# Habitat use and movement of proboscis monkeys (*Nasalis larvatus*) in a degraded and human-modified forest landscape

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# Abstract

Proboscis monkeys (*Nasalis larvatus*) are endemic to Borneo and live in habitats threatened by land clearance for agriculture, aquaculture and timber. This thesis examines the roles of structural and landscape characteristics on both short- and long-term habitat use through the first application of GPS tags to proboscis monkeys. In a comparison of four home range estimators, biased random bridges provided the best home range estimates given the GPS-collar dataset and landscape characteristics (Chapter 3). Differences in long-term ranging patterns of 10 individuals across a range of forest-block sizes and disturbance levels were examined, as well as daily and seasonal variation in movement and sleeping site selection. Using Light Detection and Ranging (LiDAR) structural metrics of the forest, as well as landscape characteristics, forest with taller canopies, forests in close proximity to river edges were found to be of particular importance to proboscis monkeys, and plantation edges were avoided (Chapter 4). Changes in daily and monthly movements were associated with seasonal changes in rainfall and potential food availability. Movement patterns also changed near forest edges, with faster, more direct movements near agricultural boundaries. Less rainfall, higher temperatures and brighter moon phases correlated with selection of sleeping sites in the forest interior (Chapter 5). By understanding the ranging requirements of proboscis monkeys, drone and GPS collar data were combined to inform conservation policy (Chapter 6). This thesis provides the most in-depth examination of proboscis monkey ecology to date. They appeared more generalist in their home range use and structural habitat requirements than previously realised, suggesting a higher degree of versatility and resilience to habitat loss and degradation. This study provides increased understanding of potential consequences of human-mediated disturbances and can be used to assist in the protection of this charismatic species and the management of degraded landscapes.

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## Chapter 3:

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DJS designed the study with supervision from IPV and BG; DARS and SKSSN captured and sedated the animals; DJS set the collars, collected the data, performed statistical analysis and wrote the manuscript. All authors commented on manuscript drafts.

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DJS designed the study with supervision from IPV and BG; LJE coordinated the drone missions; HK provided background on the initiative; DJS collected the tracking data, performed statistical analysis and wrote the manuscript. All authors commented on manuscript drafts.

## List of publications during PhD thesis work

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# Chapter 1  General Introduction

## 1.1  Introduction

Globally, the combined effects of habitat loss and fragmentation are considered the most important factor in declining biodiversity (Fisher and Lindenmayer 2007). Habitat fragmentation and degradation often accompany habitat loss, which results in increased numbers of fragments, a decrease in the size of these fragments, an increase in total forest edge habitats, and greater isolation between fragments (Arroyo-Rodríguez and Mandujano 2009). These processes affect many ecosystems, but especially high levels of deforestation are occurring in tropical forests across the globe (Hansen et al. 2013). This is a particular cause for conservation concern due to the very high levels of biodiversity in the tropics, with the remaining tropical forest estimated to contain between 50 and 90% of all terrestrial species (Shvidenko et al. 2005).

A side effect of habitat loss and fragmentation is that human-made forest edges are becoming more prevalent across the globe (Harper et al. 2005). Deforestation exposes the newly made forest edges to novel biotic and abiotic factors, whilst fragmentation increases the ratio of edge length to habitat area. Forest edges are dynamic zones that vary in the depth and intensity that the surrounding environment penetrates into the forest interior. These zones can influence the dynamics and distribution of animal and plant populations in the area (Lