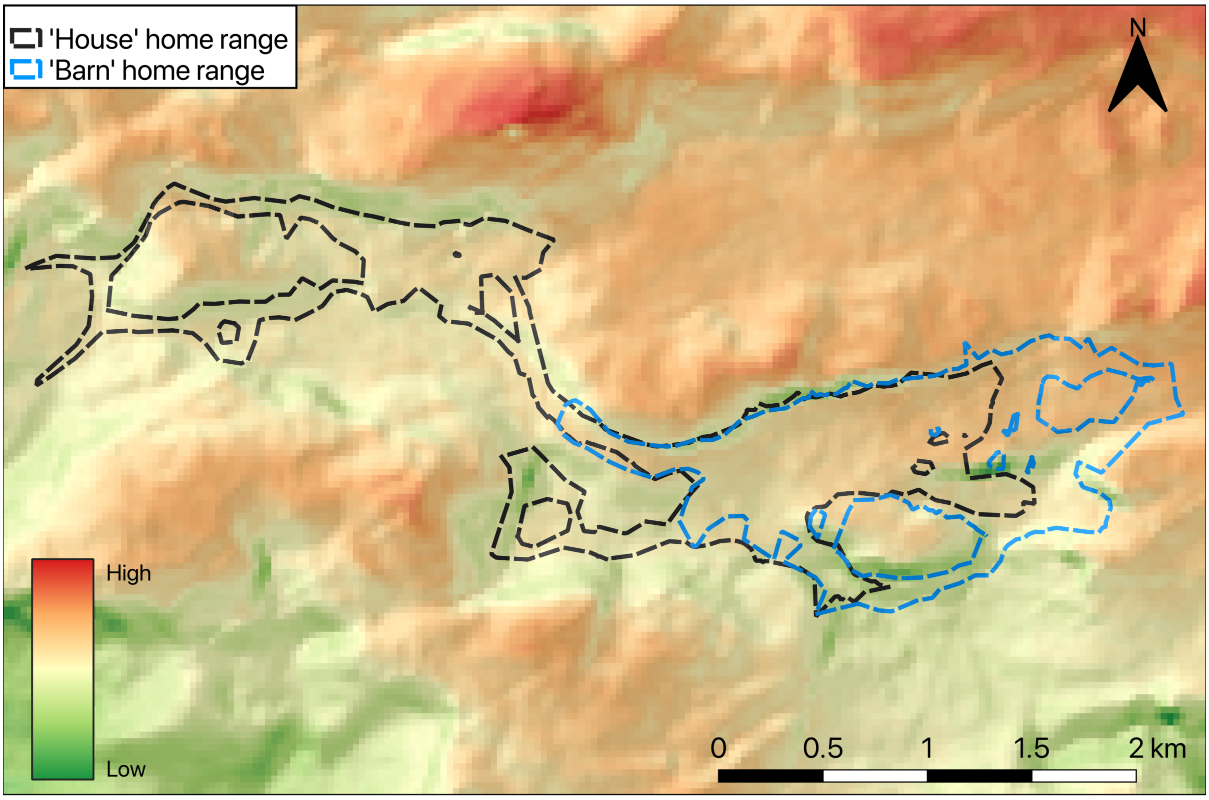

Figure 2.9. Spatial map of understory visibility across both samango groups' combined home range (2012 - 2016), at Lajuma Research Centre, Soutpansberg Mountains, South Africa.

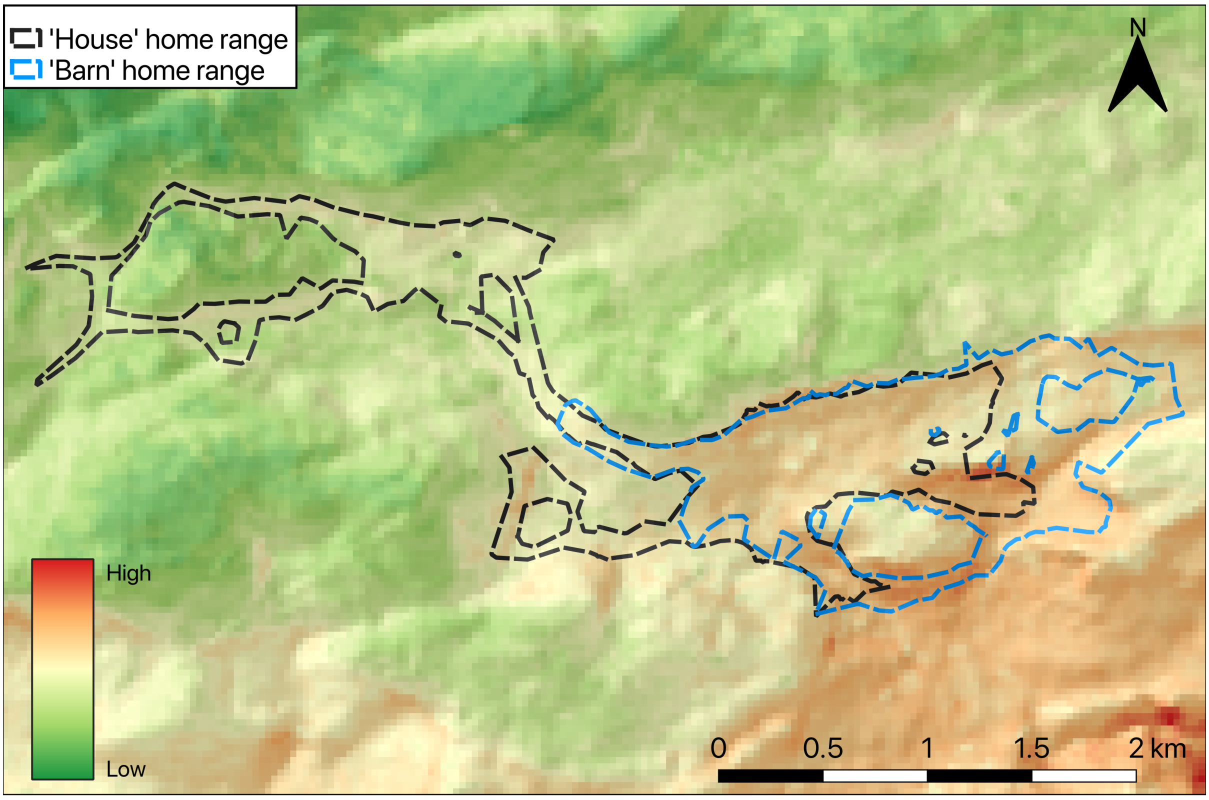

Figure 2.10. Spatial map of canopy height across both samango groups' combined home range (2012 - 2016), at Lajuma Research Centre, Soutpansberg Mountains, South Africa.

2.5.4 Landscapes of fear

Annual landscapes of fear were created for each group by using the GPS points of adult male *ka* and *katrain* calls, and group-wide alarm calls from the ad libitum sampling (see section 2.4.1: *ad libitum sampling*) to create density distributions using the Kernel Density Estimation tool in QGIS. A PLUGIN bandwidth was used for the nearest neighbour search distance due to the small sample size of alarm points in some years. This method also has superior capabilities of dealing with small sample sizes, as well as having reduced variability and increased performance when compared to least-squares cross validation (Gitzen et al., 2006). Landscapes of fear were then divided by the utilisation distribution to account for the time spent in certain areas (Willems and Hill, 2009). This process bound the annual landscape of fear by each groups' respective home range and created spatial maps of the probability of an alarm call.

2.5.5 Statistical analysis

All statistical analyses were conducted in R (v3.4 – 3.5, R Core Team, 2017; 2018). Due to the complexity of the data which often violated numerous statistical assumptions, all data were analysed using linear (LMM) and generalised linear mixed models (GLMM) (Bolker et al., 2008). These models also allow random effects to be included, whilst controlling for potentially confounding effects associated with repeated sampling. Normally distributed data was analysed using LMMs in the 'lme4' package (Bates et al., 2014), whilst non-normal data were analysed using GLMMs with a binomial, poisson or beta distribution and a logit link function in both ‘lme4’ and the ‘glmmTMB’ package (Brooks et al., 2017) in R.

Candidate models were created by including all explanatory variables of interest to assess the relative importance of each variable to the outcome of the response variable (Hurvich and Tsai, 1990). Normality and homogeneity of residuals from each model were checked by visually inspecting histograms and qqplots of the residuals, and the residuals plotted against fitted values. Collinearity between explanatory variables was assessed using Variance Inflation Factors from the vif function within the ‘car’ package, with a cut-off value of 2 (Hair et al., 2014). Significance of *P*-values of all explanatory variables were inferred at the 5% level. Confidence intervals of the explanatory variables were obtained using the confint function in the ‘lme4’ and ‘glmmTMB’ packages. Spatial autocorrelation in model residuals was identified in Chapter 5 using Moran’s I tests and accounted for by including spatial lags of the model’s residuals into the model as an “autocorrelation term” (Grueter et al., 2013).

Chapter 3

The following chapter has been formatted for submission to the journal 'Biological Conservation'.

Habitat selection of the endangered primate, the samango monkey (*Cercopithecus albogularis schwarzi*): integrating scales to prioritise habitat for wildlife management

Abstract

Habitat loss and fragmentation is one of the greatest threats facing biodiversity worldwide. Understanding resource selection and quantifying habitat connectivity in fragmented habitats is fundamental to the development of effective conservation plans. In South Africa, the arboreal samango monkey (*Cercopithecus albogularis subspp*.) is threatened due to loss and fragmentation of the indigenous forests it inhabits. The isolated population living in the Soutpansberg Mountains (*C. a. schwarzi*) is Endangered and represents the northwestern-most range of samango monkeys within South Africa. We used sequentially collected GPS points from two samango monkey groups followed between 2012 – 2016 to quantify the used and available habitat for this species within the western Soutpansberg Mountains. We developed 2nd (selection of ranging area), 3rd (selection within range) and 4th (feeding site selection) order resource selection functions (RSFs) for the samango monkey to identify important habitat features at different spatial scales. Whilst habitat productivity was the most important habitat feature at the population level, proximity to rivers, terrain ruggedness and elevation were more important on a finer scale. Through scale integration, we identified critical habitat and connectivity across the recorded samango monkey range in Limpopo Province, South Africa. We show that highly productive habitats occurring at moderate elevations and at close proximity to rivers are critical samango habitats, whilst also recognising the importance of riverine habitats and commercial plantations in connecting samango monkey populations and facilitating their long-term persistence. Protected area expansion of large forest patches and protection of forest corridors are identified as key conservation interventions for this species.

Introduction

Habitat loss and fragmentation is one of the greatest threats facing biodiversity worldwide (Fahrig, 2003; Lindenmayer and Fischer, 2006). Fragmentation can restrict populations to discrete patches of suitable habitat (Fahrig, 2003), reducing connectivity and therefore impacting metapopulation dynamics (Ricketts, 2001; Dolrenry et al., 2014). Connectivity increases gene flow between populations (Stockwell et al., 2003) which ultimately facilitates species persistence (Doerr et al., 2011) and mitigates the effects of habitat disturbance (Olds et al., 2012). Because of the increasing threat of fragmentation with global human population growth (Estrada et al., 2017), maintaining and restoring habitat connectivity is of high conservation value (Crooks and Sanjayan, 2006). Identifying important resources that influence a species' occurrence and persistence is therefore essential for effective conservation planning and preventing biodiversity loss (Kopp et al., 1998; Mayor et al., 2009).

The relative importance of a resource to a species varies with the scale of interest (Boyce, 2006), and thus conservation/management planning is highly scale-dependent (Mayor et al., 2009). Resource Selection Functions (RSFs; Manly et al., 2002) are an invaluable tool for identifying important resources required by a species at multiple scales (Boyce, 2006; DeCesare et al., 2012). RSFs are statistical models that estimate the relative probability of use of a particular resource unit by an individual or group (Manly et al., 2002) and can be used to map distribution and connectivity across the landscape. Whilst more recent methods of modelling resource selection have been developed, such as maximum entropy (MaxEnt) models (Phillips et al., 2006), they are essentially mathematically identical (Lele et al., 2013). One important yet subtle difference between the two methods however, is that MaxEnt models are commonly applied when 'used' locations have been occupied at least once over the study period, whereas RSF models typically use telemetry data where the 'used' locations may have been occupied multiple times (Lele et al., 2013).

Due to the accessibility of radio telemetry and remotely sensed environmental data, the majority of RSF studies have focussed on wide-ranging species, particularly large carnivores (Simcharoen et al., 2008; Davidson et al., 2012; Dellinger et al., 2013; Fattebert et al., 2015; Pitman et al., 2017). Despite this, RSFs may be particularly valuable in conservation planning for small-ranging and patchily distributed species living in fragmented habitats, by identifying critical habitat both within and between fragments (Harris et al., 2008). Despite the imperilled conservation status of many of the world's primates (Estrada et al., 2017) and the resolution of data gained through habituation and follows, studies using RSFs to model resource selection in primates, rather than MaxEnt models (Thorn et al., 2009; Vidal-Garcia and Serio-Silva, 2011; Sarma et al., 2015), are almost entirely lacking (Sawyer and Brashares, 2013).

The samango monkey (*Cercopithecus albogularis, subspp*; *labiatus*, *erythrarchus*, and *schwarzi*, Dalton et al., 2015) represents Africa's most southerly arboreal guenon. Its distribution throughout South Africa is closely correlated with the distribution of indigenous forest types such as Afromontane/Mistbelt, Scarp and Coastal belt forests (Lawes, 1990a; Hayward et al., 2005), which they heavily rely on for food, protection, reproduction and recruitment (Linden et al., 2016). As with other arboreal primates, it is highly susceptible to fragmentation and human-induced landscape change due to its dependence on tall, closed-canopy forests (Chapman et al., 2000). In South Africa, natural habitats are decreasing at an alarming rate due to anthropogenic conversion of land for agriculture and urbanisation (Friedmann and Daly, 2004; Kingdon et al., 2008), meaning samango monkeys must exist in isolated or semi-isolated forest fragments with little or no connectivity between patches (Linden et al., 2016). This is further compounded by the poor dispersal capabilities of samango monkeys and their reluctance to traverse open ground (Lawes, 1992, 2002; Lawes et al., 2000).

The isolated population of samango monkeys living in the Soutpansberg mountains (*Cercopithecus albogularis schwarzi*; Dalton et al., 2015), represents the most vulnerable of the three samango monkey subspecies in South Africa and is currently listed as Endangered on the national Red-List (Linden et al., 2016). Key conservation interventions for this species identified in the Red-List assessment include protected area expansion of large forest patches and the creation and maintenance of forest corridors connecting forest patches (Swart and Lawes, 1996; Lawes et al., 2000; Linden et al., 2016), whilst also highlighting the potential role of old commercial plantations to facilitate this. Resource selection studies can therefore be used to prioritise suitable habitat which can inform management plans.

Here, we estimate samango monkey resource selection within the Soutpansberg Mountains, South Africa at multiple spatial scales according to Johnson (1980): 2nd order selection (selection within geographic range), 3rd order selection (selection within home range), and 4th order selection (selection of feeding sites within home range). Through scale-integration (Johnson et al., 2004; DeCesare et al., 2012), we then identify critical habitat for both persistence within and connectivity between subpopulations across the documented samango monkey range in Limpopo Province, South Africa (hereafter 'Limpopo').

Methods

Study area and data collection

We conducted this study within the Soutpansberg Mountains, Limpopo, South Africa (29°26'05''E, 23°02'23''S, Figure 1), which forms part of the UNESCO Vhembe Biosphere Reserve, covering an area of around 6800 km^2. The Soutpansberg Mountains represent the northwestern-most range of samango monkeys within South Africa. The mountain range experiences substantial seasonal variation in rainfall and temperature, in addition to substantial variation in elevation and water availability, resulting in a variety of vegetation types (Mostert, 2006). Whilst montane grasslands exist at higher elevations, indigenous evergreen forests (described as mistbelt; Mostert, 2006; Mucina and Rutherford, 2006) dominate the south-facing ridges as a result of direct mist precipitation and the collection of groundwater from the base of the cliffs. Further down-slope of the mistbelt forest, semi-deciduous woodland and thicket forest become more abundant, whilst riverine forests occur along the streams heading down the mountains (Hahn, 2006). These vegetation types are further fragmented by farmland and commercial plantations, whilst urban settlements become more prevalent off the mountains.

All behavioural data collection followed the Association for the Study of Animal Behaviour (ASAB) Guidelines for the Treatment of Animals in Behavioural Research and Teaching (ASAB, 2012) and complied with the University's use of Live Animals in Unregulated Research guidelines (NK_EP/2016-10). All fieldwork was approved by the Life Sciences Ethical Review Process Committee and the Department of Anthropology Ethics Committee at Durham University, UK and was conducted with approved permits from Limpopo Province Department of Economic Development and Tourism (LEDET).

Location data

Data were collected on two habituated groups of samango monkeys (*Cercopithecus albogularis schwarzi*) at the Lajuma Research Centre in the western Soutpansberg Mountains. Samango monkeys are arboreal, diurnal guenons which form single-male, multi-female groups (Henzi and Lawes, 1987) normally of around 30 individuals (Lawes et al., 2013; Coleman and Hill, 2015). Home range size typically varies between 0.15 km^2 – 0.46 km^2 depending on subspecies (Linden et al., 2016). However, group sizes at Lajuma were 30 – 40 individuals ('Barn' group) and 60 – 70 individuals ('House' group respectively), with average home range sizes of 0.56 km^2 (+/- 0.07) and 0.60 km^2 (+/- 0.13) respectively. Each group was followed for an average of 8 full days every month between 2012 – 2016, with full days defined as those where a group was followed from morning sleep site to evening sleep site without losing audio-visual contact for more than 60 minutes. GPS points of the groups' location were taken using a handheld GPS device (Garmin GPSmap 64S) every 20 minutes to coincide with scan samples to collect behavioural data (Altmann, 1974). Information collected during scan samples included individuals' general behaviour (feeding, resting, social or moving).

RSFs quantify the relative importance of a particular resource unit by comparing used resource units to those available. To reduce the potential of serial autocorrelation during analysis (Gillies et al., 2006), the sample was reduced to GPS fixes every two hours between 6am – 6pm giving a maximum of seven GPS fixes per day for each scale of analysis. We defined samango monkey 'used' locations for 2nd order (selection of ranging area) analysis as all two-hourly GPS fixes for each group from 2012 to 2015 within each group's 95% home range. This resulted in 2,315 locations for Barn group and 1,961 locations for House group. 2016 locations (Barn: 851 locations, House: 872 locations) were withheld for both groups for model validation. For 3rd order analysis (selection within home range), we defined 'used' locations as all two-hourly GPS fixes within each group's core home range (50% isopleth) to investigate disproportionate use with the home range (Meyer and Thuiller, 2006). This resulted in 1,118 (Barn) and 867 (House) locations between 2012 – 2015 and 414 (Barn) and 430 (House) locations for 2016. Finally, we defined 'used' points for 4th order analysis (selection of feeding areas) as all GPS points from scan samples where feeding occurred in over 50% of the total number of scanned individuals per 5-minute sample (using a minimum scan sample size of six individuals), within each group's 95% home range. This resulted 1,532 (Barn) and 1,794 (House) locations between 2012 – 2015 and 306 (Barn) and 479 (House) locations for 2016.

Resource Selection Function training

To model habitat selection at multiple scales we built RSFs (Manly et al., 2002) in a used-available design at the 2nd, 3rd and 4th order scales (Johnson, 1980). We defined the area available to samango monkeys for selection of ranging area (2nd order selection) as the annual minimum convex polygon (MCP) for each group plus a buffer of 4km (Figure 3.1), which represents the maximum recorded day journey length for samango monkeys on site (Parker et al., in prep.). For both selection within range (3rd order) and feeding site selection (4th order), the available area was considered to be the annual 95% home range of each group (delineated using the *a*-LoCoH home range estimation method; Ryan et al. 2006; Getz et al. 2007). To sample resource availability, we generated random points using the 'Random points inside polygon' function within the 'Research Tools' toolbox in QGIS (v2.18, QGIS Development Team, 2017) within the available area designated for each order at a 1:1 ratio of used to available locations (Koper and Manseau, 2012). Whilst it is possible that some of the 'available' locations may have in fact been used (known as pseudoabsences), deterministic selection of the available sample allows RSFs to control for this by best approximating the point process likelihood (Johnson et al., 2013). We sampled landscape variables at each used and available point using the 'Point sampling tool' plugin in QGIS. Landscape variables sampled were annual EVI (Enhanced Vegetation Index, a remotely sensed measure of productivity), terrain ruggedness, elevation and distance to rivers. We opted to use EVI in our analysis over more conventional land cover classes (obtained here from the 2014 South African National Biodiversity Institute (SANBI) national land cover map) due to the greater resolution afforded by EVI composites and the increased sensitivity and responsiveness to canopy structure and composition (Pettorelli et al., 2005).

We obtained annual EVI layers of the study area from Landsat 8 datasets from Google Earth Engine (https://earthengine.google.com) at a 30 m^2 resolution. Annual EVI represents the average productivity of a given cell across a year. We used annual EVI due to the scale of analysis, and for comparability with other studies (Sawyer and Brashares, 2013). We obtained the elevation layer from NASA's Shuttle Radar Topography Mission dataset, also downloaded from Google Earth Engine at a 30 m^2 resolution. We included elevation as an explanatory variable due to the association with different habitat types across the Soutpansberg (Mostert, 2006). Terrain ruggedness was calculated from this layer using the 'Terrain Analysis' toolbox in QGIS. Finally, 'Distance to rivers' was created by downloading the WWF HydroSHEDS Flow Accumulation layer from Google Earth Engine, converting this into a presence/absence raster, and then applying the 'Proximity' function in the 'Analysis' toolbox in QGIS. Human related variables such as 'distance to roads/settlements' were excluded from analysis due to the close proximity of the groups to both farmland and small properties on the mountain range, which would heavily bias model predictions in favour of these areas. In addition, we were not able to use a 'distance to roads' variable as this was difficult to derive from the landcover maps we obtained. Furthermore, the topography of the area means it is difficult to distinguish between tar roads (which are largely avoided) and dirt roads (which may be crossed) (B. Linden pers. com.) which again may have led to spurious results.

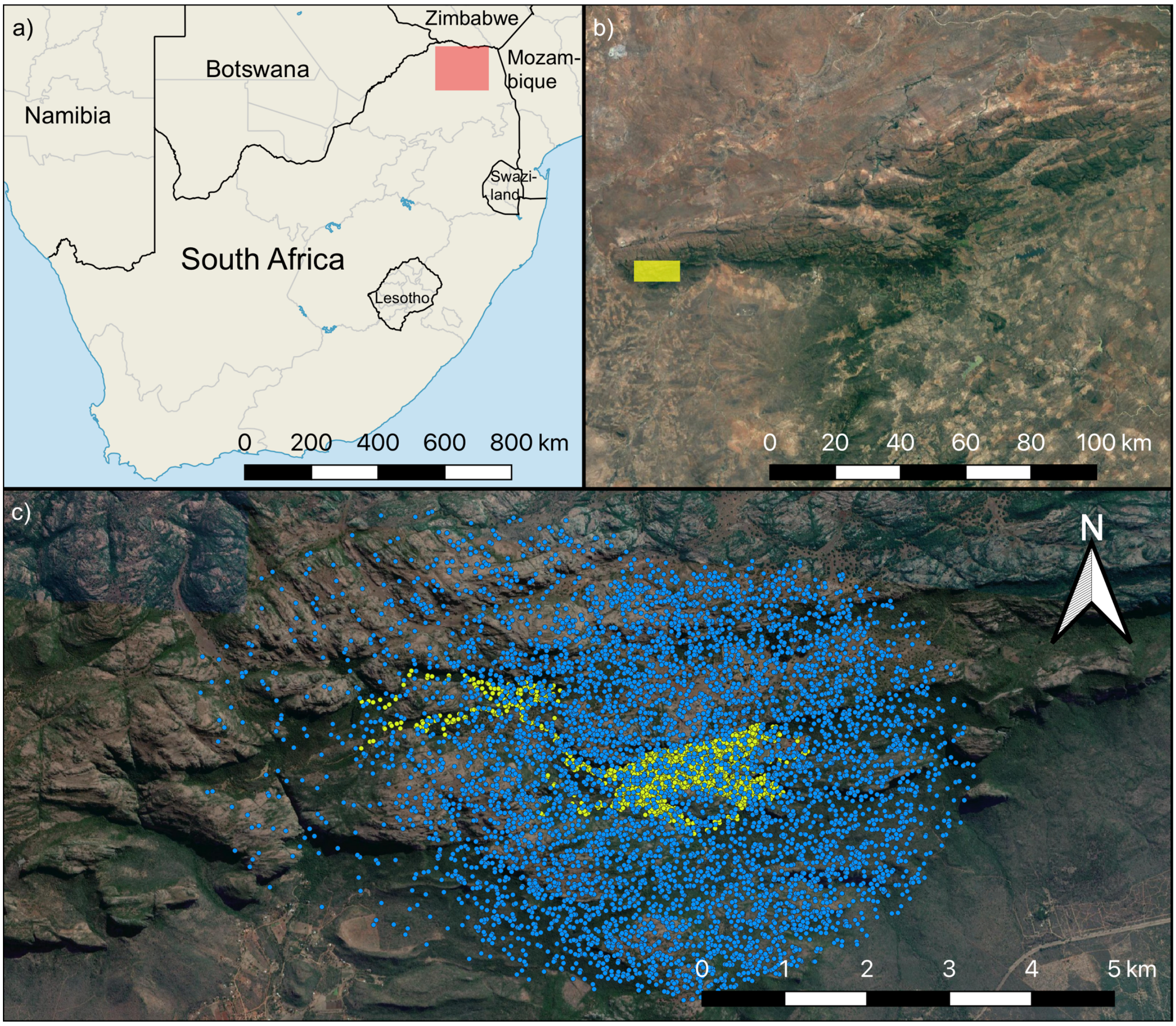

Figure 3.1: a) Location of Soutpansberg Mountains within South Africa, b) location of study area (2012 – 2016) within the western Soutpansberg Mountains, and c) resource selection function (RSF) model training points to establish selection of ranging area within the Lajuma study area. 'Barn' and 'House' group 'used' locations (yellow) were compared to randomly generated 'available' locations (blue) at a 1:1 ratio.

We designed generalised linear mixed-effects models (GLMMs) each with a binomial error structure (1; used and 0; available) and a logit link function to model annual samango monkey habitat selection at multiple scales. Analysis was carried out at the annual level for comparability with other studies (Sawyer and Brashares, 2013). We controlled for group size ('Barn/House') as this variable only has two levels and could not be included as a random variable (Bolker et al., 2008), whilst year was included as a random variable. All landscape variables sampled were included in the analysis creating a maximal model (Hurvich and Tsai, 1990). Models were fitted in R 3.4 (R Core Team, 2017) using the glmer function in the 'lme4' package (Bates et al., 2014). Model structure for each scale of analysis is given below:

use ~ ruggedness + distance to rivers + elevation + EVI + group + (1|year)

We assessed model stability by comparing the estimates of a model based on all the data with those obtained from models excluding levels of the random effects one at a time using the influence function within the 'influence.ME' package (Nieuwenhuis et al., 2012), which indicated that the models were stable. We found no evidence of collinearity between fixed effects after examining Variance Inflation Factors derived from a standard generalised linear model excluding the random effects, using the vif function within the 'car' package with a cut-off value of 2 (Hair et al., 2014). Confidence intervals were estimated using the confint function in the 'lme4' package.

RSF validation

We validated our final models using cross-validation of the withheld 2016 GPS locations of both groups, a method shown to be the most appropriate for use-availability RSF models (Johnson et al., 2006). We first projected the predicted relative probability of samango monkey use at each selection level across the study area in QGIS following Manly et al. (2002). We then reclassified raw RSF values into 10 equally sized bins (Boyce et al., 2002) and counted the frequency of 2016 used locations that fell into each bin. We used a Spearman rank correlation to test the frequencies of used locations observed in each RSF bin (Johnson et al., 2006). A significant positive correlation between RSF bin rank and frequency of used points was indicative of the predictive ability of the RSF model (Boyce et al., 2002).

RSF projection and scale-integration

The used-available designs at each scale (selection of ranging area, selection within range and feeding site selection) generate RSFs that are proportional to the probability of use (Manly et al., 2002; DeCesare et al., 2012). We spatially mapped probability of use at each order across the study area by estimating predicted RSF values per 30 m^2 pixel according to Manly et al. (2002). Predicted RSF values were scaled between 0 and 1 using a linear stretch (Johnson et al., 2004). We combined the predicted RSF values for each spatial scale to develop a scale-integrated RSF (SRSF) (Johnson et al., 2004; DeCesare et al., 2012; Pitman et al., 2017) for a given pixel and applied a linear stretch to scale RSF values between 0 and 1. To delineate critical habitat and key conservation areas to *C. a. schwarzi* across their known range within Limpopo (Linden et al., 2016), we spatially mapped habitat where probability of use was > 0.5.

Results

Cross-validation of our RSFs with the withheld 2016 points revealed a strong positive correlation between RSF bin rank and number of observed points (Spearman rank correlation: selection of ranging area: r_s, 0.92, $P<0.001$; selection within range: r_s, 0.79, $P=0.007$; selection of feeding sites: r_s, 0.83, $P=0.003$), thus demonstrating the predictive capabilities of the models in delineating probability of samango monkey use across the Soutpansberg Mountains.

Selection of ranging area

Areas of high productivity (indicated by EVI) were the most important habitat feature when establishing samango monkey home ranges (Figure 3.2a, Table 3.1), suggesting a clear preference for tall-canopy, dense forests. Elevation and distance to rivers were also important at this order, as samango monkeys established home ranges at moderate elevations and at distances further from rivers and streams.

Selection within home range

Within the home range, samango monkeys disproportionately used areas close to rivers/streams and at high elevations (Figure 3.2b, Table 3.1). Areas of low terrain ruggedness were also preferred within the home range, whilst areas of high productivity were again selected for.

Feeding site selection

When selecting feeding sites, samango monkeys strongly selected for areas of low terrain ruggedness and high elevations (Figure 3.2c, Table 3.1). Proximity to rivers/streams was again an important habitat feature at this order. In contrast to selection of ranging area and within range, habitat productivity did not influence the selection of feeding sites.

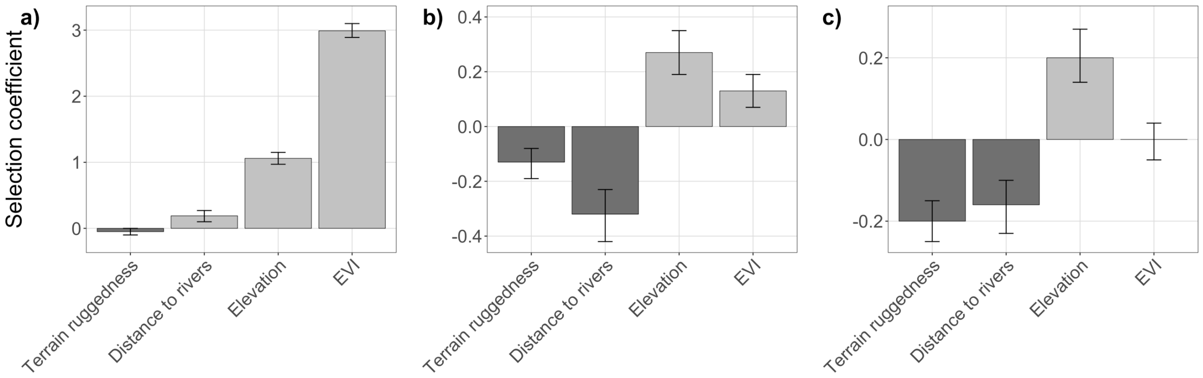

Figure 3.2. Selection coefficient estimates and 95% confidence intervals of landscape variables for selection of ranging area (a), selection within range (b) and feeding site selection (c) for samango monkeys (*C. a. schwarzi*) at Lajuma Research Centre, South Africa.

Table 3.1. Coefficient estimates and key statistics for selection of ranging area, selection within range and feeding site selection RSFs, for habitat use of samango monkeys (*C. a. schwarzi*) in the Soutpansberg Mountains, South Africa from 2012 – 2015.

Coefficient	ß	SE	CI_{lower}	CI_{higher}	*P*
Ranging area					
Intercept	-0.09	0.31	-0.85	0.66	(1)
Ruggedness	-0.05	0.03	-0.10	0.00	0.058
Distance to rivers	**0.19**	0.04	0.10	0.27	<0.001
Elevation	**1.06**	0.05	0.97	1.15	<0.001
EVI	**2.99**	0.05	2.89	3.10	<0.001
Group (House)	-0.02	0.05	-0.13	0.09	0.734
Within range					
Intercept	-0.13	0.05	-0.24	-0.03	(1)
Ruggedness	**-0.13**	0.03	-0.19	-0.08	<0.001
Distance to rivers	**-0.32**	0.05	-0.42	-0.23	<0.001
Elevation	**0.27**	0.04	0.19	0.35	<0.001
EVI	**0.13**	0.03	0.07	0.19	<0.001
Group (House)	**0.22**	0.07	0.08	0.36	0.002
Feeding site					
Intercept	-0.06	0.04	-0.13	0.01	(1)
Ruggedness	**-0.20**	0.02	-0.25	-0.15	<0.001
Distance to rivers	**-0.16**	0.04	-0.23	-0.10	<0.001
Elevation	**0.20**	0.03	0.14	0.27	<0.001
EVI	0.00	0.02	-0.05	0.04	0.875

Group (House)	0.10	0.05	0.00	0.20	0.051

EVI, enhanced vegetation index. (1) not shown because of having no meaningful interpretation.

RSF projection

Projecting the relative probability of samango monkeys establishing home ranges across the western Soutpansberg Mountains (Figure 3.3) indicated that areas of high productivity and intermediate to high elevation on the southern slopes had the highest probability of use. These areas were associated with the indigenous forest (mistbelt), woodland and thicket habitat layers from the SANBI land cover map. The apparent suitability of field and farms off the mountain was an artefact of their high EVI resulting from fertilisation and pivot irrigation.

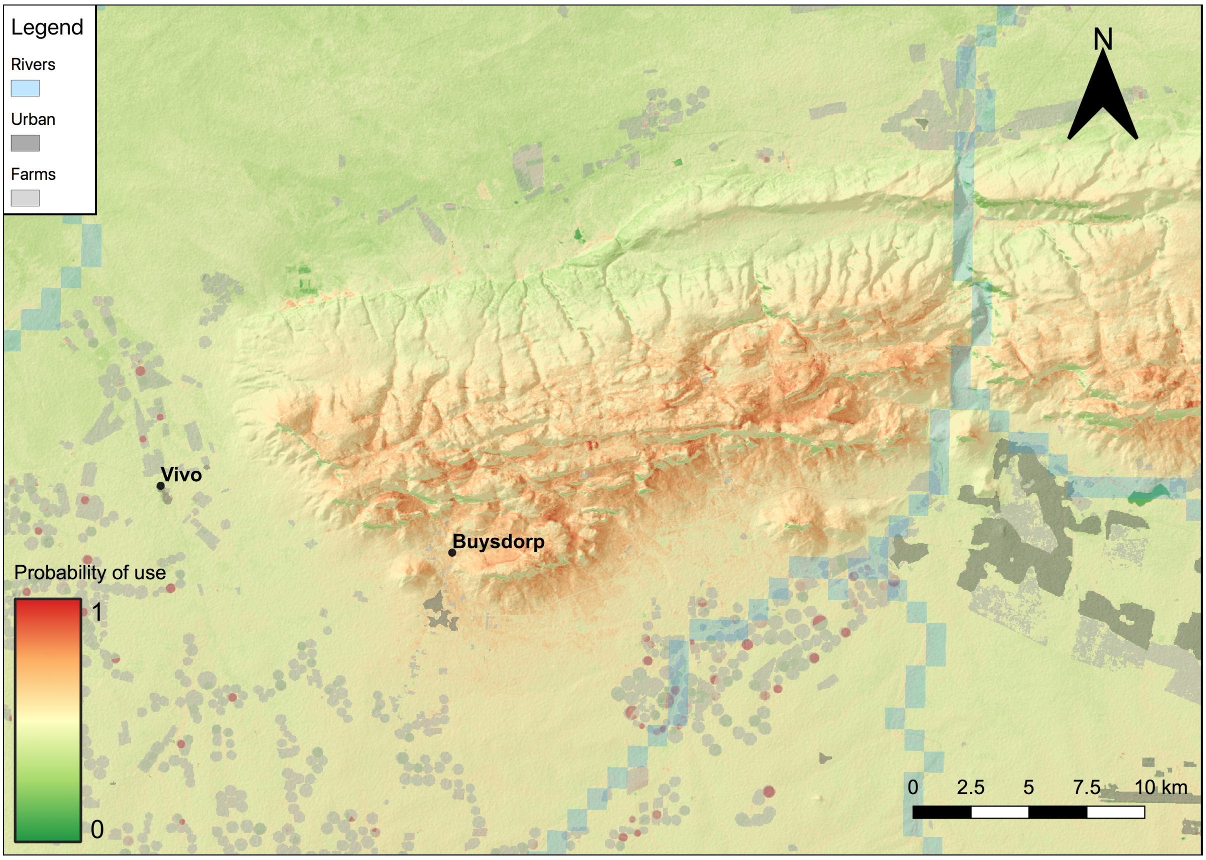

Figure 3.3. Probability of habitat selection by samango monkeys (*C. a. schwarzi*) across the western Soutpansberg Mountains, South Africa, with respect to selection of ranging area. Farms, urban settlements and rivers are also shown.

The projected scale-integrated RSF (SRSF) predicting use across the recorded *C. a. schwarzi* range identified highly productive areas occurring at intermediate to high elevations and close proximity to rivers as critical samango monkey habitat (Figure 3.4). The Blouberg, western Soutpansberg and northern Drakensberg Mountains in particular were identified as key conservation areas for samango monkeys in Limpopo. Despite the significant fragmentation and lack of connectivity between these key areas, we highlight the potential of riverine habitats and commercial plantations as possible corridors to connect fragmented subpopulations. Whilst not identified as crucial habitat, the Woodbush Forest Reserve may be particularly important for linking the Drakensberg populations in the south to the Soutpansberg populations in the north. Samango monkeys have already been recorded here (Linden et al., 2016), whilst the potential suitability of surrounding commercial plantations in facilitating movement between patches (Wimberger et al., 2017) may make this a key area for increasing connectivity between subpopulations.

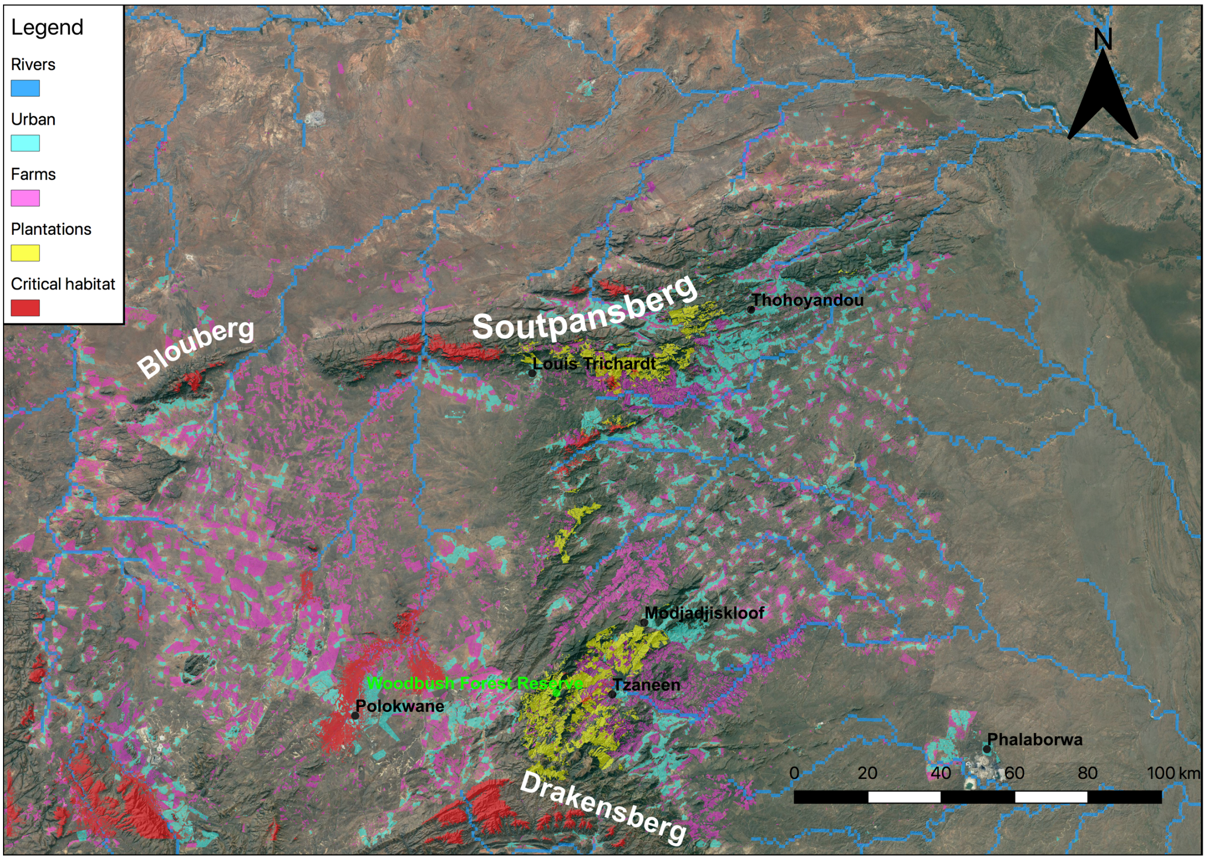

Figure 3.4. Scale-integrated RSF (SRSF) highlighting critical samango monkey habitat (probability of use > 0.5) across the Blouberg, Soutpansberg, and Drakensberg Mountains, representing the recorded range of *C. a. schwarzi* in Limpopo, South Africa. Rivers, urban settlements, farms and commercial plantations are also shown.

Discussion

This study investigated resource selection at multiple spatial scales of the endangered samango monkey in the Soutpansberg Mountains, South Africa. Through scale integration, we identified critical habitat and connectivity across the documented samango monkey range in Limpopo Province (Linden et al., 2016). We identified the habitat features that drive samango monkey resource selection whilst demonstrating that, despite being a small-ranging species, resource selection in this species is scale-specific (Boyce, 2006; DeCesare et al., 2012). We showed here that whilst habitat productivity (indicated by EVI) was the main driver predicting samango monkey distribution at the population level, proximity to rivers, elevation and terrain ruggedness became more important at finer-scales of selection. These findings highlight the importance of considering scale when understanding resource selection by a species of interest.

We found that habitat productivity was the most important habitat feature when establishing samango monkey home ranges (2nd order selection). Highly productive areas, identified through EVI, were also associated with tall-canopy, dense vegetation types from the SANBI land cover map such as the indigenous mistbelt forest, and to a lesser extent woodland and thicket, demonstrating the importance of these habitat types to samango monkeys (Lawes, 1990a; Lawes and Piper, 1992; Hayward et al., 2005). Samango monkeys rely heavily on these forest types (particularly the mistbelt forest) for food, protection, reproduction and recruitment (Linden et al., 2016; Nowak et al., 2017). As such, availability of these forests has been shown to influence their ranging patterns (Parker et al., in prep.). Although samangos can utilise matrix and non-forested habitat whilst foraging, dispersing and moving between forest patches (Lawes and Piper, 1992; Heikamp, 2008; Wimberger et al., 2017), they are ultimately restricted by access to indigenous forest patches (Nowak et al., 2017; Wimberger et al., 2017; Parker et al., in prep.). Moderate to high elevations were also important in establishing samango home ranges, most likely a consequence of the distribution of indigenous mistbelt forest occurring at these elevations on the south-facing cliffs of the mountain (Mostert, 2006). Habitat suitability decreases either side of these elevations, with montane grasslands occurring at very high elevations and woodland, thicket and farmland become more prevalent at lower elevations (Mostert, 2006). The probability of home ranges being established increased as distance to rivers increased, likely a consequence of avoiding human settlements and farmlands which occur at lower elevations and closer to rivers

(Mostert, 2006). Terrain ruggedness was not an important habitat feature at this order of selection, possibly due to the occurrence of the most suitable habitat type, the indigenous mistbelt forest, occurring on the flat south-facing plateaus of the mountain (Mostert, 2006).

Proximity to rivers and elevation were strongly selected for both within the home range (3rd order selection) and when selecting feeding sites (4th order selection). Riverine habitats are known to be an important habitat for samango monkeys (Lawes, 1992; Skinner and Chimimba, 2005; Linden et al., 2016), due to their vegetative structure and composition which includes important fruit species in the samango monkey diet (Linden et al., 2015). Similarly, selection for high elevations even at these finer scales of selection may be as an indirect result of the selection for tall-forest habitats, such as the indigenous forest, which even within the home range occurred at higher elevations and as thin strips along the south-facing cliffs of the mountains (Mostert, 2006). Since the samango monkeys rarely climbed tall cliffs, their core ranging area tended to be associated with the indigenous forest at the base of these cliffs and ranging intensity declined as they moved downslope from these areas. This was further supported by the positive selection towards EVI within the home range, which is known to correlate with tall, dense vegetation (Huete et al., 2006). The disproportionate use of highly productive areas within the home range is understandable given the location of important fruit species (Linden et al., 2015; Wimberger et al., 2017) and reduced predation risk (Coleman and Hill, 2014; Nowak et al., 2017) afforded by the tall, dense canopy in these areas, in addition to the location of sleeping trees (Coleman, 2013). Areas of low terrain ruggedness were also strongly selected for both within the home range and when selecting feeding sites, further demonstrating an avoidance of tall, steep cliffs and a preference towards the forest habitats that occur on the flat plateaus of the mountain range (Mostert, 2006).

In contrast, EVI was not important when selecting feeding sites. As samangos are able to utilise less productive matrix habitat and non-forested areas when foraging or moving between forest patches (Lawes and Piper, 1992; Skinner and Chimimba, 2005; Wimberger et al., 2017), habitat productivity may not be critical when establishing feeding sites. More importantly, samango monkeys are likely to enter low productivity (and potentially high-risk) habitats for the purpose of feeding particularly during seasonal food shortages in winter (Coleman, 2013). Since feeding levels are higher in winter this would serve to remove the link to food availability on the annual basis. Furthermore, samango monkeys are capable of incorporating large proportions of leaves into their diet owing to their gut morphology (Bruorton and Perrin, 1991), and so samangos are still capable of increasing feeding levels in areas of lower productivity by increasing the consumption of leaves (Lawes, 1990a; Skinner and Chimimba, 2005; Wimberger et al., 2017).

The SRSF predicting use across the recorded *C. a. schwarzi* range in Limpopo identified highly productive areas occurring at moderate elevations and close proximity to rivers as critical samango monkey habitat for both the persistence within and connectivity between subpopulations. Critical habitat across this range is highly fragmented although the largest, most continuous patches occur within the western Soutpansberg, Blouberg and northern Drakensberg Mountains. Despite this fragmentation, we show that riverine habitats may be important in connecting isolated patches and facilitating the persistence of subpopulations. In addition, we recognise the potential of commercial plantations in connecting patches

(Linden et al., 2016), particularly due to the ability of samangos to utilise these areas when moving between indigenous forest patches (Wimberger et al., 2017). Commercial plantations may be particularly important in connecting the Soutpansberg populations to those in the Woodbush area and further south to the Drakensberg Mountains. We also identify the Woodbush Forest Reserve and nearby areas (Modjadjiskloof and Tzaneen) as key conservation areas due to the subpopulations already existing there in large, continuous indigenous forest patches (Linden et al., 2016). In addition, the surrounding commercial plantations may be targeted in order to help connect neighbouring populations and facilitate the persistence of subpopulations in this area. On a much finer scale, highly productive matrix habitats planted with exotic species, such as residential gardens and agricultural areas, may help to increase connectivity and facilitate movement between smaller forest patches (Wimberger et al., 2017).

Samango monkey distribution across Limpopo is therefore ultimately limited by the availability of highly productive habitats occurring at moderate elevations and within close proximity to rivers. Ongoing deforestation in indigenous forest regions and riverine habitats is therefore the greatest, most immediate threat facing samango monkeys across South Africa (Lawes et al., 2000; Lawes, 2002; Linden et al., 2016). In the Soutpansberg Mountains, deforestation in indigenous mistbelt regions has resulted in the fragmentation of larger indigenous forest patches and the loss and degradation of riverine habitats acting as corridors (Armstrong and Van Hensbergen, 1996). Our SRSF delineates this fragmentation of suitable habitat across Limpopo, whilst also highlighting the lack of suitable connecting habitat linking Soutpansberg subpopulations of *C. a. schwarzi* to possible subpopulations north in Zimbabwe and east in Mozambique (Groves, 2001; Dalton et al., 2015; Linden et al., 2016). This presents a major threat to a species which is unable to re-colonise forest patches and is susceptible to local extinctions in small forest fragments (Lawes et al., 2000; Lawes, 2002). Consequently, small forest patches < 1.5 km^2 are generally unable to support samango groups due to their poor dispersal capabilities and reluctance to travel over open ground (Lawes et al., 2000). This is of particular concern to *C. a. schwarzi* which, of the three samango monkey subspecies, typically occupy the largest home ranges (Linden et al., 2016).

Loss and fragmentation of contiguous forests increases the edge effect on forest patches, bringing samangos into closer and more frequent contact with human settlements and infrastructure, increasing rates of morbidity and mortality (Linden et al., 2016). Minimising the disturbance in and around large contiguous forest patches is therefore a key management strategy for this species (Lawes et al., 2000), as is the expansion of protected areas and proper management of indigenous forests, particularly Afromontane (including mistbelt) and Scarp forests (Eeley et al., 1999; Linden et al., 2016). Current protected areas in the Soutpansberg Mountains (such as Lesheba Wilderness Reserve and Happy Rest Nature Reserve) only represent a small area and lack connectivity, whilst protection within the eastern range of the mountains is almost entirely absent. In light of our results, reclaiming and restoring non-viable areas, particularly in areas where indigenous forest previously existed, should be a priority for the management of this species (Linden et al., 2016). In addition, protection of forest corridors, including riparian habitats along rivers and streams, should also be a key focus in order to link viable habitats and facilitate samango monkey dispersal (Swart and Lawes, 1996; Linden et al., 2016). Further loss and fragmentation of suitable habitats will likely lead to a reduction in population densities and therefore threaten the long-term viability of these subpopulations (Lawes et al., 2000). On a more local scale, forest managers should be trained to reduce disturbances within forests, whilst local communities should be encouraged to plant indigenous trees, rather than exotic ones, in gardens in order to facilitate samango movement between forest patches (Linden et al., 2016). Finally, conservationists should erect bridges where roads inhibit samango movement between forest patches, in order to encourage dispersal and reduce mortality in these areas (Linden et al., 2016).

An important consideration of this study is that resource selection was modelled based on location data of two samango groups. As such, the probability of samango use could only be projected so far. One improvement therefore, would be to validate the scale-integrated projection across Limpopo with location data from other samango groups, particularly those in the eastern part of the mountain range near Thohoyandou, and in the Woodbush Forest Reserve near the Drakensburg Mountains (Linden et al., 2016). These results would also benefit from the integration of location data from other samango subspecies, such as *C. a. erythrarchus* in Kwa-Zulu Natal and *C. a. labiatus* in the Eastern Cape (Dalton et al., 2015), in order to prioritise samango habitat and inform management plans across South Africa. This will help to ensure the long-term viability of this endangered species through the protection of suitable habitat that links populations.

In summary, habitat productivity is the most important feature for samango monkey habitat selection at the population level, whilst elevation, proximity to rivers and terrain ruggedness are more important on a finer scale. Our projection of critical habitat across Limpopo highlights the fragmentation and lack of connectivity between samango monkey subpopulations (Dalton et al., 2015; Linden et al., 2016), owing largely to the anthropogenic conversion of land for agriculture and urbanisation. In order to maintain the long-term viability of this species, conservation plans should be focussed towards reclaiming and restoring areas of indigenous forest and natural corridors connecting suitable habitat, whilst minimising disturbance in and around these indigenous forest patches.

Chapter 3 summary

Our findings here show that resource and habitat use of the samango monkey is scale-specific at the species level. This chapter was specifically interested in the habitat features that influence *where* samango monkeys use space, whilst the next chapter takes this further to explore *how* samangos use space, by looking at ranging patterns and resource use at the group level.

Chapter 4

The following chapter has been submitted to the journal 'PLoS ONE'.

Access to indigenous forest patches in a fragmented landscape predicts ranging patterns in the endangered samango monkey (*Cercopithecus albogularis schwarzi*)

Abstract

Understanding the behavioural flexibility of threatened species in response to the spatiotemporal distribution of resources in fragmented habitats is increasingly important for assessing their long-term viability in an increasingly human-dominated landscape. Due to ongoing deforestation and forest fragmentation, forest-dwelling species are becoming increasingly isolated and negatively impacted. The endangered samango monkey (*Cercopithecus albogularis schwarzi*) living in the Soutpansberg Mountains, South Africa, is considered a forest specialist. Here, we explore how different measures of habitat productivity influence ranging patterns in the samango monkey. Detailed data were recorded on the monthly ranging patterns of two habituated samango monkey groups between 2012 and 2016. We used linear mixed models to explore how estimates of ground-based food availability, two measures of remotely sensed habitat productivity and indigenous forest use influenced ranging patterns in the samango monkey. We found that monthly home range size decreased as more highly productive areas (above a remotely sensed threshold) and more indigenous forest were incorporated into the home range. In addition, day journey length decreased as more highly productive areas were incorporated into the home range. In contrast, estimates of ground-based food availability and mean productivity across the home range did not influence ranging patterns. These findings highlight the dietary flexibility of the samango monkey, and that whilst samangos can utilise matrix habitat in order to acquire food resources, access to highly productive habitat and indigenous forest is crucial. Conservation efforts should therefore focus on preserving indigenous forest patches and minimising disturbance in and around these patches, whilst continuing to connect forest fragments in order to facilitate movement between patches.

Introduction

Habitat loss and fragmentation are the most significant causes of global biodiversity loss (Fahrig, 2003; Lindenmayer and Fischer, 2006). Within forest biomes, loss and fragmentation of habitat has accelerated at an unprecedented rate due to the anthropogenic conversion of land for agriculture and urbanisation (Haddad et al., 2015). Many species rely on continuous natural forest patches for foraging, reproduction and shelter. Fragmentation of these patches increases the likelihood of population declines through genetic isolation, microclimate change, decreased availability of resources (Saunders et al., 1991), increased predation risk and increased competition (Gabriel, 2013). Understanding how a species adapts to living in fragmented habitats, particularly how they respond to habitat boundaries and matrix quality, is essential to determine the extent to which they can persist in an increasingly fragmented and human-dominated landscape (Fahrig, 2007; Wilson et al., 2016).

Studies on ranging behaviour are central to behavioural ecology, as movement is key to successful foraging, mating and dispersal (Zeller et al., 2012). However, movement in fragmented landscapes is largely restricted by the availability of suitable habitat and surrounding matrix habitats (Eycott et al., 2012). Resources are often distributed unevenly in time and space across the landscape, which is exacerbated in fragmented environments. Individuals may therefore need to exploit the habitat matrix in order to obtain sufficient resources (Law and Dickman, 1998). The ability to utilise this matrix habitat therefore largely determines the susceptibility of a species to fragmentation (Fahrig, 2007).

One of the most significant advances in ecological and conservation studies has been the application of remotely sensed data, which has greatly enhanced our understanding of animal movement patterns (Kerr and Ostrovsky, 2003; Turner et al., 2003; Pettorelli et al., 2011; Neumann et al., 2015). Vegetation indices such as the Normalised Difference Vegetation Index (Tucker and Sellers, 1986) and the Enhanced Vegetation Index (Huete et al., 2002) (NDVI and EVI respectively) are well-known correlates of photosynthetic activity and have consistently been used as indicators of primary productivity (Paruelo et al., 1997), plant phenology (Justice et al., 1985) and canopy structure (Gamon et al., 1995). One of the main advantages of these vegetation indices is their ability to monitor productivity over vast geographical scales and at regular time intervals (Huete et al., 2006; Lu et al., 2015). Because of this, the majority of studies applying remotely sensed data to animal ecology have been biased towards wide-ranging species (birds: Evans et al., 2006, carnivores: Nilsen et al., 2005, ungulates: Ito et al., 2006; Leimgruber et al., 2001). In contrast, the majority of finer-scale studies typically use field-based estimates of productivity due to the increased resolution and detail afforded by these methods (Jones, 1990; Tufto et al., 1996). Despite the advantages of both of these methods, studies directly comparing their effectiveness are lacking (Gordo, 2007; Villamuelas et al., 2016; Willems et al., 2009). Furthermore, whilst the potential benefits of applying remotely sensed data to smaller-ranging species are great, particularly in fragmented habitats, studies on primates are almost entirely lacking (Zinner et al., 2002; Willems et al., 2009). Furthermore, the potential of using remotely sensed data to monitor ranging patterns in folivorous primates, or primates capable of consuming large proportions of leaves, remains hugely underutilised.

The samango monkey (*Cercopithecus albogularis subspp.*: Dalton et al., 2015) is threatened in South Africa (Linden et al., 2016), where it is becoming increasingly isolated and negatively impacted as a result of ongoing forest fragmentation and deforestation due to historic logging and the conversion of land for commercial pine (Von dem Bussche and Van der Zee, 1985) and black wattle (McMahon, 1977) forestry plantations and agriculture (Lawes, 1992; Friedmann and Daly, 2004; Kingdon et al., 2008). They are primarily arboreal and form single-male, multi-female groups (Henzi and

Lawes, 1987), averaging around 30 individuals (Lawes et al., 2013; Coleman and Hill, 2015). Being a forest specialist, its distribution is largely restricted to areas of tall-canopy, evergreen indigenous forests such as Afromontane/mistbelt, scarp and coastal belt forests (Lawes, 1990a; Skinner and Chimimba, 2005). Samango monkeys are predominantly frugivorous with fruit comprising 52 - 91% of their diet (Lawes et al., 1990; Coleman and Hill, 2015; Linden et al., 2015). However, unlike most other forest guenons samango monkeys display considerable dietary flexibility, with leaves comprising up to 44% of the diet, and insects, flowers, seeds and fungi also being consumed in smaller amounts (Coleman and Hill, 2015; Linden et al., 2015). During periods of fruit scarcity, samango monkeys are able to increase leaf consumption largely owing to their gut morphology, which facilitates the extraction of protein by breaking down cellulose in plant cell walls (Bruorton and Perrin, 1991). This dietary flexibility allows the primarily arboreal samango monkey to utilise a range of matrix habitat when foraging and moving between forest patches during periods of low fruit availability (Lawes, 1990a; Skinner and Chimimba, 2005; Wimberger et al., 2017). Despite this, they are reluctant to disperse over open ground and inhabit small and isolated forest fragments (Lawes, 1992, 2002; Lawes et al., 2000; Madisha et al., 2017).

The isolated subpopulation of samango monkeys living in the Soutpansberg Mountains (*C. a. schwarzi*; Dalton et al., 2015) is currently listed as Endangered on the national Red-List (Linden et al., 2016), and represents the most vulnerable of the three samango monkey subspecies within South Africa (Linden et al., 2016). Understanding the factors that influence ranging patterns in the samango monkey is critical for assessing the extent to which they can persist in an increasingly fragmented and human-dominated landscape. The aim of this study was to explore monthly ranging patterns of the samango monkey over a five-year study period in relation to different measures of habitat productivity. Whilst there are potentially many other factors which may influence ranging patterns, such as inter-group encounters (Isbell, 1983), weather conditions (Clutton-Brock and Harvey, 1977; Isbell, 1983), sleep site locations (Albert et al., 2011), predation (Anderson et al., 2005), location of favourite fruiting trees/water sources (Di Bitetti, 2001; Zhou et al., 2011), these are not the focus of this study and are explored elsewhere.

Given that samango monkeys incorporate a large proportion of leaves in their diet, and that remotely sensed measures of productivity can be used as indicators of leaf availability (Paruelo et al., 1997), we explored the potential of using remotely sensed data to explain ranging patterns in the samango monkey, and whether this method can more accurately predict ranging patterns compared to more commonly utilised ground-based measures of productivity. In addition, we investigated the importance of highly productive areas of the landscape on samango monkey ranging patterns, and whether these areas are independent of habitat type. We predicted that samango monkey home range size and day journey length would increase as resources become more spatially dispersed (Kaplin, 2001; Boyle et al., 2009). Given that samango monkeys can utilise matrix habitat when availability of indigenous food items is low (Wimberger et al., 2017), we predicted that home range size and day journey length would decrease when more highly productive habitat and more indigenous forest habitat was incorporated into the home range.

Methods

Study site

We conducted fieldwork as part of the Primate and Predator Project based at the Lajuma Research Centre, a privately owned property at the western edge of the Soutpansberg Mountains, South Africa (23°02’23”S, 29°26’05”E). Across the mountain range there is substantial seasonal variation with cool, dry winters (mean seasonal temperature 16°C and mean seasonal total rainfall 16 mm) and hot, wet summers (mean seasonal temperature 20°C and mean seasonal total rainfall 561 mm), resulting in substantial variation in the spatial and temporal distribution of resources (Willems, 2007). The south-facing cliffs also trap moisture resulting in small, fragmented patches of tall-canopy indigenous mistbelt (Mucina and Rutherford, 2006) and riparian forests, separated both naturally and anthropogenically by various matrix habitat including semi-deciduous woodlands, thicket, montane grasslands, farmland and residential gardens. Altitude at the field site ranges from 1150 – 1750 m.

Data collection

We followed two well-habituated groups of samango monkeys; ‘Barn’ (30 – 40 individuals) and ‘House’ (60 – 70 individuals), for an average of eight full days every month over a period of five years between February 2012 and December 2016. Full days were defined as days where a group was followed from morning sleep site to evening sleep site, without losing audio-visual contact for more than 60 minutes. This resulted in 105 sample months across the two groups, with 72 months containing eight full days or more. Only months containing a minimum of eight full days were used in subsequent analyses. Gaps in the data occurred between August – September 2013 ('Barn'), February – April 2012 and August – November 2013 ('House' group respectively). During each full day, we collected instantaneous scan samples (Altmann, 1974) on as many individuals as possible within a five-minute window, at 20 minute intervals (e.g. 12:20, 12:40, 13:00) on a handheld PDA (Psion Teklogix Workabout Pro 3). Information collected during each scan sample and used in this study included: date, time, group ID, general behaviour (e.g. feeding) and specific behaviour (e.g. foraging). In addition, a GPS point (Garmin GPSmap 64S) of the group's location was also taken with each scan sample to an accuracy of within 5 m, resulting in 113,373 locations for 'Barn' group and 113,458 locations for 'House' group.

All behavioural data collection followed the Association for the Study of Animal Behaviour (ASAB) Guidelines for the Treatment of Animals in Behavioural Research and Teaching (ASAB, 2012) and were covered by the Liverpool John Moores University's use of Live Animals in Unregulated Research Protocol (NK_EP/2016-10). All fieldwork was approved by the Life Sciences Ethical Review Process Committee and the Department of Anthropology Ethics Committee at Durham University, UK and was conducted with approved permits from Limpopo Province Department of Economic Development and Tourism (LEDET).

Environmental monitoring in the field

We counted the number of leaves, fruit and seed pods for 20 individually marked trees of 24 different species (480 trees in total) within the first two weeks of every month, over the five-year study period. Trees were selected to give a representation of various habitat types, whilst also being considered important feeding trees for samango monkeys (Coleman, 2013; Linden et al., 2015). Items were counted on an individually marked branch on each tree, and then scaled up to give an estimate for each tree based on the estimated number of branches for that tree. Where there were no items on the marked branch but items on the tree, either the total number of items were counted on the tree where possible, or estimates were made for the whole tree based on the number of items on another branch and the estimated number of branches for that tree. In addition, we used randomly generated 5 m^2 vegetation plots across the study area (n = 702) and identified all trees with a diameter at breast height > 10 cm at a height of 1 m where possible.

Remote sensing of the environment

We downloaded monthly EVI composites for the entire Soutpansberg Mountains across the study period from the Landsat 7 & 8 databases from Google Earth Engine (https://earthengine.google.com), to a resolution of 30 m^2. Monthly composites were used for comparability with the scale of other food availability estimates. EVI represents the difference in Earth surface reflectance patterns between the red and near-infrared parts of the electromagnetic spectrum, whilst taking into account the reflectance of the blue band (Eidenshink and Faundeen, 1994). Values range from - 1.0 (indicating non-vegetated areas) to + 1.0 (densely vegetated areas) (Huete et al., 2002). We used EVI in this analysis as this method is more sensitive to changes in areas of high biomass, canopy differences, canopy structure and plant phenology when compared to other vegetation indices such as NDVI (Huete et al., 2002); factors which make this a more reasonable measure when exploring ranging patterns in forest-dwelling species.

Home range and day journey length calculation

Utilisation distributions delineating home ranges were calculated using adaptive localised convex hulls (*a*-LoCoH) analysis (Getz and Wilmers, 2004; Getz et al., 2007), due to its superior ability of dealing with hard boundaries and its compatibility of coping with temporally close data points compared to other home range estimation methods (Getz and Wilmers, 2004; Ryan et al., 2006; Getz et al., 2007). Home ranges were created within the ‘*t*-LoCoH’ package (Lyons et al., 2013) in R 3.4 (R Core Team, 2017), using the maximum distance between monthly GPS points for each group as the *a*-value to allow correct construction of isopleths (Getz et al., 2007). Home ranges (in km^2) for each group were calculated on a monthly basis, with total home range size delineated by the 95% volume isopleth (Silverman, 1986; Worton, 1989), and core home range size delineated by the 50% volume isopleth (Börger et al., 2006; Getz et al., 2007). Monthly home ranges were then loaded into QGIS 2.18 (QGIS Development Team, 2017) to derive productivity estimates. Monthly mean day journey length (DJL) was calculated by summing the straight-line distance (in km) between sequential GPS points across a full day and averaging across DJLs for each month in R.

Food availability estimates

To calculate the monthly estimates of food availability for each food item, we averaged the total number of leaves, fruit and seed pods counted for each tree per month (n = 20) across each species (n = 24), giving a monthly mean value per food item per species across the study period. This value was then multiplied by the estimated number of trees per species within each group's combined total annual home range, to give a monthly food availability estimate per food item per species. Total food availability per food item was then calculated by summing the estimates for that item across the 24 tree species. The estimated number of trees within each group's range was calculated by dividing the total combined area of each group's annual home range by the area of a veg plot (5 m^2), and then multiplying this figure by the mean number of trees per species across all the vegetation plots (n = 702). In addition, we calculated the total food availability for the top five most commonly consumed food items per species (which respectively contributed over 60 % of the samango diet) to determine the influence of commonly consumed food items on ranging patterns. To do this we summed the total number of scans recorded feeding and foraging on a particular food item of a particular species and then calculated this as a proportion of the total number of scans recorded feeding/foraging over the study period, and took the top five species of each item from this list. Finally, we summed the total monthly food availability estimate per food item for each of the top five most consumed food species to give an estimate of the monthly availability of the most commonly eaten food items. The most commonly consumed species of seeds only comprised of four species as these were the only species eaten with any regularity across the study period, and so only four species were used in this estimate.

Home range productivity and indigenous forest estimates

Monthly EVI composites where cloud cover did not impede the study area by > 30% were used in all analyses. For months where cloud cover was > 30%, we selected the clearest image from the 16-day EVI composites. Composites were loaded in QGIS and mean EVI values within the 95% and 50% home range were extracted using the 'zonal statistics' plugin. EVI was run with a zero, one and two-month time lag in subsequent analyses to allow for any possible lag in food availability predicted by these remotely sensed measures. EVI values for months where data was missing completely were estimated using linear regression between EVI values and month (coded as a numeric variable), with a quadratic term (month^2) for each year respectively. Whilst estimating missing values in this way doesn't account for other factors that predict variation in EVI (e.g. ecological or physical factors), only 11 out of 118 samples months were missing and, as such, estimated values are likely to be representative. Additionally, as mean productivity across the home range may not precisely match the availability of productive habitat, we measured the proportion of highly productive remotely sensed cells within each group's home range. To do this we clipped EVI rasters by values > 0.5 within the home range using the 'Raster Calculator', a value which represents dense vegetation (Huete et al., 2006). Finally, to calculate the proportion of home range that included indigenous forest, we used the 'indigenous forest' layer of the 2014 SANBI South African national landcover map (30 m^2 resolution) and calculated this as a proportion of each monthly home range using the 'LecoS' (Landscape ecology Statistics) plugin in QGIS (Jung, 2016). The SANBI 'indigenous' forest layer is derived from a combination of seasonal maximum NDVI values (from images taken between April 2013 and April 2014), forest biome boundaries (from the SANBI database), and shadow and altitude terrain parameters (from NASA's Shuttle Radar Topography Mission database).

Statistical analysis

We used linear mixed-effects models with a Gaussian error structure to determine the effects of habitat productivity and indigenous mistbelt forest use on the ranging patterns of samango monkeys. For each of the home range variables (total home range, core home range and day journey length), separate models assessed the effect of productivity (remotely sensed, field sampled and highly productive cells) and proportion of indigenous forest incorporated into the home range. We included day length (calculated using the daylength function in R), number of days sampled and group as control variables, as the number of daylight hours (Hill et al., 2003) and group size (Takasaki, 1981) are known to influence ranging patterns, whilst more sample days per month is likely to create larger home range estimates. Month and year were included as random variables. Models were fitted in R 3.4 (R Core Team, 2017) using the lmer function of the 'lme4' package (Bates et al., 2014). We checked for normality and homogeneity of residuals by visually inspecting histograms and qqplots of the residuals, and the residuals plotted against fitted values. Collinearity between fixed effects were inspected using Variance Inflation Factors (VIF) from the vif function within the 'car' package. VIF values were derived from a standard linear model excluding the random effects, with all values < 1.5 indicating no collinearity between variables (Hair et al., 2014). *P*-values for the individual effects were based on likelihood ratio tests comparing the full with respective reduced models dropping one fixed effect at a time (R function drop1), with significance inferred at the 5% level. To allow for likelihood ratio tests we fitted the models using Maximum Likelihood (Bolker et al., 2008), and used Akaike's Information Criterion (Burnham and Anderson, 2002) to infer goodness of fit between separate models.

Results

Annual mean home ranges were similar between the two groups ('Barn': 0.56 km^2 (+/- 0.07) and 'House': 0.60 km^2 (+/- 0.13)). Delineation of the home ranges showed substantial variation in both size and location of both groups' ranges (Figure 4.1), and demonstrates the reluctance of samango monkeys to traverse large open areas whilst using thin forest corridors to connect parts of the home range.

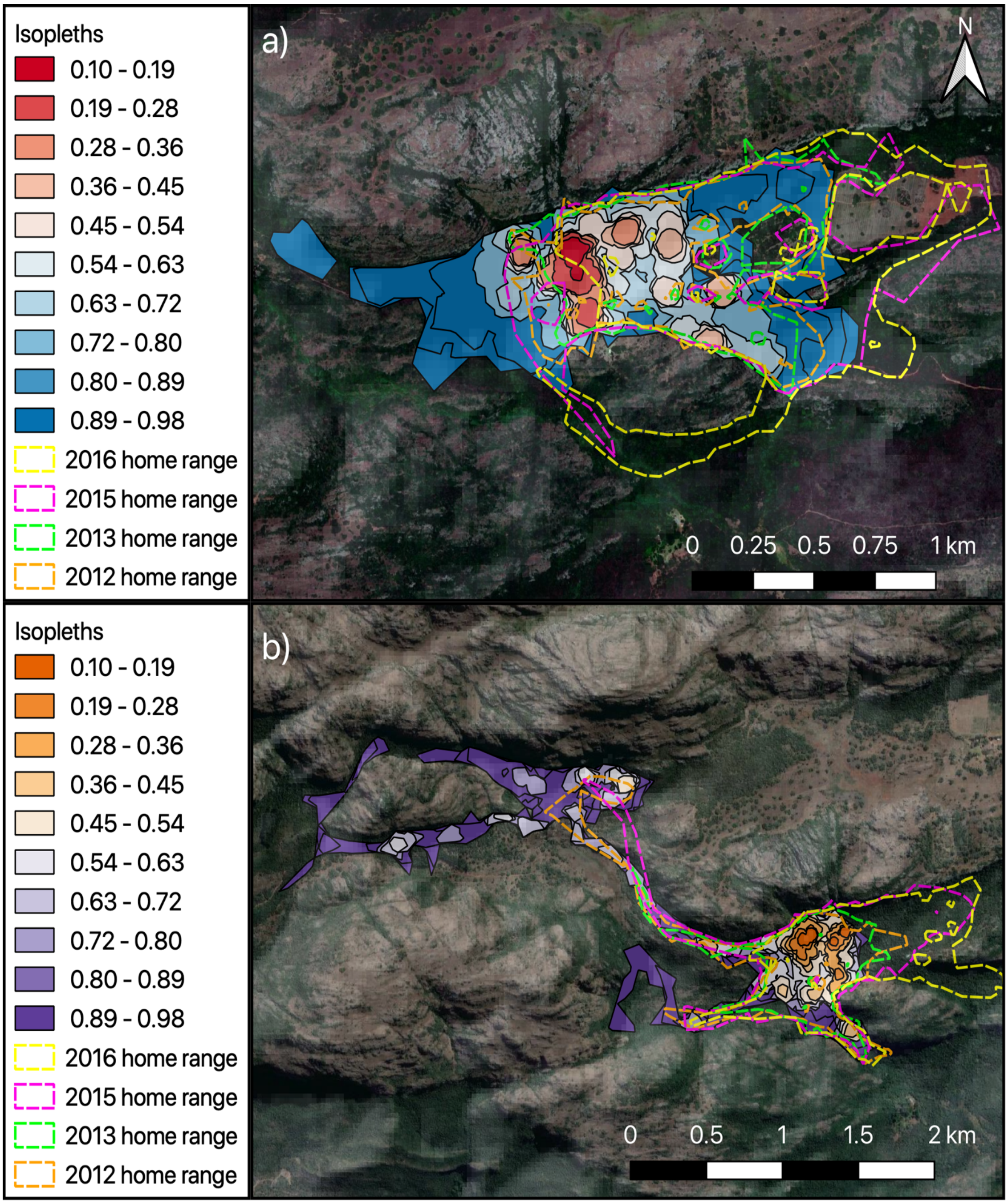

Figure 4.1. Annual utilisation distributions (UDs) showing the variation in home range size and location for both 'Barn' (a) and 'House' (b) groups at Lajuma Research Centre, Soutpansberg Mountains, South Africa. UDs are shown for 2014, which were the largest annual ranges recorded for both groups, with outlines of UDs from other years shown for comparison. Total home range is delineated as isopleths ≤ 0.98. Core home range is delineated as isopleths ≤ 0.5.

Effect of habitat productivity on ranging patterns

There was no effect of total food availability (Table 4.1) or the availability of most commonly eaten food items (Table 4.2) on monthly home range size or mean monthly DJL. There was no effect of mean productivity across the home range (indexed by EVI) on either monthly home range size or mean monthly DJL (Table 4.3). This also held when introducing a one and two-month time lag into the analysis to account for possible delays in food availability (Appendix Table 1). Whilst mean productivity across the home range did not influence ranging patterns, we found that the proportion of highly productive remotely sensed cells within the home range was significantly associated with a decrease in both monthly total home range and mean monthly DJL (Table 4.4). However, the proportion of highly productive cells within the home range did not correlate with monthly core home range size.

Table 4.1. Coefficient estimates and key statistics of models predicting effect of total food availability on total home range size, core home range size, and day journey length.

Variable	Estimate	SE	CI_{lower}	CI_{upper}	*t*-value	*P*
HR^{tot}						
Intercept	0.268	0.153	-0.041	0.600	(1)	(1)
$Leaves^{tot}$	-0.013	0.011	-0.036	0.009	-1.230	0.241
$Fruit^{tot}$	-0.006	0.008	-0.021	0.009	-0.816	0.416
$Seeds^{tot}$	-0.005	0.008	-0.022	0.012	-0.603	0.551
Daylength	-0.005	0.012	-0.032	0.020	-0.435	0.664
Days	**0.007**	0.002	0.003	0.012	3.100	0.003
Group	-0.006	0.013	-0.032	0.020	-0.451	0.653
HR^{core}						
Intercept	0.128	0.052	0.022	0.243	(1)	(1)
$Leaves^{tot}$	-0.006	0.004	-0.014	0.002	-1.576	0.146
$Fruit^{tot}$	-0.001	0.003	-0.006	0.005	-0.192	0.847

Seeds^{tot}	-0.003	0.003	-0.010	0.003	-1.109	0.284
Daylength	-0.006	0.004	-0.015	0.003	-1.309	0.195
Days	0.001	0.001	0.001	0.003	1.027	0.329
Group	-0.001	0.005	-0.001	0.004	-0.146	0.885
DJL						
Intercept	-0.220	0.266	-0.747	0.317	(1)	(1)
Leaves^{tot}	0.020	0.025	-0.032	0.071	0.774	0.450
Fruit^{tot}	-0.018	0.020	-0.057	0.021	-0.910	0.364
Seeds^{tot}	-0.002	0.021	-0.045	0.041	-0.108	0.915
Daylength	**0.138**	0.022	0.094	0.181	6.344	<0.001
Days	0.009	0.007	-0.005	0.022	1.323	0.208
Group	-0.009	0.034	-0.077	0.059	-0.268	0.789

HR^{tot}, total monthly home range size; HR^{core}, core monthly home range size; DJL, mean monthly day journey length. Leaves^{tot}, total availability of leaves; fruit^{tot}, total availability of fruit; seeds^{tot}, total availability of seed pods. (1) not shown because of having no meaningful interpretation.

Table 4.2. Coefficient estimates and key statistics of models predicting effect of availability of most commonly eaten food items on total home range size, core home range size, and day journey length.

Variable	Estimate	SE	CI$_{lower}$	CI$_{upper}$	*t*-value	*P*
HR^{tot}						
Intercept	0.291	0.153	-0.024	0.623	(1)	(1)
Leaves^{com}	-0.011	0.011	-0.034	0.012	-1.023	0.329
Fruit^{com}	-0.005	0.007	-0.020	0.010	-0.673	0.502
Seeds^{com}	-0.005	0.008	-0.022	0.012	-0.603	0.554
Daylength	-0.007	0.013	-0.034	0.019	-0.572	0.568
Days	**0.007**	0.002	0.002	0.012	2.840	0.006
Group	0.003	0.015	-0.026	0.032	0.183	0.857
HR^{core}						
Intercept	0.124	0.051	0.020	0.237	(1)	(1)
Leaves^{com}	-0.007	0.004	-0.015	0.001	-1.758	0.103
Fruit^{com}	0.001	0.003	-0.005	0.007	0.336	0.738
Seeds^{com}	-0.004	0.003	-0.010	0.003	-1.153	0.271
Daylength	-0.005	0.004	-0.014	0.003	-1.266	0.213
Days	0.001	0.001	-0.001	0.003	0.815	0.431
Group	0.003	0.006	-0.009	0.014	0.491	0.630

DJL						
Intercept	-0.365	0.251	-0.861	0.130	(1)	(1)
Leaves^{com}	-0.016	0.023	-0.061	0.029	-0.705	0.483
Fruit^{com}	-0.023	0.019	-0.061	0.015	-1.217	0.225
Seeds^{com}	-0.013	0.021	-0.056	0.029	-0.626	0.535
Daylength	**0.150**	0.020	0.110	0.190	7.464	<0.001
Days	0.007	0.007	-0.007	0.021	1.033	0.321
Group	0.012	0.037	-0.062	0.086	0.316	0.753

HR^{tot}, total monthly home range size; HR^{core}, core monthly home range size; DJL, mean monthly day journey length. Leaves^{com}, availability of top five most commonly eaten leaves; fruit^{com}, availability of top five most commonly eaten fruit; seeds^{com}, availability of top five most commonly eaten seed pods. (1) not shown because of having no meaningful interpretation.

Table 4.3. Coefficient estimates and key statistics of models predicting effect of mean EVI across the home range on total home range size, core home range size, and day journey length.

Variable	Estimate	SE	CI$_{lower}$	CI$_{upper}$	*t*-value	*P*
HR^{tot}						
Intercept	0.387	0.155	0.062	0.719	(1)	(1)
EVI	0.057	0.059	-0.062	0.177	0.958	0.346
Daylength	-0.018	0.013	-0.047	0.010	-1.346	0.187
Days	**0.008**	0.002	0.003	0.013	3.410	0.001
Group	-0.005	0.013	-0.031	0.021	-0.385	0.701
HR^{core}						
Intercept	0.166	(1)	0.054	0.054	(1)	(1)
EVI	0.015	0.406	0.023	-0.031	0.061	0.524
Daylength	-0.009	3.648	0.005	-0.020	0.000	0.056
Days	0.001	1.128	0.001	-0.001	0.003	0.288
Group	-0.001	0.016	0.005	-0.011	0.010	0.900
DJL						
Intercept	-0.294	0.231	-0.750	0.163	(1)	(1)
EVI	-0.085	0.133	-0.351	0.184	-0.636	0.532
Daylength	**0.148**	0.021	0.105	0.190	6.960	<0.001
Days	0.007	0.007	-0.006	0.021	1.125	0.284
Group	-0.007	0.034	-0.075	0.061	-0.208	0.836

HR^{tot}, total monthly home range size; HR^{core}, core monthly home range size; DJL, mean monthly day journey length. EVI, mean enhanced vegetation index within the total monthly home range. (1) not shown because of having no meaningful interpretation.

Table 4.4. Coefficient estimates and key statistics of models predicting effect of proportion of highly productive cells within the home range on total home range size, core home range size, and day journey length.

Variable	Estimate	SE	CI_{lower}	CI_{upper}	*t*-value	*P*
HR^{tot}						
Intercept	0.320	0.131	0.044	0.600	(1)	(1)
Productive cells	**-0.006**	0.003	-0.011	-0.001	-2.309	0.029
Day length	-0.005	0.011	-0.029	0.018	-0.451	0.652
Days	**0.007**	0.002	0.002	0.011	2.815	0.006
Group	-0.005	0.013	-0.031	0.021	-0.400	0.690
HR^{core}						
Intercept	0.151	0.047	0.051	0.256	(1)	(1)
Productive cells	-0.001	0.001	-0.003	0.001	-1.086	0.323
Day length	-0.007	0.004	-0.016	0.002	-1.636	0.110
Days	0.001	0.001	-0.001	0.003	0.826	0.419
Group	-0.001	0.005	-0.011	0.010	-0.121	0.904
DJL						
Intercept	-0.321	0.219	-0.754	0.112	(1)	(1)
Productive cells	**-0.013**	0.006	-0.024	-0.001	-2.156	0.033
Day length	**0.157**	0.019	0.119	0.194	8.300	<0.001
Days	0.005	0.007	-0.008	0.019	0.821	0.429
Group	-0.005	0.034	-0.071	0.062	-0.135	0.893

HR^{tot}, total monthly home range size; HR^{core}, core monthly home range size; DJL, mean monthly day journey length. (1) not shown because of having no meaningful interpretation. Productive cells, proportion of highly productive remotely sensed cells within the total monthly home range.

Effect of proportion of home range including indigenous forest

The proportion of home range that was indigenous forest was significantly associated with a decrease in both monthly total and core home range size (Figure 4.2, Table 4.5), with smaller home range sizes increasingly focussed on indigenous forest. However, the proportion of home range containing indigenous forest was not related to mean monthly DJL.

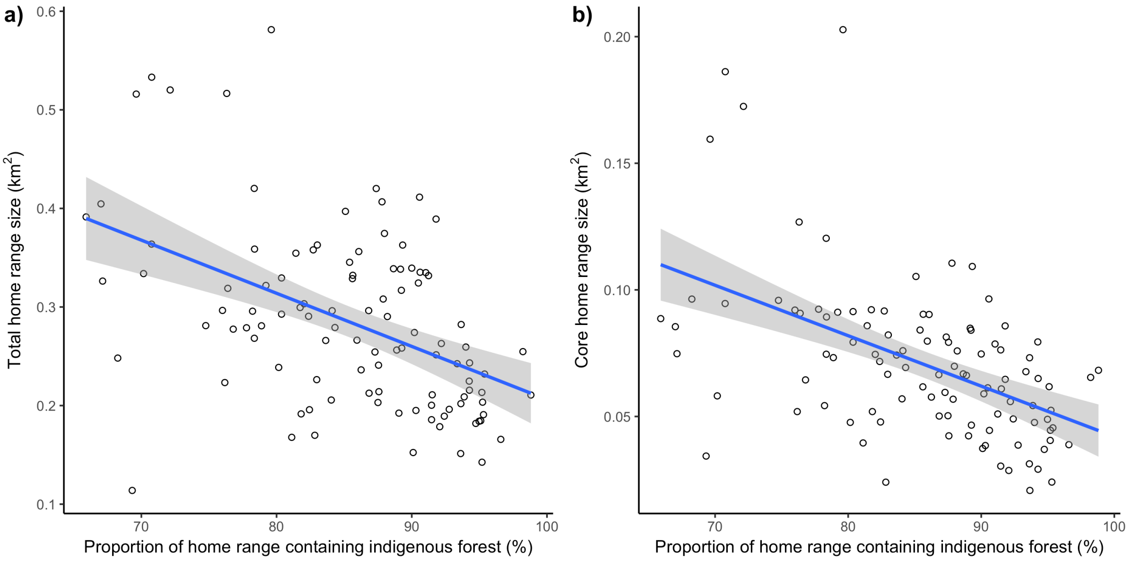

Figure 4.2. Effect of proportion of home range including indigenous forest on total home range size (a) and core home range size (b).

Table 4.5. Coefficient estimates and key statistics of models predicting effect of proportion of home range containing indigenous forest on total home range size, core home range size, and day journey length.

Variable	Estimate	SE	CI_{lower}	CI_{upper}	*t*-value	*P*
HR^{tot}						
Intercept	0.564	0.141	0.264	0.854	(1)	(1)
Forest	**-0.004**	0.001	-0.006	-0.002	-4.237	<0.001
Day length	-0.004	0.011	-0.027	0.019	-0.357	0.722
Days	**0.007**	0.002	0.003	0.012	3.413	0.001
Group	0.008	0.013	-0.016	0.034	0.677	0.502
HR^{core}						
Intercept	0.248	0.047	0.149	0.344	(1)	(1)

Forest	**-0.002**	0.000	-0.002	-0.001	-4.780	<0.001
Day length	-0.004	0.004	-0.012	0.003	-1.178	0.248
Days	0.001	0.001	-0.001	0.002	0.984	0.335
Group	0.005	0.005	-0.004	0.015	1.101	0.277
DJL						
Intercept	-0.038	0.256	-0.545	0.468	(1)	(1)
Forest	-0.004	0.002	-0.009	0.001	-1.618	0.110
Day length	**0.149**	0.018	0.113	0.186	8.124	<0.001
Days	0.009	0.006	-0.004	0.022	1.369	0.192
Group	0.008	0.035	-0.062	0.077	0.218	0.828

HR^{tot}, total monthly home range size; HR^{core}, core monthly home range size; DJL, mean monthly day journey length. (1) not shown because of having no meaningful interpretation. Forest, proportion of home range containing indigenous forest.

The proportion of home range containing indigenous forest was also significantly positively correlated with the proportion of highly productive cells within the home range (likelihood ratio test: $t = 4.20$, df = 1, $P < 0.001$), suggesting that these highly productive cells are disproportionately found within this habitat type. Proportion of home range containing indigenous forest best explained variation in home range size compared to remotely sensed and field sampled estimates of productivity, based on log likelihood ratio tests and model information criterion. In addition, proportion of highly productive cells is a better predictor of total home range size and DJL than both EVI and field sampled estimates of productivity for this species (Table 4.6).

Table 4.6. Candidate model set and model selection results for total home range size, core home range size and day journey length.

Ranging variable	Model	Fixed effects	LogLik	ΔLogLik	AIC	ΔAICc	*w*
Total home range	5	Proportion istbelt + Day length + Days + Group	133.3	7.8	-250.5	-17.4	1.00
	4	Highly productive cells + Day length + Days + Group	127.5	2.0	-238.9	-5.8	0.00
	1	EVI + Day length + Days + Group	125.5	0.0	-235.1	-2.0	0.00
	2	Total leaves + Total fruit + Total seeds + Day length + Days + Group	126.0	0.5	-232.0	-0.2	0.00
	3	Common leaves + Common fruit + Common seeds + Day length + Days + Group	125.9	0.4	-231.8	0.0	0.00
Core home range	5	Indigenous forest + Day length + Days + Group	236.3	9.9	-456.5	-20.3	1.00
	4	Highly productive cells + Day length + Days + Group	226.7	0.3	-437.4	-1.2	0.00
	1	EVI + Day length + Days + Group	226.4	0.0	-436.9	-0.7	0.00
	3	Common leaves + Common fruit + Common seeds + Day length + Days + Group	227.7	1.3	-435.5	-0.6	0.00
	2	Total leaves + Total fruit + Total seeds + Day length + Days + Group	227.5	1.1	-434.9	0.0	0.00
Day journey length	4	Highly productive cells + Day length + Days + Group	31.3	1.5	-46.6	-5.7	0.61
	5	Indigenous forest + Day length + Days + Group	30.3	0.5	-44.6	-3.7	0.23
	1	EVI + Day length + Days + Group	29.2	-0.6	-42.4	-1.5	0.08
	3	Common leaves + Common fruit + Common seeds + Day length + Days + Group	30.1	0.3	-40.3	-0.7	0.05
	2	Total leaves + Total fruit + Total seeds + Day length + Days + Group	29.8	0.0	-39.6	0.0	0.03

LogLik, log likelihood; ΔLogLik, difference in log likelihood compared to the best model; AIC_C, Akaike information criterion corrected for small sample size; ΔAIC_c, difference in AIC_c compared to the best model; w, Akaike weight.

EVI, enhanced vegetation index; highly productive cells, proportion of highly productive cells within the home range; indigenous forest, proportion of home range containing indigenous forest; common leaves, fruit and seeds, availability of most commonly eaten leaves, fruit and seeds respectively.

Discussion

Understanding how a species responds to the spatiotemporal distribution of resources in fragmented habitats is increasingly important for assessing their long-term viability (Fahrig, 2007; Wilson et al., 2016). Here, we investigated the effects of different measures of resource availability on the ranging patterns of the endangered samango monkey in the Soutpansberg Mountains, South Africa. We found that total home range size and DJL decreased as more highly productive remotely sensed cells were incorporated into the home range. In addition, both total and core home range size decreased as more indigenous forest was incorporated into the home range. These findings suggest that samango monkeys are capable of utilising the habitat matrix and non-forested patches due to their dietary flexibility (Coleman and Hill, 2015), but that access to natural patches of indigenous forest is key to samango monkey ranging patterns.

We found no effect of total food availability or availability of the top five most commonly eaten food items on home range size or DJL. Whilst samango monkeys are predominantly frugivorous (Lawes, 1991; Skinner and Chimimba, 2005; Linden et al., 2015), they show a large degree of dietary flexibility, with leaves, seeds, flowers, insects and even exotic species contributing to the samango diet (Coleman and Hill, 2015; Linden et al., 2015; Wimberger et al., 2017). In addition, samangos at Lajuma are also frequently recorded eating grasses, herbs, tree sap, roots, moss and fungi (pers. obs.), even when preferred fruits are available. As such, samangos may not need to range further into non-preferred habitats in order to find high-quality food items when availability of commonly consumed food items is low; instead they can exploit a range of food items in preferred habitats and surrounding matrix habitat which are readily available and easily located (Hemingway and Bynum, 2005). Due to the clumped and patchy distribution of fruiting trees across Lajuma (Coleman, 2013), it further pays to be flexible when commonly eaten fruits are available in order to reduce competition for access to food patches (Peng-Fei et al., 2015), particularly given the large group sizes of samangos.

We found no relationship between mean productivity across the home range (indexed by EVI) and either home range size or DJL. Similar to food availability, mean productivity across the home range is likely an uninformative measure when exploring ranging patterns, as the home range is likely to incorporate areas of lower productivity which samangos rarely access or only use as corridors to more productive areas (Lawes, 2002). As a consequence, mean values may mask areas or periods of high productivity. Willems et al. (2009) similarly found no correlation between maximum NDVI across the home range and core home range size in vervet monkeys (*Chlorocebus pygerythrus*) at the same field site, but found a negative association between DJL and maximum NDVI. However unlike samangos, vervets are not predominantly forest-dwelling (Willems and Hill, 2009) and so daily ranging patterns may be suitably explained by productivity across the home range, as vervets are more capable of utilising open habitats which are largely inaccessible to samangos.

Whilst mean productivity across the home range was uninformative, we found that both total home range size and DJL significantly decreased as the proportion of highly productive remotely sensed cells within the monthly home range increased. As this measure of productivity was derived from EVI, a measure of primary productivity (Paruelo et al., 1997), these highly productive cells are therefore indicative of the most densely vegetated areas of the home range. Whilst these areas might also contain important fruit species (Wimberger et al., 2017), the ability of samangos to incorporate a large proportion of leaves in their diet may serve to reduce some aspects of ranging patterns by incorporating more of these highly productive areas into the home range. The lack of relationship observed with core home range is likely a result of the consistency in the spatial and temporal availability and distribution of highly productive habitat in these areas, in addition to the location of important resources such as sufficient sleeping trees (Kaplin, 2001). We also found that the proportion of highly productive cells and indigenous forest within the home range were positively correlated, indicating that the most productive areas of the landscape are disproportionately found within the indigenous forest.

We found that both total and core home range size significantly decreased as more indigenous forest was incorporated into the home range. Reliance on fragments of natural forest is commonly observed in frugivorous species such as bats and primates (Ripperger et al., 2015), which typically reduce their ranging area by incorporating more natural forest fragments into the home range (Chaverri et al., 2007; Palminteri and Peres, 2012; Campera et al., 2014). Similarly, our results demonstrate the importance of the indigenous forest as a highly productive habitat to samango monkeys and that in order to live at reasonable population densities, samangos must have access to indigenous forest patches (Linden et al., 2016). These forests are key for samango monkey reproduction and recruitment (Linden et al., 2016), and are perceived as safer habitats by samangos (Coleman and Hill, 2014; Nowak et al., 2017). As a result, the majority of sleeping trees, which are typically the tallest trees in the home range, are disproportionately found within these tall-canopy forests. The indigenous forest also contains important indigenous fruits such as figs (Linden et al., 2015), which contribute significantly to the samango diet (Coleman, 2013; Linden et al., 2015). Indeed, samango monkeys in the Eastern Cape preferentially forage on indigenous fruits and seeds when available regardless of the availability of exotic species (Nowak et al., 2017; Wimberger et al., 2017). However, whilst samangos at Lajuma are capable of exploiting the surrounding matrix, access to indigenous forest patches is clearly key (Wimberger et al., 2017). By incorporating more indigenous forest into the home range, samangos are able to access more preferred food items (Coleman, 2013; Linden et al., 2015) and so do not need to exploit matrix habitat as intensively.

In contrast, the proportion of indigenous forest within the home range did not influence DJL. Whilst indigenous forest may be important for daily ranging patterns in terms of connectivity between forest patches (Swart and Lawes, 1996), the daily distance travelled appears to be more influenced by the time available for foraging (indicated by day length) in this study (Hill et al., 2003). However, other factors such as weather (Isbell, 1983; Hill, 1999), inter-group encounters (Yamagiwa and Mwanza, 1994), predator avoidance (Willems and Hill, 2009; Coleman and Hill, 2014), mating season dynamics (Erlinge et al., 1990) and sleep site location (Albert et al., 2011) may also be important. In addition, day journey length may not be a reliable measure when exploring ranging patterns in samango monkeys, as their reluctance to traverse open ground may superficially increase travel paths when going round rather than through open areas. Based on log likelihood ratio tests and model information criterion we found that proportion of indigenous forest within the home range best explained variation in home range size when compared to other measures of productivity, when controlling for other variables. These models therefore demonstrate that access to the indigenous forest is key to explaining variations in home range size in the samango monkey.

Our findings suggest that ranging patterns in samango monkeys may not be influenced by food availability *per se*, but the availability of food items in suitable, highly productive habitat. As such, measures of highly productive habitat/habitat type derived from remotely sensed data may be able to accurately predict ranging patterns in arboreal primates that consume large proportions of leaves, and future studies should explore this approach further. Whilst samango monkeys can utilise matrix habitat to access important resources (Skinner and Chimimba, 2005; Heikamp, 2008; Wimberger et al., 2017), they are generally unable to occupy small or isolated forest patches (Swart et al., 1993; Lawes, 2002). Additionally, they are poor dispersers in comparison to other forest-dwelling mammals and are reluctant to travel and disperse over open ground as a result of increased predation risk (Lawes et al., 2000; Madisha et al., 2017; Nowak et al., 2017). Due to the dietary flexibility of samango monkeys, access to suitable matrix habitat may allow samangos to exploit other food items and may therefore help to mitigate the effects of habitat loss and fragmentation by increasing connectivity and encouraging movement between fragments, providing samangos also have access to indigenous forest patches (Wimberger et al., 2017). Given this, the availability of highly productive indigenous forest habitat is not only important to samango monkey ranging patterns, but also to the persistence and viability of populations long-term (Swart and Lawes, 1996).

Across South Africa, metapopulations are declining owing to increasing habitat loss and a lack of corridors connecting suitable habitats (Lawes, 2002). This is particularly relevant for the isolated subpopulations in the Soutpansberg Mountains which are unlikely to receive any rescue effect from neighbouring populations (Linden et al., 2016). Therefore, in order for samango monkeys to persist in an increasingly fragmented and human-dominated landscape, access to indigenous forest patches is crucial. The primary focus of management plans should therefore be on expanding protected areas and properly managing areas of indigenous forest (Linden et al., 2016). The expansion of protected areas should focus on reclaiming and restoring non-viable areas, particularly areas such as riparian forests which facilitate the growth of indigenous forests (Linden et al., 2016). In addition, minimising disturbance in and around large habitat patches (Lawes et al., 2000) and continuing to connect forest fragments is also crucial in order to ensure the viability of subpopulations and subsequently, metapopulations (Swart and Lawes, 1996). For the Soutpansberg populations of samango monkeys, key conservation areas to ensure long-term persistence are forest patches in the eastern Soutpansberg which are naturally larger than areas in the western part of the mountain range, but are also under greater pressure from urbanisation (Linden et al., 2016).

Chapter 4 summary

Our findings here show that resource use and availability of highly productive habitat influences ranging patterns in the samango monkey. The next Chapter explores how behaviour varies spatially across the home range in relation to the variation in perceived predation risk, habitat features associated with perceived predation risk and resource availability.

Chapter 5

The following chapter has been formatted for submission to the journal ‘Behavioural Ecology’.

Behavioural responses to spatial variation in predation risk and resource availability in an arboreal primate

Abstract

The fear of being eaten may cause prey species to preferentially perform behaviours throughout their home range depending on the variation in perceived predation risk. Here, we explored how behaviour of the predominantly arboreal samango monkey (*Cercopithecus albogularis schwarzi*), varied spatially across the home range according to perceived predation risk, habitat features associated with risk, resource availability and distance from sleep site. We used acoustically distinct alarm calls to develop landscapes of fear for two samango monkey groups. In addition, we created spatial maps of seasonal fruit availability, understory visibility and canopy height, to explore the spatial variation in behaviour using generalised linear mixed models. We found that areas of high perceived risk were associated with an increase in the proportion of individuals feeding, increased number of near neighbours, and a decrease in the proportion of individuals resting, moving and being vigilant. Feeding also increased in areas of reduced understory visibility and where canopy height was lower whilst vigilance also increased in more densely vegetated areas, both likely an indirect

response to perceived predation risk in these areas. Areas of high fruit availability were also associated with fewer individuals resting and being vigilant, likely a response to individuals prioritising feeding in these areas. Finally, the proportion of individuals being vigilant decreased in areas used less often and when group cohesion increased, potentially mitigating any impact of risk associated with these areas by sharing the vigilance load between individuals. These findings suggest that neighbour distance may be the primary response to entering areas of high perceived risk.

Introduction

Understanding how animals utilise their environment over both space and time is one of the central issues in behavioural ecology (Willems and Hill, 2009). The way in which animals utilise space within their home range is largely determined by the distribution of resources and the presence of predators within their environment (Schoener, 1971; Mangel and Clark, 1986). Whilst resource distribution largely influences individuals directly as a result of local availability, the effect of predation can be both direct, resulting from the fitness costs of mortality, and indirect via the adjustment of behaviours to reduce the risk of mortality. These indirect costs of predation affect almost every aspect of prey behaviour and ecology (Lima, 1998; Caro, 2005) and, as such, animals often face a trade-off between resource acquisition and predator avoidance (Lima and Dill, 1990). In some cases, the perceived risk of predation is so high, that prey species preferentially forage in food-poor areas where predation risk is considerably lower. This trade-off has been observed in a wide range of taxa, including birds (Suhonen, 1993), fish (Dill and Fraser, 1984), cetaceans (Heithaus and Dill, 2002), ungulates

(Hernández and Laundré, 2005; Acebes et al., 2013; Cappa et al., 2014) and primates (Cowlishaw, 1997a).

Much of the current work exploring behavioural responses to predation risk has focussed on the foraging/vigilance trade-off, whilst largely ignoring other behavioural responses (Laundré et al., 2001; Heithaus and Dill, 2002; Campos and Fedigan, 2014). In a novel approach, Cowlishaw (1997a) explored activity budgets in a population of desert baboons in response to predation risk. Desert baboons (*Papio cynocephalus ursinus*) responded to predation risk from leopards (*Panthera pardus*) and lions (*Panthera leo*) by spending more time feeding in low-risk habitats where food availability was low. Baboons also preferred the safest habitats for other activities such as resting and grooming, indicating a clear avoidance for high-risk areas within their environment. However, predation risk in this study was assumed based on the hunting strategies of the predators rather than perceived risk by the prey species or indeed knowledge of actual predator locations.

How animals perceive predation risk spatially across their environment is often conceptualised as the "landscape of fear" (Laundré et al., 2001; Willems and Hill, 2009; Coleman and Hill, 2014), which is highly predator-specific (Shultz et al., 2004; Willems and Hill, 2009; Cresswell and Quinn, 2013). Whilst quantifying predator-specific predation risk can be difficult for the majority of species, primates are a notable exception in that the predator-specific alarm responses of some species are easily recognisable and can be easily attributed to specific predators (Cheney and Seyfarth, 1981), whilst also providing information on the location of predators (Willems and Hill, 2009). In addition, the majority of primate species can be readily habituated, and thus detailed data on ranging patterns, resource availability and perceived predation risk can be collected (Willems and Hill, 2009; Coleman and Hill, 2014).

Predator-specific landscapes of fear have been shown to influence how primates use space within their home range. White-faced capuchins (*Cebus capucinus*) in Costa Rica perceived high and middle forest layers with reduced predation risk and were more vigilant nearer the ground, likely reflecting the higher perceived risk from snakes and terrestrial predators associated with these areas (Campos and Fedigan, 2014). Vervet monkeys (*Chlorocebus pygerythrus*) in the Soutpansberg Mountains, South Africa, avoided areas of their home range associated with high perceived risk from baboons (*Papio ursinus*) and leopards (Willems and Hill 2009). Similarly, samango monkeys (*Cercopithecus albogularis schwarzi*) at the same field site avoided areas associated with high perceived risk from African crowned (*Stephanoaetus coronatus*) and Verreaux's eagles (*Aquila verreauxii*). Samangos also avoided areas associated with risk, such as in more densely vegetated areas where visibility was reduced and where canopy height was low. Whilst an avoidance of areas associated with risk is clear in primates, these areas are still part of the monkeys' home range and it is currently unclear how individuals trade-off specific behaviours when in these areas.

Here, we explored the spatial variation in behaviour of the arboreal samango monkey to perceived predation risk, habitat features associated with risk, resource availability and distance from sleep site in a fragmented, multipredator environment in the Soutpansberg Mountains, South Africa. The samango monkey (*Cercopithecus albogularis spp.*) is South Africa's only exclusively forest-dwelling primate, and is largely confined to the distribution of tall-canopy indigenous forests across South Africa (Linden et al., 2016). Across the mountain range, there is substantial seasonal fluctuation in rainfall and temperature and differences in water availability with changing elevation result in a variety of vegetation types (Mostert, 2006). These highly seasonal and environmental conditions lead to substantial variation in the spatial and temporal distribution of resources (Willems, 2007). In addition, samango monkeys are exposed to a range of predators at this location, including leopard, African crowned eagle, Verreaux's eagle and African rock python (*Python sebae*).

We expected that groups would only enter high-risk areas for behaviours that significantly enhance fitness. As feeding is fundamental to survival (Schoener, 1971; Pyke, 1984), we expected feeding to increase in high-risk areas relative to other behaviours. We also predicted that grooming and resting behaviours would be more common in areas where perceived risk was lowest (Cowlishaw, 1997a), as these behaviours are risky and do not depend on location-specific resources. Although individuals need to move to feed, we expected that moving would also be less common in high-risk areas due to the potential of walking into an ambush (Hopcraft et al., 2005), and that individuals would only enter these areas to access important food sources before retreating to safer areas. As increasing vigilance and group cohesion are common antipredator strategies adopted by prey species (Maisels et al., 1993; Brown, 1999; Laundré et al., 2001; Coleman, 2013), we predicted that individual vigilance and the number of nearby individuals would both increase in high-risk areas (Teichroeb and Sicotte, 2012; Campos and Fedigan, 2014), but that vigilance would decrease with increasing group size (Roberts, 1996; Treves, 1998). In addition, we also predicted that vigilance and the number of nearby individuals would decrease in areas close to sleep sites, as these areas are used more intensively (Coleman and Hill, 2014) and are typically associated with areas of reduced predation risk (Anderson, 1998; Albert et al., 2011).

In addition to perceived risk we investigated the effect of understory visibility and canopy height on samango behaviour. Areas of reduced visibility reduce the chance of detecting predators (Hill and Weingrill, 2007; Jaffe and Isbell, 2009) whilst offering increased ambush opportunities for predators (du Bothma and Le Richie, 1986; Tchabovsky et al., 2001), whereas areas closer to the ground are frequently associated with increased risk in arboreal species (Emerson et al., 2011). Therefore, both these habitat features represent indirect measures of predation risk (Cowlishaw, 1997b; Valeix et al., 2009; Coleman and Hill, 2014). Due to the importance of feeding to an individual's fitness, we expected feeding to increase in areas of reduced visibility and lower canopy height relative to other behaviours. Finally, we considered the effect of resources by using a measure of fruit availability. We expected feeding to occur more when in areas of high fruit availability (Whitten, 1988), whilst behaviours such as resting and grooming would decrease in these areas, instead being reserved for fruit-poorer areas. Whilst other factors such as temperature and rainfall (which change over the course of the day) may influence the time devoted to certain behaviours (Hill et al., 2004; Korstjens et al., 2010; Coleman, 2013), they are unlikely to have much influence on behaviour spatially and are not explored here.

Methods

Study species and study site

Samango monkeys are primarily arboreal, diurnal guenons that live in single-male, multi-female groups (Henzi and Lawes, 1987) of around 30 individuals (Lawes et al., 2013; Coleman and Hill, 2015). They are predominantly frugivorous but are capable of supplementing their diet with a large proportion of leaves (Beeson et al., 1996; Coleman and Hill, 2015), with seeds (Linden et al., 2015), flowers and insects (Butynski, 1990; Kaplin, 2001) also contributing to the diet albeit in smaller amounts. Samangos, like other forest guenons, use the tallest trees located in mature or indigenous forest as sleep site locations (Kaplin, 2001). Whilst some of these trees are located in close proximity to a crowned eagle’s nest on site (Coleman, 2013), the diurnal nature of these raptors (Trapani et al., 2006) means sleep sites are still selected to reduce predation risk (Albert et al., 2011), particularly from terrestrial predators.

We conducted fieldwork in the western Soutpansberg Mountains, South Africa, as part of the Primate and Predator Project at the Lajuma Research Centre (23°02’23”S, 29°26’05”E). Altitude at the field site ranges from 1150 – 1750 m. Climate at the study site is described as temperate, with highly seasonal conditions resulting in cool, dry winters from April to September and hot, wet summers from October to March (Willems, 2007). These conditions give rise to a variety of microclimates which result in substantial variation in the diversity of both flora and fauna (Brock et al., 2003; Willems, 2007). The south-facing cliffs of the mountain are dominated by the tall-canopy, indigenous mistbelt forest due to the direct mist precipitation and collection of groundwater from the base of the cliffs (Mucina and Rutherford, 2006). These forests exist in a mosaic of secondary shorter forests such as riparian forests, semi-deciduous woodlands and thicket (Mostert, 2006), which are further fragmented by montane grasslands, farmland and residential gardens.

Whilst potential predators include the leopard and the African rock python, the African crown eagle, and to a lesser extent the Verreaux's or black eagle, are the main predators of the samango monkey due to its primarily arboreal nature (Cordeiro, 2003; Coleman and Hill, 2014). Venomous snakes such as the black mamba (*Dendroaspis polylepis*), puff adder (*Bitis arietans*) and Mozambique spitting cobra (*Naja mossambica*), whilst not directly preying on samangos, still present a significant mortality-risk if encountered and may therefore influence antipredator behaviour. However, as observed with other arboreal guenons attacks by venomous snakes are rarely recorded (Foerster, 2008) and are almost always discovered and avoided well before they actually become dangerous (Smith et al., 2008; Fuller, 2013). As such, snakes were not assumed to have a significant influence on antipredator behaviour of samangos at Lajuma.

Data collection

We collected behavioural data on two habituated groups of samango monkeys (‘Barn’, 30 – 40 individuals and ‘House’, 60 – 70 individuals) between February 2012 and December 2016, for an average of eight full days per month. Full days consisted of maintaining audiovisual contact with the group from morning sleep site to evening sleep site, without losing contact for more than 60 minutes. During follows, we used instantaneous scan samples (Altmann, 1974) within a five-minute window to collect information on as many individuals as possible, using a handheld PDA (Psion Teklogix Workabout Pro 3). Scans samples occurred at 20-minute intervals (e.g., 12:20, 12:40, 13:00), with a GPS point of the group’s location recorded with each scan sample using a GPS device (Garmin GPSmap 64S). Information collected during each scan sample included: date, time, group ID, age-sex class, general behaviour (e.g. feeding, social), specific behaviour (e.g. foraging, grooming given), height from ground (m), vigilance and number of nearest neighbours within 5 m. However, data on vigilance was only recorded from April 2014 meaning only three years of data were available on this behaviour. General behavioural categories explored in this study included the following specific behaviours:

feeding (feeding and foraging), social (grooming given/received), resting (sitting, standing, huddled, lying and sleeping), moving (walking and running) and vigilance (scanning, looking up/down).

To specify spatial variation in perceived predation risk, we followed the approach of Coleman and Hill (2014) using the samango monkeys' acoustically distinct alarm calls, particularly the *ka* and *katrain* calls which have an unambiguous association with aerial predators (Fuller, 2013). However, samango monkeys do not appear to have predator-specific alarm calls for terrestrial predators (Coleman, 2013; Fuller, 2013) such as snakes or leopards, possibly due to the low frequency with which they are encountered due to their primarily arboreal nature (Coleman, 2013). Whilst group-wide alarm calls cannot always be attributed to a specific predator guild, a large proportion of these calls are associated with antipredator behaviour from aerial predators, such as individuals jumping down from the canopy, looking up and scanning the sky. The location and details of all *kas*, *katrains* and group-wide alarm calls were recorded on an all occurrence basis, resulting in a total of 1,110 alarm calls across both groups over the five-year study period, with the context known for 210 calls (eagle: 198, snake: 12). A further 323 calls were associated with antipredator behaviour in response to raptors (e.g. jumping into trees, moving down from canopy, scanning sky etc.), meaning 47% of calls were associated with raptors. Whilst no context could be established for the remaining 557 calls, these calls are still informative as they indicate the monkeys' perception of risk (Willems and Hill, 2009; Campos and Fedigan, 2014) and, as such, all alarm calls were used to create the landscapes of fear. Whilst this resulted in landscapes indicating overall perceived risk from multiple predator guilds, the large proportion of calls associated with raptors meant the landscapes of fear were predominantly focussed on this predator guild.

We collected monthly phenological data (number of leaves, fruit, seeds and flowers) from 20 individually marked trees of 24 species (480 trees in total) every month over the five-year study period. We calculated estimates for the whole tree if there were items on the tree but not on a specified marked branch. We selected tree species due to the relative importance of each species to the diet of the samango monkey (Coleman, 2013; Linden et al., 2015), whilst also giving a representation of various habitat types across the study area. For the purpose of this analysis, we used only the numbers of fruits (in addition to seed pods of *Acacia spp*.) to calculate seasonal food availability. Despite leaves (40.1%) contributing more than fruit (37.7%) to the diet of samangos at Lajuma, they are readily available across the home range, even during periods of fruit scarcity (Coleman, 2013). Samangos have also been shown to compete over access to fruit due to the spatial and temporal unpredictability of this food item (Payne et al., 2003). As such, fruit availability is more likely to influence behaviour in samangos compared to other food items.

We used randomly generated 5 x 5 m^2 vegetation plots across the study site (n = 702) to calculate food availability, habitat visibility and canopy height throughout the home ranges. Within each plot, we identified all trees with a diameter > 10 cm at a height of 1 m and recorded the following measurements: height, diameter at breast height (DBH), crown diameter and perpendicular crown diameter. We calculated mean crown diameter for each tree by averaging the latter two measurements which was used in later estimates of fruit availability. To estimate understory visibility, we counted the number of squares on a 0.8 m^2 chequerboard with 0.1 m^2 cells at a distance of 5 m and 10 m, and at a height of 0 m and 1.25 m, for each of the four cardinal point directions from the northwest corner of each vegetation plot, resulting in 16 chequerboard measurements per plot. To get an estimate of understory visibility per plot, we averaged the number of chequerboard squares counted across the 16 chequerboard measurements per plot. We estimated mean canopy height per plot by averaging the height across all trees sampled in each plot.

Data processing

We imported all data into QGIS 3.0 (QGIS Development Team, 2018) with the cell size of all output rasters set to 30 m^2 to be consistent with the resolution of our base maps. We then created utilisation distributions, landscapes of fear and fruit availability maps to spatially map the various landscapes across the study area. In addition, we also imported behaviour data into QGIS for visualisation.

We created annual home ranges delineating the utilisation distribution of each group using adaptive localised convex hulls (*a*-LoCoH) analysis (Getz and Wilmers, 2004; Getz *et al.*, 2007). This home range estimation method is particularly useful for small ranging species living in fragmented landscapes, as it has a superior ability of identifying hard boundaries and parts of the range which aren’t used (Ryan et al., 2006), whilst also dealing with temporally close data points (Getz and Wilmers, 2004; Ryan et al., 2006; Getz et al., 2007; Coleman and Hill, 2014). We calculated home ranges using the ‘*t*-LoCoH’ package (Lyons et al., 2013) in R 3.5 (R Core Team, 2018), using the distance between the widest points within each groups’ respective annual home range as the *a*-value to allow for the correct construction of isopleths (Getz et al., 2007).

We created annual landscapes of fear for each group using the ‘Kernel Density Estimation’ tool in QGIS to create density distributions of GPS points for all alarm calls recorded for each year for each group, resulting in five alarm calls layers for each group. A PLUGIN bandwidth was used for the nearest neighbour search distance due to its reduced variability and increased performance when compared to least-squares cross validation (Gitzen et al., 2006) and its ability to operate with small sample sizes which was evident in some of our sample years. We then calculated the annual landscape of fear by dividing the alarm call layer by the utilisation distribution (Willems and Hill, 2009) to account for the time spent in certain areas of the home range. This process also bound the annual landscape of fear by each groups’ respective home range.

We estimated fruit availability at the seasonal level as we deemed this the most appropriate scale given the difficulties in predicting monthly fruit availability at this field site (Coleman, 2013), and due to the scale of other variables used in this analysis. We calculated seasonal (wet versus dry season) fruit availability maps for each year across the study period by summing the monthly fruit availability estimates across each season, across the 20 trees for each of the 24 species sampled as part of the phenology data collection. We then applied a linear regression to predict the total availability of fruit per season as a function of either mean crown diameter or DBH measured for each of the 20 trees of each of the 24 species (Coleman, 2013). We applied these seasonal fruit availability estimates to each individual of each species within each vegetation plot based on mean crown diameter or DBH, and calculated the total fruit availability per plot per season by summing the total fruit availability estimate for all individuals within each plot. We imported all vegetation plots into QGIS and extracted the following landscape variables for each plot using the ‘Point Sampling Tool’:

annual mean EVI (a remotely sensed measure of productivity), elevation, terrain ruggedness and distance to rivers/streams. We then ran a linear regression to predict the total seasonal fruit availability for each vegetation plot as a function of these landscape variables. As each landscape variable was a significant predictor of fruit availability, we were able to spatially map the seasonal fruit availability for each year across the home range using the ‘Raster Calculator’ and applying the regression coefficients to predict a value for seasonal fruit availability for each 30 m^2 raster cell. Similarly, we used the mean understory visibility and mean canopy height measurements sampled from the vegetation plots and used a linear regression to predict these measurements based on the aforementioned landscape variables. Finally, we created spatial maps of understory visibility and canopy height by applying the regression coefficients to the ‘Raster Calculator’ in QGIS to predict a value for each 30 m^2 raster cell.

Statistical analysis

Using the GPS point associated with each scan sample, we extracted values for the landscape of fear, fruit availability, habitat visibility and canopy height in QGIS. We also calculated the distance from morning sleep site using the ‘Distance Matrix’ tool in QGIS and extracted these distances for each scan sample. We used the ‘dplyr’ package (Wickham et al., 2017) in R to calculate the number of individuals displaying a particular behaviour (feeding, grooming, resting, moving and vigilant) as a proportion of the total number of individuals recorded within each five-minute scan sample. We confined all analyses to data on adult females to remove any bias in age-sex class, and also as this age-sex class comprises the greatest proportion of samango groups and is therefore likely to experience the landscape of fear most. In addition, restricting analyses in this way also reduces the possible error from variability in age-sex class sampled in each scan sample, whilst also reducing potential bias from including a single adult male who was regularly sampled. We used a minimum threshold of five individuals per scan sample to remove biases resulting from a small number of individuals within each scan sample. For our vigilance analysis, we also calculated the mean number of nearest neighbours per scan sample as an additional variable. Finally, we also used the mean number of nearest neighbours per scan sample to explore this variable as a function of perceived predation risk, habitat features associated with risk, fruit availability and distance from sleep site.

We used generalised linear mixed models (GLMMs) with a beta error structure to model the proportion of individuals feeding, grooming, resting, moving and vigilant per scan sample across the five-year study period. In addition, we used a linear mixed model with a Gaussian error structure to model the mean number of nearest neighbours. We included the landscape of fear, fruit availability, understory visibility, canopy height and distance from morning sleep site as predictor variables. We also included the average number of nearest neighbours per scan sample as an additional predictor in our vigilance model. Group ID was included in each model to control for the effect of group size on behaviour, whilst month and year were included as crossed random effects. All models were fitted in R using the glmmTMB function in the ‘glmmTMB’ package (Brooks et al., 2017), and the ‘lmer’ function in the ‘lme4’ package (Bates et al., 2014) for the nearest neighbours model. No collinearity between fixed effects was evident, as Variance Inflation Factors (VIF) using the vif function within the ‘car’ package all indicated values below 1.5 (Hair et al., 2014). Significance for *P*-values of the individual effects was inferred at the 5% level. Due to the spatial nature of the response variable in all our models, we examined the residuals for each model for evidence of autocorrelation. Visual inspection of correlograms using the spline.correlog function in the ‘ncf’ package and semivariograms using the variogram function in the ‘gstat’ package in R, indicated no spatial autocorrelation between the residuals and lagged distance. However, Moran’s I tests on the residuals of each model indicated autocorrelation was present, albeit only at very short distances. We accounted for any autocorrelation by creating spatial lags of the residuals from each model (in GeoDa v1.12; Anselin et al., 2006), and including these lags as an additional “autocorrelation term” in each of the final models, an approach that has similarly been adopted before (Grueter et al., 2013). Finally, we checked for normality and homogeneity of residuals from the final models by visually inspecting the residuals plotted against fitted values.

Results

Visualisation of behaviours across the home range showed areas of higher and lower intensity for each behaviour that varied between years (Figure 5.1). In addition, visualisation of the landscapes of fear showed that areas of perceived higher risk were relatively consistent for both groups between years (Figure 5.2).

The proportion of individuals feeding significantly increased when in areas of high perceived risk, as well as in areas with dense understory vegetation and lower canopy height (Table 5.1), whilst fruit availability and distance from sleep site had no effect. In contrast, grooming was not influenced by perceived predation risk or measures of habitat structure associated with risk. Grooming was also not influenced by fruit availability or distance from sleep site. The proportion of individuals resting significantly decreased in high-risk areas and also in areas where fruit availability was high. Habitat structure and distance from sleep site did not influence resting. The landscape of fear was the only variable influencing the proportion of individuals moving, with moving decreasing in high-risk areas. Interestingly, the proportion of vigilant individuals decreased in high risk areas and also in areas of high fruit availability. Individuals were also less vigilant in areas of increased understory visibility. Vigilance also decreased in areas further away from the morning sleep site, whilst individuals were also less vigilant when the number of near neighbours increased. However, canopy height did not influence vigilance. Finally, individuals increased the number of nearby neighbours when in high-risk areas and as distance from morning sleep site increased (Table 5.2), whilst understory visibility, canopy height and fruit availability had no effect.

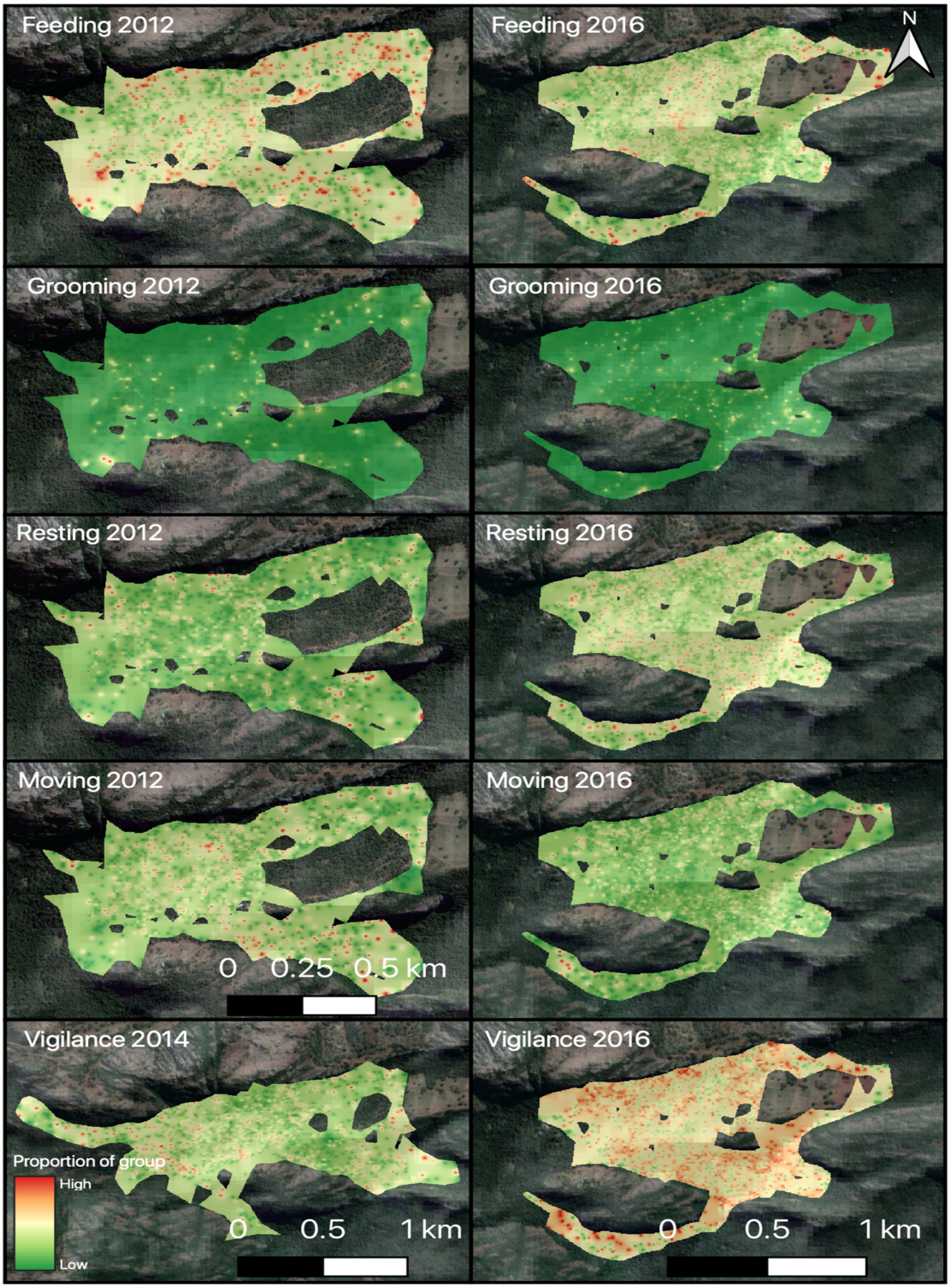

Figure 5.1. Comparison between the proportion of 'Barn' group feeding, grooming, resting, moving and vigilant for 2012 and 2016 at Lajuma Research Centre, Soutpansberg Mountains, South Africa. Proportion of group vigilant is shown for 2014, as opposed to 2012, due to onset of data collection for this behaviour (scale is independent).

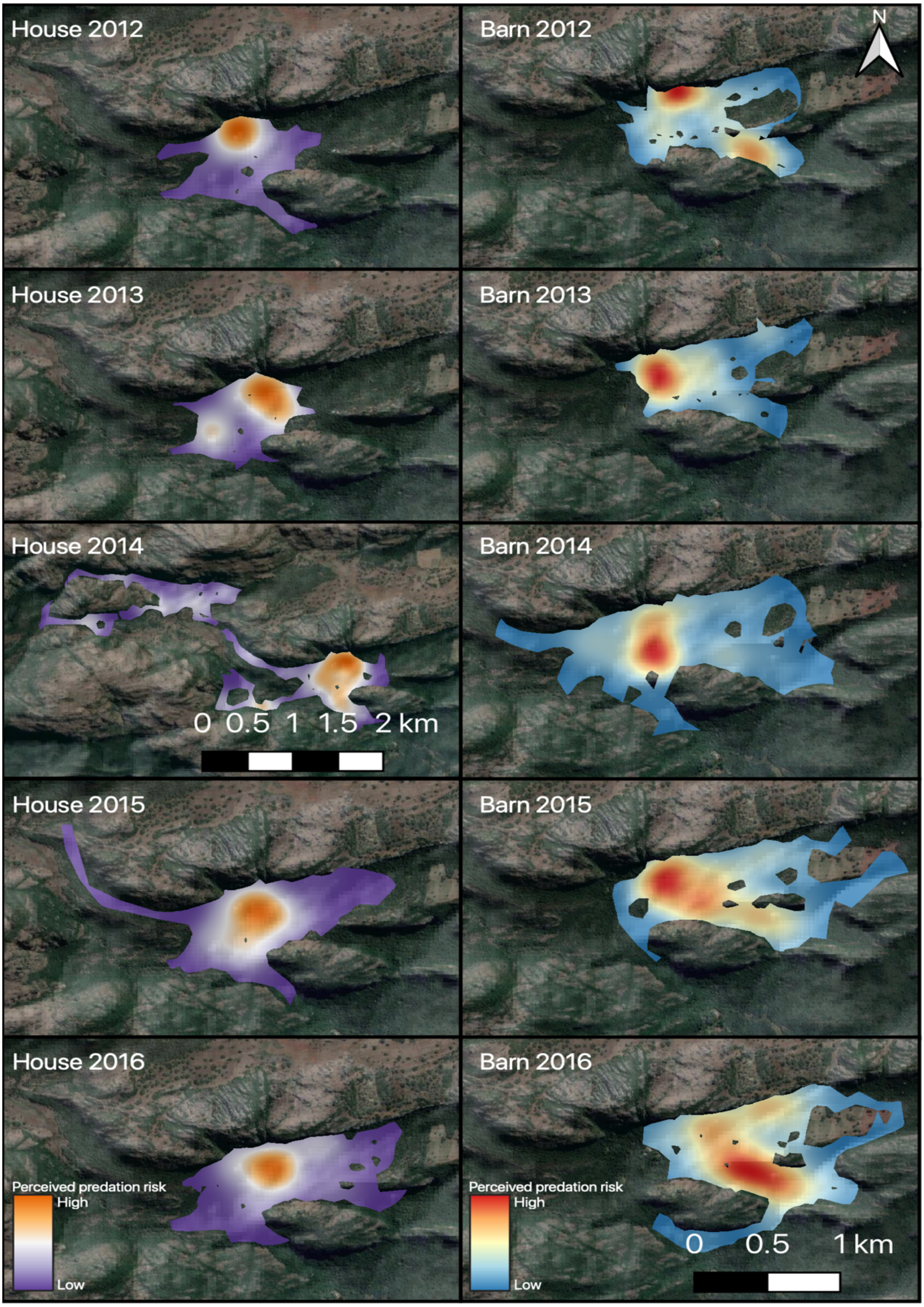

Figure 5.2. Spatial distributions of annual landscapes of fear for both 'House' and 'Barn' group at Lajuma Research Centre, Soutpansberg Mountains, South Africa, from 2012 – 2016 (scale for 'House 2014' is independent).

Table 5.1. Parameter estimates and key statistics of spatial GLMMs for proportion of individuals feeding, grooming, resting, moving and being vigilant, as a function of perceived predation risk (landscape of fear), fruit availability, understory visibility, canopy height and distance to sleep sites.

Coefficient	ß	SE	z-value	CI$_{lower}$	CI$_{higher}$	*P*
Feeding						
Intercept	-0.619	0.140	(1)	-0.894	-0.344	(1)
Landscape of fear	**0.069**	0.032	2.176	0.007	0.130	0.030
Fruit availability	0.054	0.067	0.798	-0.078	0.185	0.425
Understory visibility	**-0.075**	0.036	-2.095	-0.145	-0.005	0.036
Canopy height	**-0.081**	0.033	-2.421	-0.147	-0.015	0.016
Sleep site	0.027	0.031	0.866	-0.034	0.088	0.387
Ac.term	**1.226**	0.191	6.403	0.851	1.601	<0.001
Group (House)	0.072	0.066	1.100	-0.056	0.200	0.271
Grooming						
Intercept	-2.440	0.058	(1)	-2.553	-2.326	(1)
Landscape of fear	0.015	0.025	0.600	-0.034	0.064	0.548
Fruit availability	-0.041	0.025	-1.660	-0.089	0.007	0.097
Understory visibility	0.031	0.028	1.110	-0.023	0.084	0.268
Canopy height	0.032	0.026	1.230	-0.019	0.084	0.218
Sleep site	0.007	0.025	0.270	-0.042	0.055	0.790
Ac.term	**1.152**	0.286	4.020	0.591	1.714	<0.001
Group (House)	0.118	0.053	2.220	0.014	0.222	0.027
Resting						
Intercept	-1.661	0.130	(1)	-1.916	-1.406	(1)
Landscape of fear	**-0.062**	0.031	-2.013	-0.123	-0.002	0.044
Fruit availability	**-0.121**	0.060	-2.016	-0.239	-0.003	0.044
Understory visibility	-0.012	0.032	-0.363	-0.074	0.051	0.717
Canopy height	0.027	0.031	0.863	-0.034	0.087	0.388
Sleep site	0.027	0.029	0.932	-0.029	0.083	0.352
Ac.term	**0.671**	0.338	1.983	0.008	1.334	0.047
Group (House)	0.081	0.059	1.366	-0.035	0.197	0.172
Moving						
Intercept	-1.340	0.115	(1)	-1.565	-1.116	(1)
Landscape of fear	**-0.146**	0.027	-5.389	-0.199	-0.093	<0.001
Fruit availability	0.010	0.057	0.175	-0.102	0.122	0.861
Understory visibility	-0.052	0.033	-1.568	-0.118	0.013	0.117
Canopy height	-0.030	0.032	-0.932	-0.093	0.033	0.351

Sleep site	-0.012	0.029	-0.422	-0.070	0.045	0.673
Ac.term	**1.235**	0.241	5.127	0.763	1.707	<0.001
Group (House)	**-0.164**	0.060	-2.746	-0.280	-0.047	0.006
Vigilance						
Intercept	-0.573	0.487	(1)	-1.528	0.382	(1)
Landscape of fear	**-0.095**	0.039	-2.443	-0.171	-0.019	0.015
Fruit availability	**-0.516**	0.122	-4.228	-0.755	-0.277	<0.001
Understory visibility	**-0.181**	0.046	-3.913	-0.271	-0.090	<0.001
Canopy height	-0.063	0.041	-1.526	-0.144	0.018	0.127
Sleep site	**-0.109**	0.038	-2.849	-0.184	-0.034	0.004
Neighbours	**-0.270**	0.045	-5.978	-0.358	-0.181	<0.001
Ac.term	0.830	0.458	1.815	-0.067	1.727	0.070
Group (House)	**-0.279**	0.079	-3.545	-0.433	-0.125	<0.001

Sleep site, distance to nearest sleep site; neighbours, number of nearest neighbours; ac.term, autocorrelation term. (1) not shown because of having no meaningful interpretation.

Table 5.2. Parameter estimates and key statistics of spatial LMM for mean nearest neighbours as a function of perceived predation risk (landscape of fear), fruit availability, understory visibility, canopy height and distance to sleep sites.

Coefficient	ß	SE	t-value	CI_{lower}	CI_{higher}	*P*
Nearest neighbours						
Intercept	0.551	0.131	(1)	0.293	0.809	(1)
Landscape of fear	**0.079**	0.028	2.763	0.023	0.134	0.006
Fruit availability	0.033	0.061	0.532	-0.088	0.153	0.595
Understory visibility	0.058	0.032	1.775	-0.006	0.121	0.076
Canopy height	0.050	0.032	1.548	-0.013	0.113	0.122
Sleep site	**0.063**	0.030	2.108	0.004	0.121	0.035
Ac.term	**0.219**	0.047	4.674	0.127	0.310	<0.001
Group (House)	-0.094	0.060	-1.573	-0.211	0.023	0.116

Sleep site, distance to nearest sleep site; neighbours, number of nearest neighbours; ac.term, autocorrelation term. (1) not shown because of having no meaningful interpretation.

Discussion

The indirect costs of predation are often recognised as the most important constraint on prey behaviour (Lima, 1998), yet are among the most difficult to quantify. Previous studies have either focussed on the behavioural responses to variation in predation risk either in terms of space use (Laundré et al., 2001; Heithaus and Dill, 2002; Valeix et al., 2009; Willems and Hill, 2009; Coleman and Hill, 2014), or the foraging/vigilance trade-off (Dill and Fraser, 1984; Suhonen, 1993; Heithaus and Dill, 2002; Hernández and Laundré, 2005), and thus have largely ignored specific behavioural responses (Cowlishaw, 1997a). Whilst samango monkeys have previously been shown to avoid areas of high perceived predation risk within their home range, particularly from eagles (Coleman and Hill, 2014), these areas are still part of the monkeys' home range, and it is unknown what individuals do when in these high-risk areas. Here, we investigated the spatial variation in behaviour of the samango monkey in response to perceived predation risk, habitat visibility, canopy height, fruit availability and distance from sleep site. We found that perceived predation risk, and habitat measures associated with risk, significantly influenced samango monkey behaviour across the home range.

The areas perceived as high-risk were relatively consistent for both groups across the study period. This is largely attributed to the presence of an African crowned eagle's nest located on the cliff face at the rear of the tall indigenous forest between the northernmost edges of both groups' home range (Coleman, 2013). In addition, the landscapes of fear for Barn group also show high perceived risk to the southeast areas of the home range, which can be attributed to the location of a black eagle's nest (Coleman, 2013). These visualisations of the landscape of fear, in addition to the large proportion of calls associated with raptors, suggests that this is the most important predator guild that influences the samango monkey's landscape of fear.

Feeding

Samango monkeys actively avoid areas of their home range perceived as the highest risk from their main predator, the African crowned eagle (Coleman and Hill, 2014). However, we show here that when entering areas of high risk, samango monkeys increase the amount of feeding relative to other behaviours. Because food acquisition is fundamental to an individuals' survival (Schoener, 1971; Pyke, 1984), the benefits of accessing important resources (such as higher quality or temporally available food items) may sometimes outweigh the potential costs of predation. For example, common squirrel monkeys (*Saimiri sciureus*) increased time spent feeding on artificial high-reward food platforms where predation risk was high, when availability of natural fruit was low during the dry season (Stone, 2007). Similarly, Milne-Edwards' sifakas (*Propithecus diadema edwardsi*) in the Madagascan rainforest spend more time feeding in the fruit-rich but high-risk canopy where risk from raptors is greatest (Wright, 1998). A similar foraging/risk trade-off also appears to be the case here. The tall indigenous forest contains many important fruit species for the frugivorous samango monkey (Coleman, 2013; Linden et al., 2015; Wimberger et al., 2017), many of which are large, isolated species which fruit asynchronously (Coleman, 2013). However, certain parts of these forests are also where risk from eagles is greatest due to the location of their nests (Coleman and Hill, 2014). As such, accessing isolated and finite resources in these high-risk areas may outweigh the potential predation costs during months where overall fruit availability across the landscape is low (Coleman, 2013). Another possibility is the foraging constraints imposed by group size. In a study on desert baboons in Namibia, groups avoided feeding in high-risk food-rich habitats, instead preferring to feed in the low-risk food-poor habitats (Cowlishaw, 1997a). However, there was a weak association with group size and feeding time in the riskiest habitat, with the largest groups spending more time feeding in the riskier woodland habitat. As within-group feeding competition increases with group size (Watts, 1985), larger groups may be under greater pressure to forage in riskier habitats where food is more abundant and competition is reduced. The unusually large size of samango groups at Lajuma may mean a similar relationship is present here.

Samango monkeys also actively avoid areas of reduced understory visibility and low canopy height within their home range (Coleman and Hill, 2014). However, we found that when entering these areas, the proportion of individuals feeding increased relative to other behaviours. Areas of reduced visibility tend to be densely vegetated, meaning predators have improved camouflage (Tchabovsky et al., 2001) and ambush opportunities (du Bothma and Le Richie, 1986). In addition, arboreal primates often show a vertical axis of fear, with areas closer to the ground associated with increased risk (Emerson et al., 2011), particularly from terrestrial predators. Both of these factors influence the monkeys' perceived risk via reduced predator detection (Hill and Weingrill, 2007; Jaffe and Isbell, 2009) or reduced ease of escape (Lima, 1992; Hart et al., 1996) respectively. Therefore, an increase in feeding in these areas is understandable given this is a behaviour essential to an individual's survival.

We found no relationship between fruit availability and the proportion of individuals feeding. Whilst we would expect the predominantly frugivorous samango monkey to increase feeding when in areas of high fruit availability, the lack of any relationship may reflect the samango monkeys' foraging/risk trade-off (Lima and Dill, 1990), whilst also highlighting their dietary flexibility. During the wet season when fruit availability across the home range is high (Coleman, 2013), samango monkeys may preferentially feed in relatively fruit-poorer but lower risk habitats (Cowlishaw, 1997a) due to their ability to exploit a rich habitat matrix and consume large amounts of leaves (Coleman and Hill, 2015; Linden et al., 2015; Wimberger et al., 2017). The ability to increase leaf consumption in these areas may allow feeding levels to remain high and successfully mitigate any effects on energy requirements from foraging in fruit-poor areas relative to the surrounding areas. In contrast however, when fruit availability across the home range is low during the dry season, samango monkeys may be willing to take more risks in order to access isolated and finite food items.

Grooming

We found no effect of landscape of fear, habitat measures associated with risk, fruit availability or distance from sleep site on the proportion of individuals grooming across the home range. Whilst we expected grooming to be more common in lower-risk areas, it may simply be that grooming is less affected by environmental factors in this species, and instead is more influenced by social factors such as intra-group conflicts, increases in social tension and inter-group encounters (Terry, 1970; Henzi and Barrett, 1999; Koyama et al., 2006). Furthermore, whilst Cowlishaw (1997a) found that desert baboons preferred the safest habitats for grooming, he also acknowledged that this may simply be a consequence of the baboons' diurnal activity and that behaviours such as grooming and resting are more common at dawn and dusk which, coincidentally, is where the safest habitat is located. Similarly, grooming in samango monkeys may also be associated with their diurnal behaviour and less influenced by perceived predation risk.

Resting

Whilst feeding is fundamental to an individual's fitness and may therefore influence risk-taking decisions, resting is an inherently high-risk behaviour and even though some resting is 'enforced', such as during digestion or thermoregulation (Korstjens et al., 2010), it should be avoided in high-risk areas. Indeed, we found that samango monkeys rested less in high-risk areas, instead reserving this behaviour for safer areas. Avoidance of high-risk areas for resting is commonly observed in various species. Desert baboons reserved all resting behaviour for the hills, which as a result of the increased visibility was perceived as the safest of habitats (Cowlishaw, 1997a). Similarly, Milne-Edwards' sifakas (*Propithecus diadema edwardsi*) use daytime resting sites lower in the canopy which offer greater protection from aerial predators (Wright, 1998), whilst in bottlenose dolphins (*Tursiops aduncus*), resting occurred almost exclusively in deep waters which were perceived as the safest habitats from tiger sharks (*Galeocerdo cuvier*) (Heithaus and Dill, 2002).

Resting was also less common in areas of high fruit availability. Being predominantly frugivorous, it seems reasonable that samangos would prioritise feeding in these areas in order to increase fruit consumption, whilst reserving resting for more fruit-poor areas where individuals can recuperate and digest (Korstjens et al., 2010). Whilst we may therefore expect a positive relationship between fruit availability and feeding, the ability of samangos to increase leaf consumption in areas or periods of fruit scarcity (Coleman, 2013) may allow feeding levels to remain high, thus masking any relationship with fruit availability. One important consideration with this finding is that resting is multi-faceted, yet was explored as a single behaviour here. Resting ranged as part of the data collection from 'sleeping' (which we would only expect in safe areas) to pauses in other activities (such as ‘sitting’), perhaps to aid vigilance. A useful future direction would therefore be to separate these behaviours further in order to increase our understanding of how samangos manage risk.

Moving

We found that moving significantly reduced when in areas of high perceived risk. Moving, like resting, is also a risky behaviour, especially when moving into unfamiliar areas which increases the risk of predation (Isbell et al., 1990). Similarly, moving in high-risk areas can increase the likelihood of ambush from terrestrial predators (du Bothma and Le Richie, 1986). Furthermore, whilst moving in this instance was considered to be ‘walking’ and ‘running’ behaviours, it may be that walking decreases in high risk areas but running increases in order to escape these areas quickly. Whilst specific behaviours were not explored as part of this analysis, future work may benefit from exploring this in more detail. Alternatively, samangos may move less in high-risk areas as a consequence of spending more time feeding on large trees with abundant resources where individuals can feed without moving between patches (Whitten, 1988).

Vigilance

Contrary to our predictions, samango monkeys were less vigilant in areas of high perceived risk. The relationship between vigilance and predation risk has long been recognised as one of the most common anti-predator responses (Brown, 1999; Laundré et al., 2001), and our findings contrast those of other studies (Cowlishaw, 1997b; Laundré et al., 2001). One possibility for the relationship observed involves the foraging/vigilance trade-off, in that as samangos increase time spent feeding in high-risk areas, there may be less time available to spend being vigilant (Coleman, 2013). However, feeding and vigilance are not incompatible in primates, and so a more likely explanation may be that samangos mitigate the potential costs of this trade-off by increasing the number of nearby neighbours (Roberts, 1996; Cowlishaw, 1998; Treves, 1998; Teichroeb and Sicotte, 2012). This strategy may reduce predation risk due to the "dilution effect" (Maisels et al., 1993), or perhaps more likely due to the sharing of the vigilance load between individuals (McNamara and Houston, 1992; Cowlishaw, 1998). Indeed, we found that the proportion of individuals being vigilant significantly reduced when the number of nearby neighbours increased, thereby allowing samangos to be less vigilant in high-risk areas. Vigilance also decreased in areas of increased understory visibility. The effect of habitat visibility on vigilance is a finding consistent with other studies (Metcalfe, 1984; Chapman, 1985; Burger, 2001; Enstam and Isbell, 2004; Whittingham et al., 2004) due to the increased chance of predator detection in areas of increased visibility (Hill and Weingrill, 2007; Jaffe and Isbell, 2009). Whilst many arboreal primates associate the ground with increased risk (Emerson et al., 2011; Teichroeb and Sicotte, 2012) and therefore increase vigilance accordingly (Teichroeb and Sicotte, 2012; Campos and Fedigan, 2014) no such relationship was observed here. One possibility for a lack of relationship observed here is that samangos may mitigate the increased perceived risk associated with areas closer to the ground by increasing the number of nearby individuals, thereby "diluting" the chances of predation (Maisels et al., 1993) whilst switching to group vigilance (McNamara and Houston, 1992; Cowlishaw, 1998).

Samango monkeys were also less vigilant in areas of high fruit availability, likely a result of the foraging/vigilance trade-off (Cowlishaw, 1997b; Coleman, 2013) or possibly also a consequence of sharing the vigilance load whilst individuals clump together at resources

(Stevenson et al., 1998; Koenig, 2002; Basabose, 2004). Samangos were also less vigilant in areas of the home range use less intensively, indicated by distance from sleep site. Whilst this relationship seems contradictory, reducing individual vigilance in less familiar areas may again be a consequence of grouping behaviour (McNamara and Houston, 1992; Cowlishaw, 1998), as samangos increased the number of nearby neighbours as distance from sleep site increased.

Number of neighbours

Group cohesion significantly increased in high-risk areas, where the number of near neighbours increased. This grouping effect may successfully mitigate the risk of predation by deterring predators (Maisels et al., 1993) or by sharing the vigilance load between individuals (McNamara and Houston, 1992). As previously mentioned, the number of near neighbours also increased with increasing distance from morning sleep site. As these areas are used less intensively (Coleman and Hill, 2014) and are therefore more unfamiliar, increasing the number of nearby neighbours in these areas may be another antipredator response to increased perceived predation risk associated with these areas (Isbell, 1994). Similarly, despite the close proximity of some sleep sites to the crowned eagle’s nest (Coleman, 2013), the diurnal nature of these raptors means that the location of sleep sites within the tall indigenous forest are inherently safer (Smith et al., 2008; Albert et al., 2011), and so increasing the number of nearby individuals may not be necessary in these areas. These findings suggest that neighbour distance is the main response to predation risk; while animals only go into the highest risk areas to feed, risk can be managed across the rest of the range by varying the number of neighbours which subsequently reduces any effect of risk on other behaviours.

One potentially influential factor on perceived risk not explored here is that of intergroup encounters (Chapman, 1990). Encounters between groups can be perceived as risky due to the risk of injury and death (Arseneau-Robar et al., 2017). However, whilst encounters between samangos can be aggressive, they rarely result in injury or death (Lawes and Henzi, 1995). Intergroup encounters did not influence the intensity of space use in samangos at the same field site (Coleman and Hill, 2014), and so it was assumed that encounters between groups would not influence perceived risk. Additionally, the presence of human observers throughout data collection potentially influenced the likelihood of intergroup encounters across the home range, particularly when contrasting habituated and non-habituated groups. As a consequence, any measure of the frequency of intergroup encounters is likely to be biased towards areas of overlap between habituated groups.

In conclusion, behaviour varied spatially across the home range in relation to the perceived risk of predation, both directly resulting from the landscape of fear and indirectly as a result of habitat visibility and canopy height, whilst fruit availability and distance from sleep sites also influenced some behaviours. Due to the direct result of mortality from successful predation, the presence of predators influences the behaviour of prey species indirectly (Lima and Dill, 1990). As such, prey species often disproportionately use areas within their home range (Laundré et al., 2001; Willems and Hill, 2009; Coleman and Hill, 2014), or preferentially perform behaviours depending on risk (Cowlishaw, 1997a). Whilst only adult females were included in analyses here, as they comprise the largest proportion of age-sex classes in samango groups and are likely to experience the landscape of fear most, this is also a potential limitation of the study and results may therefore not necessarily be applicable to the species as a whole. The spatial variation in behaviour resulting from perceived predation risk explored here is a novel analysis, and future studies should explore this relationship in other species to help improve knowledge on space use. In addition, an important future direction would be to explore the spatial variation in behaviour in comparison to the utilisation distribution of predators.

Chapter 5 summary

Our findings here show that perceived predation risk, resulting both directly from the landscape of fear and indirectly from habitat visibility and canopy height, significantly influences the spatial variation in behaviour of the samango monkey. The next chapter will explore whether this variation in perceived risk influences anxiety-related behaviours.

Chapter 6

The following chapter has been formatted for submission to the journal ‘Animal Behaviour’.

Perceived predation risk increases anxiety in a wild primate, the samango monkey (*Cercopithecus albogularis schwarzi*)

Abstract

The fear of being eaten can manifest as anxiety in prey species. Whilst previous studies have shown an increase in anxiety-related behaviours in primates (such as scratching and self-grooming) when exposed to a predator, it remains largely unknown whether perceived predation risk can invoke anxiety. We collected focal observations from adult females from two groups of samango monkey over a 12-month period to explore whether scratching increased in areas associated with higher perceived predation risk. We used a paired t-test to investigate scratching as an anxiety-related behaviour in this species, comparing the rate of scratching after a stressful event (an eagle alarm call) relative to a control period. We used a generalised linear mixed model to predict the rate of scratching as a function of the landscape of, understory visibility, canopy height, distance from sleep site and the number of near neighbours, whilst controlling for season. We found scratching occurred significantly more often following an eagle alarm call, indicating this may be a reliable anxiety-related behaviour. In addition, scratching increased in areas further away from morning sleep sites, indicating that samangos may be more anxious due to the perceived risk associated with areas used less

often. Whilst the landscape of fear, habitat visibility and canopy height did not influence scratching, samangos may adopt other behavioural strategies to mitigate the risk of anxiety in these areas. We propose that scratching may be a useful indicator of anxiety in wild primates and can help to improve knowledge on the environmental factors that induce stress in wild populations.

Introduction

Fear is an adaptive emotional response which serves to modify an individual’s behaviour in order to avoid potentially dangerous situations (Nelson et al., 2003). Fear can manifest as anxiety, the apprehension over anticipation of potentially threatening stimuli, which is critical to an individual’s survival (Coleman and Pierre, 2014). Whilst anxiety serves as a short-term coping mechanism, long-term anxiety can lead to chronic stress which can negatively impact the reproductive success and survival of individuals (Wingfield and Romero, 2000; Cox et al., 2010; Crespi et al., 2013). In wild animals, the most significant stimuli that invokes anxiety in prey species is that of predators (Brown, 1999). In addition to the direct effects of predation in terms of mortality, predation also has indirect effects which can influence nearly all aspects of prey behaviour (Lima, 1998). As such, even in the direct absence of predators, prey should maintain a baseline level of anxiety due to the constant possibility of predation (Brown, 1999). However, this baseline can vary over space or time depending on the varying risk of predation, such as in safe versus risky habitats or depending on time of day (Brown, 1992, 1999; Brown and Kotler, 2004). Understanding the variation in this baseline, particularly in the direct absence of predators, can provide important information on the environmental factors that induce anxiety.

Predator-induced anxiety has been extensively explored in numerous species (Apfelbach et al., 2005), particularly mice (Berton et al., 1998; Belzung and Griebel, 2001), rats (Hendrie et al., 1996) and zebrafish (Blaser et al. 2010; Maximino et al. 2010) using predator models. In primates, including humans, anxiety or stress is typically assessed using faecal glucocorticoids (Rangel-Negrín et al., 2009; Foerster and Monfort, 2010; Crespi et al., 2013). However, recent evidence suggests elevated levels of glucocorticoids do not necessarily mean an individual is anxious or stressed (Beehner and Bergman, 2017). As such, behavioural indicators of anxiety may therefore be more informative. Displacement behaviours such as scratching, self-grooming, body-shaking and yawning (Maestripieri et al., 1992), typically referred to as self-directed behaviours (SDBs), have long been recognised as manifestations of anxiety in nonhuman primates (hereafter, primates) (Baker and Aureli, 1997). Scratching in particular was shown to be the most reliable indicator of anxiety in a study on captive chimpanzees (Baker and Aureli, 1997). Whilst anxiety can be detrimental to an individual in terms of psychological stress (Maestripieri et al., 1992), it can also be beneficial in terms of increasing vigilance or evoking predator-specific alarm calls (Stevenson and Poole, 1976), which in turn helps to reduce the risk of predation (Lima and Dill, 1990; McNamara and Houston, 1992; Brown, 1999).

Whilst some studies cite vigilance as a measure of anxiety (Barros et al., 2000; Coleman and Pierre, 2014), vigilant individuals are not necessarily anxious. Indeed, anxiolytics such as lorazepam have been shown to reduce SDBs, such as scratching, in captive cynomolgus macaques (*Macaca fascicularis*) whereas anxiogenic compounds increase these behaviours

(Schino et al., 1996), thus validating SDBs as anxiety-related behaviours. In contrast, whilst some anxiogenics have been shown to increase vigilance (Palit et al., 1998), anxiolytics appear to have mixed or negative effects (Schino et al., 1991, 1996; Barros and Tomaz, 2002; Barros et al., 2007), meaning vigilance may represent a state of arousal as well as anxiety. Therefore, despite many studies linking vigilance to other behavioural contexts (Allan and Hill, 2018), evidence for vigilance as a measure of anxiety is somewhat mixed and SDBs appear to be the most reliable indicators of anxiety in primates.

The majority of work exploring predator-induced anxiety in primates thus far has focussed on captive individuals, particularly macaques (rhesus, *Macaca mulatta* and cynomolgus, *Macaca fascicularis*) and marmosets (*Callithrix penicillate*) using predator confrontation tests (Barros et al., 2000, 2004; Barros and Tomaz, 2002). These tests present a taxidermied predator to the study subject in a randomly encountered manner, recording the response of the subject on each occasion (Barros et al., 2000). Responses in marmosets typically involved an increase in alarm calls, vigilance and SDBs including self-grooming and scratching (Barros et al., 2004). However, some behaviours stopped following habituation to the stimulus. Whilst studies on wild primates are lacking, wild-reared rhesus macaques showed higher levels of anxiety, indexed by behavioural disturbance, when exposed to a snake compared to their laboratory-reared counterparts (Mineka et al., 1980). However, in both sets of studies, habituation to the stimuli showed marked individual differences, demonstrating the importance of considering individual variation in anxiety (Mineka et al., 1980; Nelson et al., 2003; Barros et al., 2004).

In addition to studies exploring the direct effects of predation on anxiety in wild primates, studies exploring the indirect effects of predation are also lacking (Tkaczynski et al., 2014). Prey species are known to adopt a variety of anti-predator behaviours depending on perceived predation risk (Lima and Dill, 1990). Individuals may avoid areas they perceive to be higher risk (Suhonen, 1993; Cowlishaw, 1997a; Laundré et al., 2001; Heithaus and Dill, 2002; Acebes et al., 2013; Coleman and Hill, 2014), increase their vigilance (Brown, 1999) or increase the number of nearby individuals (McNamara and Houston, 1992), if accessing these high risk areas is necessary. Habitat structure also plays an important role in a prey's perceived risk (Cowlishaw, 1998; Valeix et al., 2009), as visibility affects the ease of escape of prey species (Lima, 1992) whilst affording predators camouflage and ambush opportunities (Hopcraft et al., 2005). In arboreal species canopy height may also influence perceived risk, with areas lower to the ground viewed as 'riskier' habitats (Emerson et al., 2011; Nowak et al., 2014). Furthermore, primates living in groups compete for central positions due to the increased perceived risk of being at the periphery of the group (Tkaczynski et al., 2014). It is therefore possible that these behavioural responses are modulated by anxiety.

In addition to habitat structure, social factors may also influence anxiety and the display of SDBs, such as competition during mating season (Sclafani et al., 2012), agonistic interactions (Aureli, 1997; Castles and Whiten, 1998) and the proximity of higher ranking conspecifics (Castles et al., 1999). Despite this association between SDBs and anxiety in primates, these behaviours, particularly self-grooming, also play a role in hygiene (Maestripieri et al., 1992) and have been shown to correlate with seasonal temperature and humidity (Ventura et al., 2005). Such environmental conditions may be also be linked to increased ectoparasite load.

Finally, studies on anxiety often show marked differences between individuals (Mineka et al., 1980; Nelson et al., 2003; Barros et al., 2004), particularly between age and sex classes (Rangel-Negrín et al., 2009), and controlling for these individual differences is therefore paramount in studies exploring anxiety.

Here, we explored how perceived predation risk influences scratching rate, an anxiety-related behaviour, in the arboreal samango monkey (*Cercopithecus albogularis schwarzi*). The population living in the Soutpansberg Mountains, South Africa, live in a fragmented and highly seasonal environment. In addition, samangos are at risk of predation from multiple predators, including African crowned eagle (*Stephanoaetus coronatus*), leopard (*Panthera pardus*) and African rock python (*Python sebae*). The impact of predation from eagles in particular has been shown to be the key driver of their ranging behaviour (Coleman and Hill, 2014) and an important determinant of behaviour (Parker et al., in prep.). As a result, samangos are expected to experience anxiety from living in a seasonal, multi-predator environment.

To validate scratching as an anxiety-related behaviour, we predicted that the rate of self-scratching would increase after a predator-specific alarm call (Fuller, 2013) relative to a control period. We predicted that areas of high perceived risk from predation would be associated with an increase in scratching, which may indicate an increase in anxiety associated with these high-risk areas. Similarly, we also predicted that scratching would increase as canopy height decreased due to the increased perceived risk associated with areas closer to the ground in arboreal primates (Emerson et al., 2011; Campos and Fedigan, 2014;

Nowak et al., 2014). Scratching was also believed to increase in areas of reduced understory visibility, as a result of the reduced likelihood of detecting a predator (Cowlishaw, 1997b; Hill and Weingrill, 2007) and the increased potential for ambushes (du Bothma and Le Richie, 1986; Shultz, 2001; Hopcraft et al., 2005). We also predicted that samangos would scratch more in areas of the home range used less often (Coleman and Hill, 2014), indicated by distance from morning sleep site. Finally, due to the increased perceived risk associated with increasingly isolated individuals (Tkaczynski et al., 2014), we predicted that scratching would increase when individuals were more isolated, indicated by fewer nearby neighbours. To our knowledge, this study represents a novel approach to exploring anxiety in wild primates in relation to perceived predation risk in the direct absence of a predator.

Methods

Study species and field site

The samango monkey is a predominantly arboreal, diurnal guenon that lives in single-male, multi-female groups (Henzi and Lawes, 1987) of around 30 individuals (Coleman and Hill, 2015; Lawes et al., 2013), with breeding season typically taking place during the dry season (May – July). They are predominantly frugivorous although are capable of consuming large proportions of leaves (Beeson et al., 1996; Coleman and Hill, 2015), whilst also consuming items such as seeds (Linden et al., 2015; Wimberger et al., 2017), flowers and insects (Butynski, 1990; Kaplin, 2001) albeit in smaller amounts. They are heavily reliant on areas of tall indigenous forest for food and shelter (Linden et al., 2016; Wimberger et al., 2017), with the tallest trees in these forests being used repeatedly as sleep sites due to the reduced risk of predation associated with these trees (Smith et al., 2008; Albert et al., 2011).

We conducted fieldwork as part of the Primate and Predator Project at the Lajuma Research Centre (23°02’23”S, 29°26’05”E), at the western edge of the Soutpansberg Mountains, South Africa. Across the mountain range there is substantial seasonal variation, with hot, wet summers from October to March and cool, dry winters from April to September. These conditions result in a variety of vegetation types (Mostert, 2006), including the tall-canopy indigenous mistbelt forest (Mostert, 2006; Mucina and Rutherford, 2006) which dominates the south-facing cliffs as a result of direct mist precipitation and groundwater collection. The mistbelt forest exists in a mosaic of shorter secondary forests such as semi-deciduous woodland, thicket and riverine forests (Hahn, 2006), which are further fragmented by montane grasslands, residential properties, farmlands and commercial plantations.

Data collection

We followed two well-habituated groups of samango monkeys (‘Barn’, 30 – 40 individuals and ‘House’, 60 – 70 individuals) between August 2016 and August 2017. We collected five-minute focal samples (Altmann, 1974) using the ‘Prim8’ app (McDonald and Johnson, 2014) on a mobile smart phone (Samsung Galaxy S5). Focals were collected on identifiable adult females (through ear tags and/or distinguishing features; *n* = 19 across both groups) to remove age and sex biases in anxiety (Rangel-Negrín et al., 2009) and any potential bias from including a single adult male in analysis who was regularly sampled. The same individual was not sampled more than twice per day, and only once in the morning session (before 13:00) and once in the afternoon session (after 13:00). Groups were followed from morning to evening sleep site, with focals collected at 20-minute intervals (e.g., 12:20, 12:40, 13:00) where possible. Only focals lasting the full five minutes were used in analysis, resulting in a total of 252 focals over the study period. Information collected during each focal sample included the date, time, individual ID, group ID, the number of nearest neighbours within 5 m (continuously sampled throughout the five minute sample), and the frequency of self-scratching (quick, repetitive movements of the hand or foot through fur; Barros et al., 2000). Scratching was recorded as separate bouts when separated by a period of five seconds or more (Castles et al., 1999). We also recorded the individual’s location for each focal sample using a handheld GPS (Garmin GPSmap 64S). Behavioural data collection and fieldwork was approved by the University’s use of Live Animals in Unregulated Research protocol (NK_EP/2016-10) and followed the Association for the Study of Animal Behaviour (ASAB) Guidelines (ASAB, 2012). Permits for fieldwork were approved by the Limpopo Province Department of Economic Development and Tourism (LEDET).

To determine perceived predation risk across the home range we followed the approach of Coleman and Hill (2014); using the acoustically distinct alarm calls of adult male samango monkeys (Fuller, 2013) in addition to group-wide alarm calls. Adult male alarm calls such as the *ka* and *katrain* have an unambiguous association with aerial predators (Fuller, 2013), whilst predator-specific alarm calls for terrestrial predators, such as leopards and snakes, do not appear to exist (Coleman, 2013; Fuller, 2013). A lack of specific alarm calls for terrestrial predators is likely a consequence of how infrequently these predator guilds are encountered (Coleman, 2013). In addition, group-wide alarm calls can be attributed to a range of predator guilds, but are commonly associated with raptor antipredator behaviour such as jumping down from the canopy, looking up and scanning the sky. The location and detail of all *ka*, *katrain* and group-wide alarm calls were recorded on an all-occurrence basis between August 2016 – August 2017. This resulted in a total of 356 alarm calls between both groups across the study period, with 83 calls directly associated with a predator (eagle: 74, snake: 9). A further 129 calls were associated with antipredator behaviour from aerial predators (e.g. jumping into trees, coming down from canopy, looking up towards the sky etc.) meaning 59.6% of calls were associated with raptors. We used all alarm calls to create the landscapes of fear, giving an overall spatial map of perceived risk. We also used these alarm calls to validate scratching as an anxiety-related behaviour in this species.

We collected measures of habitat structure using randomly generated 5 m^2 vegetation plots across the study site (n = 702) to give a representation of the various vegetation types (Mostert, 2006). Within each plot, we visually estimated the height of all trees with a diameter at breast height > 10 cm and averaged the height of all these trees to give an estimate of mean canopy height per plot (in m). In addition, we estimated understory visibility for each plot by averaging the number of chequerboard squares counted on a 0.8 m^2 board with 0.1 m^2 cells, at a height of 0 m and 1.25 m and at a distance of 5 m and 10 m, for each of the four cardinal point directions at the northwest corner of each plot. This resulted in 16 chequerboard measurements per plot.

Data processing

All data were imported in QGIS 3.0 (QGIS Development Team, 2018) with the cell size of all output rasters set to 30 m^2, which was consistent with the base map resolution. To calculate the annual landscape of fear for each group, we first created annual utilisation distributions using adaptive localised convex hulls (a-LoCoH) analysis (Getz and Wilmers, 2004; Getz *et al.*,

2007) in the '*t*-LoCoH' package (Lyons et al., 2013) in R 3.5 (R Core Team, 2018). This method uses the greatest distance between recorded location points within each group's respective annual home range as the *a*-value to allow for the correct construction of isopleths (Getz et al., 2007). Annual landscapes of fear for each group were then created using the Kernel Density Estimation tool in QGIS using a PLUGIN bandwidth (Gitzen et al., 2006). This method creates density distributions based on the recorded GPS locations of all recorded alarm calls for each group, resulting in an annual landscape of fear for each group across the study period. These alarm call layers were then divided by the respective utilisation distribution of each group for each year (Willems and Hill, 2009), to account for the time spent in certain areas of the home range and to bind the landscape of fear to each group's range.

We created spatial maps of understory visibility and canopy height using the mean measurements calculated from the vegetation plots. The GPS points of each vegetation plot were imported into QGIS 3.0 (QGIS Development Team, 2018) and the following landscape variables were extracted for each plot using the 'Point Sampling Tool' in QGIS: mean annual EVI (a remotely sensed measure of productivity), elevation, terrain ruggedness and distance to rivers/streams. We then applied a linear regression to predict the mean understory visibility and mean canopy height of each plot based on these landscape variables, with each landscape variable being a significant predictor for each of these measurements. Spatial maps of understory visibility and canopy height were then created using the 'Raster Calculator' in QGIS and applying the regression coefficients from each model to give a habitat structure value for each 30 m^2 cell.

Statistical analysis

We imported the GPS points from all focal samples into QGIS. We then calculated the distance of each focal sample from morning sleep site as a measure of how frequently areas are used, using the ‘Distance Matrix’ tool in QGIS. Values for each of these variables were derived for each focal sample using the ‘Point sampling tool’ plugin in QGIS. We used the ‘dplyr’ package (Wickham et al., 2017) in R 3.5 (R Core Team, 2018) to calculate scratching as a rate per focal sample (frequency per five minutes), in addition to calculating the average number of nearest neighbours within 5 m for each focal.

To validate scratching as an anxiety-related behaviour, we compared the rate of scratching per focal within 10 minutes of an eagle alarm call to the rate of scratching from focals up to one hour before the recorded alarm. Rate of scratching before and after an alarm was compared within the same individual (*n* = 10) using a paired t-test with the t.test function in R. We used a generalised linear mixed model with a poisson error structure to predict the rate of scratching as a function of the landscape of fear, understory visibility, canopy height, distance from sleep site and the number of nearby individuals from the focal individual, whilst also controlling for season (wet vs dry). We controlled for individual differences in anxiety by including individual ID nested within group ID as a random factor. Models were fitted in R using the glmmTMB function in the ‘glmmTMB’ package (Brooks et al., 2017). We ran glms excluding the random effects and used the vif (Variance Inflation Factor) function from the ‘car’ package to investigate collinearity between our predictors. We found no evidence of collinearity with all values below 2.0 (Hair et al., 2014). We also found no evidence of spatial autocorrelation after running a Moran’s I test on the model residuals.

Results

Rate of scratching significantly increased up to 10 minutes after an eagle alarm call relative to a control period up to one hour before the alarm (*t*(9) = - 4.30, *P* = 0.002, Figure 6.1), thus validating this behaviour as an anxiety-related behaviour in samango monkeys. As such, anxiety was defined as scratching in the context of this analysis.

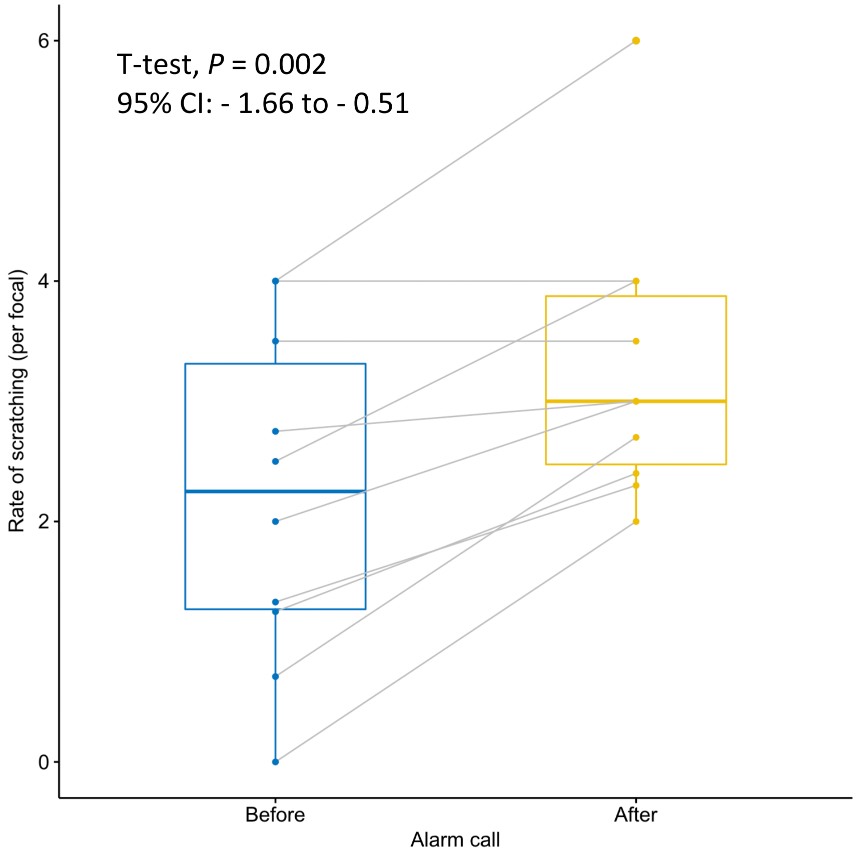

Figure 6.1. Rate of scratching (frequency per five-minute observation) up to one hour before and up to 10 minutes after an adult male alarm call, in 10 identified samango monkeys Lajuma Research Centre, Soutpansberg Mountains, South Africa.

We found that the rate of scratching significantly increased as distance from morning sleep site increased (Table 6.1). In addition, scratching was also more common in the hot, wet season compared to the cool, dry season. Interestingly, perceived predation risk, nor any environmental measures of perceived risk, influenced the rate of scratching. Finally, scratching was not influenced by the number of nearby individuals from the focal individual.

Table 6.1. Coefficient estimates and key statistics of GLMM expressing scratching as a function of landscape of fear, understory visibility, canopy height, distance from morning sleep site, number of nearby neighbours and season.

Coefficient	ß	SE	z-value	CI_{lower}	CI_{higher}	*P*
(Intercept)	0.502	0.129	(1)	0.250	0.754	(1)
Fear	0.074	0.063	1.177	-0.049	0.197	0.239
Understory visibility	0.085	0.068	1.258	-0.048	0.218	0.208
Canopy height	0.042	0.070	0.602	-0.095	0.179	0.547
Nearest neighbours	0.085	0.061	1.409	-0.033	0.204	0.159
Sleep site	**0.130**	0.060	2.186	0.013	0.247	0.029
Season(winter)	**-0.390**	0.123	-3.175	-0.630	-0.149	0.002

Fear, landscape of fear; nearest neighbours, number of nearby individuals within 5 m of focal subject; sleep site, distance from morning sleep site. (1) not shown because of having no meaningful interpretation.

Discussion

In wild animals, the fear of being eaten can make prey species anxious (Brown, 1999). Whilst predator-induced anxiety has been explored extensively in a wide-range of species (Hendrie et al. 1996; Barros et al. 2000; Apfelbach et al. 2005; Blaser et al. 2010), studies on primates (Barros and Tomaz, 2002), particularly wild primates, are lacking (Mineka et al., 1980). In a novel approach we explored how perceived predation risk, and measures of habitat structure associated with risk, influenced anxiety-related behaviour in wild samango monkeys. We found that samangos were more anxious in areas further away from morning sleep site and during the hot, wet summer season, indicating that wild primates may experience anxiety in the direct absence of a predator.

We found that the perceived presence of a predator (indicated by an alarm call) resulted in an increase in the rate of self-scratching in samango monkeys, thus validating this as an anxiety-related behaviour. Self-scratching has also been validated as an indicator of anxiety in other primates, such as chimpanzees (Baker and Aureli, 1997). Self-scratching following an encounter with a predator has also been shown in captive marmosets, which responded to repeated exposure to a taxidermied oncilla cat (*Felis tigrine*) with an increase in self-directed behaviour, including scratching (Barros et al., 2007, 2008). The increase in self-scratching following an alarm call in this study is perhaps unsurprising given the direct costs of mortality from successful predation (Barros et al., 2000, 2004). Anxiety in this case can be beneficial to an individual's survival as it elicits the appropriate antipredator response, such increasing vigilance or group density, or seeking refuge (Brown et al., 1999). Even in the period following an alarm call, maintaining a high level of anxiety may be beneficial as animals know a predator is present but are unsure whether it has left the area, and therefore risk remains high.

We found that distance from morning sleep site was the most significant predictor of self-scratching rate in samango monkeys, with an increase in scratching associated with areas further away from sleep sites. As areas further from sleep sites are used less intensively and are therefore less familiar (Lima and Dill, 1990; McNamara and Houston, 1992; Brown, 1999), they are inherently 'riskier' areas (Coleman and Hill, 2014). It therefore pays for individuals to be more anxious in order to remain alert and increase the chances of predator detection in these areas (Nowak et al., 2017). Samangos may therefore adopt certain antipredator strategies in these areas in order to reduce risk, such as increasing vigilance or the number of nearby individuals (Brown, 1999). However, despite samangos increasing group cohesion in these areas (Parker et al., in prep.) individuals still show increased anxiety in this study. Anxiety in this context may therefore not be associated with predation risk, but rather the anticipation over the increased likelihood of intergroup encounters towards the periphery of the home range (Chapman, 1990; Barrett and Lowen, 1998; Coleman, 2013). Conversely however, samangos like many arboreal primates use the tallest trees in the home range as sleep sites as these trees offer the greatest protection from predators (Chapman, 1990; Barrett and Lowen, 1998; Coleman, 2013), particularly terrestrial predators such as leopards or snakes. A more likely explanation for the observed relationship therefore may be that individuals are less anxious in these areas due to the reduced predation risk afforded by the taller trees.

Interestingly, perceived predation risk (indicated by the landscape of fear) had no effect on anxiety. Despite the increase in risk associated with these areas, many primates have been shown to increase the number of nearby individuals in these high-risk areas (Smith et al., 2008; Albert et al., 2011), including samangos (Parker et al., in prep.). Increasing group cohesion in these areas may help to reduce risk by deterring predators as a consequence of group size (Maisels et al., 1993), or by sharing the vigilance load between individuals (McNamara and Houston, 1992). Samangos may therefore increase or decrease the number of nearby individuals depending on the level of perceived risk in order to maintain a low level of anxiety. Similarly, we found that measures of habitat structure associated with risk (measured as canopy height and understory visibility here) did not influence anxiety. Whilst many arboreal primates, including samangos, view areas nearer the ground as 'riskier' (Hopcraft et al., 2005; Hill and Weingrill, 2007; Emerson et al., 2011), the presence of human observers has been shown to significantly reduce the monkeys' perceived risk of terrestrial predators (Emerson et al., 2011; Campos and Fedigan, 2014; Nowak et al., 2017). The lack of any effect of canopy height in this study may therefore be a consequence of human observers being present during data collection. Primates are also known to associate areas of reduced visibility with increased predation risk (Cowlishaw, 1997b; Coleman and Hill, 2014) and whilst we found no effect of habitat visibility on anxiety here, the presence of human observers may again obscure any possible relationship.

One of the most common stressors in primates is that of fellow group members (Cowlishaw, 1997b; Hill and Weingrill, 2007). Both conflict between (Dunbar, 1988) and the dominance rank (Castles and Whiten, 1998; Castles et al., 1999) of nearby individuals can increase anxiety in the focal individual. In addition, individuals at the periphery of a group may experience more anxiety due to the increased perceived risk of being more isolated (Tkaczynski et al., 2014). Whilst we found no effect of the number of nearby individuals on anxiety, the low level of aggression in this species likely serves to reduce anxiety resulting from conspecifics (Lawes, 1990; Payne et al., 2003). Another potential determinant of perceived risk, and therefore anxiety, is that of other groups (Chapman, 1990; Coleman, 2013). However, due to the influence of human observers on perceived risk (Nowak et al., 2014), encounters in this study were likely biased towards habituated groups due to the "shield" effect of human observers, thereby reducing any impact on anxiety. As such, the impact of intergroup encounters on anxiety was not explored here.

Finally, we found that season strongly influenced the rate of self-scratching, with samangos scratching significantly more often in the hot, wet summer months compared to the cool, dry winters. The summer months at Lajuma are associated with an increase in fruit availability (Coleman, 2013) and so it may be reasonable to expect an increase in anxiety during this period as a result of increased within-group aggression. However, samangos show very little within-group aggression, particularly over resources (Payne et al., 2003), and thus we can rule out any effect of fruit availability here. In contrast, a similar relationship between self-scratching and season was observed in wild Japanese macaques (Ventura et al., 2005), where scratching positively correlated with ambient temperature and relative humidity. In this instance, scratching likely does not indicate anxiety but rather serves as a hygienic function, with the increased need for pelage care possibly associated with variations in piloerection, sweating and ectoparasite load (Ventura et al., 2005). However, these functions of scratching are not mutually exclusive and so samangos may use scratching both as a mediator of anxiety and also to maintain pelage care. It is important to note that another correlate of anxiety is mating (Sclafani et al., 2012). However, we can rule out any relationship with mating here as the samango monkey breeding season in this subspecies is during the cool, dry winter months when scratching was observed to be lowest.

In conclusion, we found that distance from sleep site was the most important factor influencing anxiety in a wild primate, the samango monkey. This increased anxiety can keep individuals alert in unfamiliar areas and elicit the appropriate antipredator response if a predator is encountered, thereby reducing risk. Whilst we found no effect of habitat features associated with risk on anxiety, this may be due to the presence of human observers which reduces any perception of risk in these areas. Future studies should try to account for the effect of humans to determine whether habitat structure does indeed influence anxiety in wild primates. Another potentially important limitation is that analysis was only carried out on adult females in order to keep analysis consistent and remove any potential biases from other age-sex classes which may be exposed to different stressors (e.g. males during breeding season; Sclafani et al., 2012). However, only sampling one age-sex class in this way means that results may not necessarily be applicable to the species as a whole. To our knowledge, this is the first study exploring the relationship between perceived predation risk and anxiety in wild primates. We propose that scratching can be a useful indicator of anxiety in wild primates and can help to improve knowledge on the environmental factors that induce stress in wild populations.

Chapter 6 summary

The findings from this chapter showed that using less familiar areas of the home range can invoke anxiety in the samango monkey. The next and final chapter will summarise the findings from all the data chapters, highlighting the contributions to the field whilst suggesting future directions.

Chapter 7

Discussion

Understanding how animals use space is one of the central issues in behavioural ecology and is fundamental to the allocation of resources for wildlife management and conservation (Zeller et al., 2012). Space use is largely determined by the spatiotemporal variation in resource distribution and predation risk (Zeller et al., 2012). The main aim of this thesis was to investigate this variation in space use from species level to group level in the samango monkey. The results showed that space use at the species level is highly scale-dependent, with highly productive areas at moderate elevations and close to rivers being selected, whilst predation risk and forest availability are more influential at the group level. In addition, habitat features associated with increased predation risk (distance from sleep site) invoked anxiety in this species. This chapter serves to evaluate and integrate the main findings of each chapter whilst suggesting potential directions for future studies.

7.1 Space use at the species level

Despite being a small-ranging species, resource selection functions (RSFs) from Chapter 3 indicated that resource selection in the samango monkey is scale-specific (Boyce, 2006; DeCesare et al., 2012). Highly productive habitat drove selection at the population level, whilst elevation, proximity to rivers and terrain ruggedness were more important at finer scales of selection. These findings show the importance of considering scale in studies exploring resource selection by a species, and that in order to live at sustainable population densities, access to tall-canopy, indigenous forests is crucial. Samango monkeys rely heavily on these forests for food, reproduction and recruitment (Boyce, 2006; DeCesare et al., 2012). In addition to the significance of indigenous forest, the integrated projection from Chapter 3 also highlighted habitat at moderate elevation and in close proximity to rivers as critical samango monkey habitat. The distribution of this suitable habitat is fragmented across Limpopo Province, South Africa, and lacks connectivity between patches. This critical habitat is at risk of being further fragmented as a result of the ongoing deforestation and conversion of land for agriculture and urbanisation (Linden et al., 2016; Nowak et al., 2017). Loss of important habitat is therefore the most immediate threat facing samango monkeys across South Africa (Friedmann and Daly, 2004; Kingdon et al., 2008), and presents a major problem for a species which is susceptible to local extinctions in small forest fragments and is unable to re-colonise forest patches (Lawes et al., 2000; Lawes, 2002; Linden et al., 2016).

However, riverine habitats could be important in connecting fragments of suitable forest, therefore facilitating dispersal between isolated samango subpopulations and increasing the long-term persistence of these subpopulations. Furthermore, due to the ability of samangos to utilise exotic plant species (Wimberger et al., 2017), commercial plantations may also be important in connecting subpopulations, particularly due to the typically large area they cover. Similarly, residential gardens and agricultural areas may also be important on a finer scale due to the capacity of samangos to use these areas as part of the habitat matrix (Swart and Lawes, 1996; Nowak et al., 2017).

These results represent only the second known study using RSFs to explore scale-dependent resource selection in primates (Sawyer and Brashares, 2013). Given the imperilled status of many of the world’s primates (Estrada et al., 2017), and the importance of identifying critical habitat to inform conservation management, RSFs should be used more frequently in primate studies to establish more efficient management plans.

7.2 Space use at the group level

The results from Chapter 3 highlighted the importance of tall-canopy, indigenous forests in determining samango monkey distribution. However, these forests also appeared to have an important influence on ranging patterns too, as the results from Chapter 4 suggest. Both core and total monthly home range size decreased as more tall-canopy, indigenous mistbelt forest was incorporated into the home range. These findings further demonstrated the dependence of samango monkeys on these forest types, and that in order to maintain sustainable population densities, access to indigenous forest patches is key (Linden et al., 2016; Wimberger et al., 2017). Not only are these forests perceived as safer habitats (Coleman and Hill, 2014; Nowak et al., 2017), but they also contain important food items for samangos (Coleman, 2013; Linden et al., 2015). Samangos can therefore reduce their ranges and fulfil energy requirements by incorporating more indigenous forest into the home range. Whilst some samango groups have been shown to preferentially feed in the indigenous forest if given a choice (Wimberger et al., 2017), the study groups here are capable of utilising a rich matrix habitat when home ranges included less indigenous forest.

Highly productive habitat also influenced the total (95% isopleth) monthly home range size and day journey length (DJL), which both significantly decreased as more highly productive cells were incorporated into the home range. These cells were derived from remotely sensed composites above a specific threshold, and were positively correlated with the dense, tall-canopy indigenous forests. Samangos are therefore able to maximise their energy intake by reducing certain ranging patterns (Hall, 1962) when more highly productive habitat is used. Whilst no relationship with core (50% isopleth) monthly home range was found, this is likely due to the consistently high productivity of these areas resulting from the location of important feeding areas and sleep sites (Kaplin, 2001; Albert et al., 2011).

Interestingly, average productivity across the home range appeared to be uninformative, and it was only when looking at the availability of highly productive areas (remotely sensed cells in this case), that a relationship with ranging patterns was observed. This is perhaps surprising, given the numerous studies that have observed a relationship between remotely sensed productivity and ranging patterns in various mammals (Leimgruber et al., 2001; Zinner et al., 2002; Nilsen et al., 2005; Ito et al., 2006; Willems et al., 2009; Fullman et al., 2017). However, despite being forest-specialists, samango monkey home ranges are likely to incorporate areas of lower productivity, such as matrix habitat or corridors used to access more productive areas (Lawes, 2002). As such, using average productivity across the home range may mask areas or periods of high productivity.

As access to tall-canopy, indigenous forest patches was key to variation in home range size, it is perhaps unsurprising that food availability had no effect. If samangos incorporate more indigenous forest into the home range, which subsequently contains more important food items (Coleman, 2013; Linden et al., 2015; Wimberger et al., 2017), then accessing food in the ‘riskier’ matrix habitat (Nowak et al., 2014, 2017) becomes less of a necessity. Instead, food availability may have a greater impact on the location of the home range, rather than the size, as has been observed in other species (Willems et al., 2009; Albert et al., 2013).

This study is one of few studies to explore the effect of remotely sensed productivity on primate ranging patterns (Zinner et al., 2002; Willems et al., 2009). However, the previous studies looked at this relationship in the grivet monkey (*Cercopithecus aethiops aethiops*, Zinner et al., 2002) and vervet monkey (*Chlorocebus pygerythrus*, Willems et al., 2009), both semi-terrestrial species. In light of this, the results from this study suggest using remotely sensed productivity across the home range is uninformative for forest-dwelling species, which typically inhabit areas of consistently high productivity. Therefore, using highly productive cells above a certain threshold (derived from remotely sensed composites) is a much more informative measure when exploring the effect of remotely sensed productivity on ranging patterns in forest-dwelling species.

7.3 Spatial variation in behaviour

Chapter 3 and 4 demonstrated that space use in samango monkeys is greatly influenced by the distribution of resources in both space and time. Perhaps of more significance in terms of accessing resources however, is the spatiotemporal distribution of predators across the home range. As successful predation incurs the ultimate fitness cost to prey in terms of mortality, the presence of predators affects almost every aspect of prey behaviour (Lima, 1998). The findings from Chapter 5 confirm this, showing that perceived predation risk and habitat features associated with risk are the most significant landscapes influencing the spatial variation in samango monkey behaviour.

Whilst previous studies have shown that samango monkeys actively avoid areas within their home range where perceived predation risk is highest (Coleman and Hill, 2014), when entering these high-risk areas the proportion of individuals feeding significantly increased. As food acquisition is fundamental to an individuals' survival (Schoener, 1971; Pyke, 1984), prey species must often face a trade-off between maximising food intake whilst minimising predation risk (Lima and Dill, 1990). Many species balance this trade-off by foraging in food-poor areas where predation risk is lowest (Dill and Fraser, 1984; Suhonen, 1993; Cowlishaw, 1997a; Heithaus and Dill, 2002; Hernández and Laundré, 2005; Acebes et al., 2013; Cappa et al., 2014). However, sometimes the benefits of acquiring food, such as high-energy, temporally available or clumped items, outweighs the potential costs of predation (Wright, 1998; Stone, 2007; Wirsing et al., 2007; Stears and Shrader, 2015). Across the study area, high-energy clumped food items, such as large fruiting trees, are common (Coleman, 2013). When these trees occur in high-risk areas, particularly during months where overall fruit availability across the landscape is low (Coleman, 2013), the benefits of accessing these food items may outweigh the potential predation costs for samangos, particularly if other antipredator behaviours are adopted to reduce predation risk. Additionally, the unusually large group sizes of samangos at Lajuma may mean increased within-group competition for resources may force individuals to enter higher risk areas to access food resources (Watts, 1985).

Similarly, samangos avoid areas of reduced understory visibility and decreased canopy height within their home range (Coleman and Hill, 2014), factors indirectly associated with predation risk (Lima, 1992; Hart et al., 1996; Hill and Weingrill, 2007; Jaffe and Isbell, 2009). When entering these areas however, samangos again increased feeding relative to other behaviours in order to maximise consumption of important food resources in these risky habitats. Whilst no relationship between feeding and fruit availability was observed this is likely a result of samangos' dietary flexibility, as samangos can increase leaf consumption in areas of low fruit availability (Coleman and Hill, 2015; Linden et al., 2015; Wimberger et al., 2017), thereby maintaining high levels of feeding.

In order to minimise the potential risk of foraging in high-risk areas, samango monkeys adopt one important behavioural strategy. Samangos increase group cohesion (indicated by the number of near neighbours) in high-risk areas, thereby mitigating any potential risk associated with foraging in these areas by sharing the vigilance load between individuals and deterring predators due to the "dilution effect" (Maisels et al., 1993). High-risk areas were also associated with fewer individuals moving. Reduced moving in this case may either be to reduce the chance of walking into an ambush (du Bothma and Le Richie, 1986) or as a consequence of spending more time feeding on large fruiting trees where individuals can feed without moving between patches (Whitten, 1988).

Although perceived predation risk did not influence where individuals groomed, resting was associated with the safest areas within the home range where perceived predation risk was lowest. Whilst some resting is 'enforced', such as during digestion or thermoregulation (Korstjens et al., 2010), it is inherently a risky behaviour and should therefore be reserved for the safest areas (Cowlishaw, 1997a; Heithaus and Dill, 2002). Resting was also less common in areas of high fruit availability, possibly a result of samangos prioritising feeding in these areas whilst reserving resting for relatively fruit-poorer areas (Cowlishaw, 1997a).

Despite increasing vigilance being one of the most common antipredator strategies in response to predation risk (Brown, 1999; Laundré et al., 2001), samango monkeys showed the opposite trend which was somewhat contradictory. One possible explanation for this relationship is the foraging/vigilance trade-off (Cowlishaw, 1997b; Coleman, 2013), although as feeding and vigilance are not incompatible in primates, a more likely possibility lies in the fact samangos increase group cohesion in high-risk areas. Increasing the number of near neighbours may successfully mitigate the potential risk of being in high-risk areas by sharing the vigilance load and deterring predators due to group cohesion (McNamara and Houston, 1992; Maisels et al., 1993; Cowlishaw, 1998). Samangos were also less vigilant in areas of increased understory visibility, a finding consistent with other studies (Burger, 2001; Enstam and Isbell, 2004; Whittingham et al., 2004) due to the increased chance of detecting predators (Hill and Weingrill, 2007; Jaffe and Isbell, 2009). Vigilance also decreased in areas of high fruit availability, possibly due to the foraging/vigilance trade-off (Cowlishaw, 1997b; Coleman, 2013) or more likely as a consequence of sharing the vigilance load whilst individuals clump together at resources (Stevenson et al., 1998; Koenig, 2002; Basabose, 2004). Finally, the proportion of vigilant individuals decreased in areas further away from sleep sites. Despite this relationship appearing contradictory, samangos again increase group cohesion in these areas which may mitigate any potential risk associated with areas used less intensively.

Whilst the foraging or vigilance/risk trade-off has received much attention in a wide range of species in the literature, studies exploring the effect of perceived predation risk on other behaviours are currently lacking, particularly in primates (Cowlishaw, 1997a). The results of this study further demonstrate the impact of predation on the behavioural ecology of prey. In addition, these results show that perceived predation risk influences many aspects of samango monkey behaviour, with the distance between neighbours appearing to be the main antipredator response in successfully managing risk across the home range. Future studies should also consider more specific behaviours when exploring the effect of predation risk on prey species, and would also benefit from incorporating the utilisation distribution of predators when exploring spatial variation in behaviour of prey species.

7.4 Anxiety-related behaviour

The results of Chapter 5 demonstrated the impact of perceived predation risk on prey behaviour. However, predation risk may also influence a prey species in terms of the physiological stress response (Berton et al., 1998; Barros and Tomaz, 2002; Maximino et al., 2010; Tkaczynski et al., 2014), which can be monitored using anxiety-related behaviours (Maestripieri et al., 1992; Blaser et al., 2010). Self-scratching was validated as an anxiety-related behaviour in Chapter 6, as the rate of scratching increased after an eagle alarm call (indicating the presence of a predator) relative to a control period. These results confirm findings from captive studies, where marmosets (*Callithrix penicillate*) increased self-directed behaviours (such as scratching and self-grooming) after exposure to a taxidermied oncilla cat (*Felis tigrine*) (Barros et al., 2007, 2008).

The findings from Chapter 6 also showed that perceived predation risk associated with areas of the home range used less intensively was the only environmental variable that influenced anxiety (indicated by self-scratching) in samango monkeys, as individuals were more anxious in areas further away from the morning sleep site. It is understandable that samangos are anxious in unfamiliar and therefore inherently ‘riskier’ habitats (Coleman and Hill, 2014; Nowak et al., 2017), as being anxious in these areas can be beneficial to animals by remaining alert and eliciting the correct antipredator response (Brown et al., 1999). Despite the findings from Chapter 5 showing that samangos increase group cohesion in these areas, this reduced distance between neighbours does not appear to successfully manage anxiety. However, the increase in anxiety in these areas may not necessarily be associated with perceived predation risk, but rather anxiety in anticipation of the increased likelihood of intergroup encounters at the periphery of the home range (Chapman, 1990; Barrett and Lowen, 1998; Coleman, 2013). Conversely however, samangos were less anxious near sleep sites as the taller trees in these areas reduce the risk of predation from terrestrial predators, such as leopards or snakes (Smith et al., 2008; Albert et al., 2011).

Interestingly, the landscape of fear, nor any measures of habitat structure associated with risk, influenced anxiety in samango monkeys. Despite the increase in risk associated with these areas, the findings from Chapter 5 showed that samangos adopted various antipredator strategies in high-risk areas which may successfully manage risk, such as increasing vigilance in areas of low understory visibility and increasing the number of near neighbours in areas of high perceived risk. These behavioural responses, through predator deterrence (Maisels et al., 1993) and the sharing of the vigilance load (McNamara and Houston, 1992), may help to successfully manage any impact on anxiety resulting from being in areas of high perceived risk. In addition, the presence of human observers, which act as a “shield” from predators (Nowak et al., 2014), may successfully reduce any impact of habitat features associated with risk on anxiety.

The number of nearby individuals did not influence anxiety in samango monkeys. Despite conflict between (Castles and Whiten, 1998), and dominance rank of nearby individuals

(Castles et al., 1999) being common stressors, a lack of a relationship observed here is likely a result of the low levels of aggression reported in samango monkeys (Payne et al., 2003). However, there was a strong seasonal effect on scratching, with the rate of scratching significantly increasing in the warmer, wetter summer months. Although scratching in this case is likely a hygienic response to the increased need for pelage care resulting from environmental conditions (Ventura et al., 2005), rather than an increase in anxiety.

This study is one of few studies investigating the effect of perceived predation risk on anxiety in wild primates (Mineka et al., 1980; Nelson et al., 2003). Furthermore, this is the first study to explore the indirect effects of predation, in terms of habitat structure and distance from sleep sites, on anxiety in wild primates. As predation risk affects almost every aspect of prey behaviour (Lima, 1998), further research exploring these relationships would be hugely beneficial to understanding the environmental factors that influence anxiety in wild primates.

7.5 Conservation management plans

The findings from various chapters of this thesis have demonstrated the reliance of samango monkeys on tall canopy indigenous forests. Loss and fragmentation of suitable forest patches is therefore the greatest, most immediate threat facing samango monkeys across their range (Linden et al., 2016). This fragmentation of suitable habitat brings samangos into closer contact with humans and human infrastructure, which in turn has seen an increase in the number of mortalities resulting from road collisions and electrocutions on power lines. The key intervention strategy for this species is therefore protected area expansion and proper management of indigenous forest habitats, particularly in terms of reclaiming and restoring areas of non-viable habitat or areas where indigenous forest previously existed (Linden et al., 2016). Areas of riparian forest along streams and rivers are particularly important as they are conductive to indigenous forest growth and therefore maintain connectivity between patches of suitable habitat (Linden et al., 2016). Additionally, minimising the disturbance in and around large forest patches is also a key management strategy as these areas are essential for samango monkey movement (Linden et al., 2016). Conservation plans should therefore focus on maintaining and connecting fragments of suitable forest in order to facilitate the dispersal of mature individuals between subpopulations, which will ensure the long-term persistence of metapopulations (Swart and Lawes, 1996; Lawes et al., 2000). On a finer scale, effective forest management is also important. This includes proper training of forest guards in order to reduce poaching and potential disturbances. Furthermore, educating the surrounding communities on proper waste management and reducing accessibility to potential attractants is important in order to reduce human-wildlife conflict. Communities should also be encouraged to plant indigenous species, rather than exotic species, in order increase connectivity between forest patches whilst also making residential gardens less appealing to samangos (Wimberger et al., 2017). Finally, “monkey bridges” and warning signs should be erected where road collisions are common to encourage samango monkeys to cross roads at specific locations (Linden et al., 2016).

In the Soutpansberg, areas of priority are forest patches to the east of the mountain range, which are larger in size than patches in the west, but are under greater pressure from human disturbance (Linden et al., 2016). Protected areas in the Soutpansberg (such as Lesheba Wilderness Reserve and Happy Rest Nature Reserve) only exist in the western part of the mountain range, and currently only represent a small area and lack connectivity. Protected areas in the east are almost entirely lacking, despite this area being more densely populated by humans (Linden et al., 2016).

7.6 Methodological limitations and future directions

Throughout this thesis there are some important methodological limitations to consider. In Chapter 3, one of the greatest limitations was that data was only collected on two samango groups due to constraints with the number of field assistants and difficulty with habituating other samango groups. Whilst there are no strict guidelines on the number of individuals/groups to use in RSF models, having a larger sample size leads to more robust coefficient estimates as each individual/group will experience slightly different environmental variables which the model will account for (Koper and Manseau, 2012). Furthermore, the scale-integrated probability of use could only be projected so far based on data from two groups. Whilst the projection was consistent with recorded samango locations across the Soutpansberg, Woodbush Forest Reserve and Drakensburg Mountains (Linden et al., 2016), validating this analysis using recent samango "presence" locations across Limpopo Province should be a future aim. Management plans would also benefit from similar analyses on the other samango monkey subspecies to identify areas of priority within their range.

In Chapter 4, the remotely sensed data from the Landsat satellites used to derive measures of productivity was a relatively low resolution at 30 m^2 compared to other newer satellites, such as the Quickbird satellite (Toutin and Cheng, 2002), which has a resolution of 2.44 m^2. A greater resolution may have better distinguished between habitat types and areas of high/low productivity in a pronounced heterogenous landscape such as at Lajuma (Mostert, 2006). In addition, the resolution of the Landsat composites may have overrepresented productivity in some areas which may have influenced some results, particularly in such a small ranging species like samango monkeys. As such, future studies may benefit from using a finer resolution of remotely sensed data. The findings from this chapter also showed that measures of habitat productivity (derived from remotely sensed data) can predict ranging patterns in a forest-dwelling species, and future studies should explore this relationship further.

The analysis in Chapter 5 may have benefitted from actual predator locations in order to disentangle the relationship between perceived risk and actual risk. However, obtaining actual predator locations is often difficult without telemetry data, and was beyond the scope of this study. Furthermore, the focus of this study was concerned with the monkeys' *perceived* risk of predation, which itself is informative without predator locations. Regardless, exploring behaviour in relation to the presence of predators may be an interesting question for future studies. Another potential limitation of this chapter lies in that the proximity of both groups means they are exposed to similar predation pressures (e.g. the location of the eagle's nest). However, this is again in itself informative as both groups react similarly to the landscape of fear dominated by the same predator guild. Exploring the spatial variation in behaviour in groups exposed to slightly different predation pressures would nevertheless be beneficial.

One of the biggest limitations of Chapter 6 was how anxiety was measured. Self-directed behaviours, particularly self-scratching, are strongly linked to anxiety in nonhuman primates (Baker and Aureli, 1997). Whilst behavioural measures of anxiety are informative, physiological measures have widely been used in studies exploring anxiety and stress, particularly with the use of faecal glucocorticoids (Rangel-Negrín et al., 2009; Foerster and

Monfort, 2010; Crespi et al., 2013). However, recent evidence suggests elevated levels of glucocorticoids do not necessarily mean an individual is anxious or stressed (Beehner and Bergman, 2017). Whilst validating behavioural measures of anxiety with faecal glucocorticoids would have been beneficial, it was beyond the scope of this study and future studies should therefore look to validate this relationship.

7.7 Final conclusions

This thesis set out to investigate how ranging patterns and resource use govern space use in the samango monkey. Resource use at the species level is scale-specific. The availability of highly productive, tall-canopy indigenous forests is critical to samango monkey space use on a coarse scale, whereas other resources become more important on a finer scale. These indigenous forests are also vital to samango monkey ranging patterns, as home ranges which include more indigenous forest, and therefore important food items, can be smaller, thus reducing the energetic demand in terms of travel (Hall, 1962). Whilst resource availability has an important influence on space use, so too does the presence of predators. As a result of living in a multipredator environment, samangos adopt various antipredator strategies. Samangos not only disproportionately use areas of their home range depending on perceived predation risk (Coleman and Hill, 2014), they also increase group density and move less in high-risk areas in order to mitigate the risk of increasing feeding in these areas. These behavioural responses to perceived predation risk may also mitigate the impact of anxiety resulting from living in a multipredator environment.

Habitat loss and fragmentation of the world’s forests is occurring at an unprecedented rate (Haddad et al., 2015), which has subsequently resulted in a significant decline in global biodiversity. The main results of this thesis highlight the importance of tall-canopy, evergreen indigenous forests to samango monkey survival and persistence and, as such, management plans for this species should prioritise expansion of protected areas of large forest patches and protection of forest corridors linking suitable habitat (Linden et al., 2016). More broadly however, the results of this thesis demonstrate the importance of emerging technological and statistical techniques in conservation management of threatened species. Advances in more accurate home range estimation methods (Getz and Wilmers, 2004; Getz et al., 2007), radio telemetry (Cagnacci et al., 2010; Tomkiewicz et al., 2010), geographic information systems (GIS), and remote sensing (Huete et al., 2006, 2010), have all greatly enhanced our understanding of animal movement patterns and resource use (Pettorelli et al., 2011; Neumann et al., 2015), and future studies should continue to use and develop these methods in order to further increase our understanding of behavioural ecology.

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Appendix 1

Appendix Table 1. Coefficient estimates and key statistics predicting effect of mean EVI across the home range, with a one and two-month lag, on total home range size.

Variable	Estimate	X^2	SE	CI_{lower}	CI_{upper}	P
$HR95^1$						
Intercept	0.363	(1)	0.142	0.052	0.665	(1)
EVI^1	-0.045	0.256	0.078	-0.209	0.137	0.613
Daylength	-0.011	0.798	0.012	-0.038	0.014	0.372
Days	**0.008**	9.832	0.002	0.003	0.012	0.002
Group	-0.006	0.190	0.013	-0.032	0.020	0.663
$HR95^2$						
Intercept	0.455	(1)	0.134	0.148	0.725	(1)
EVI^2	-0.142	2.435	0.076	-0.295	0.042	0.119
Daylength	-0.013	1.486	0.010	-0.034	0.009	0.223
Days	**0.008**	10.183	0.002	0.003	0.013	0.001
Group	-0.005	0.155	0.013	-0.031	0.021	0.694

$HR95^1$, total monthly home range size model 1; $HR95^2$, total monthly home range size model 2. EVI^1, averaged enhanced vegetation index within the total monthly home range with a one-month lag; EVI^2, averaged enhanced vegetation index within the total monthly home range with a two-month lag. (1) not shown because of having no meaningful interpretation.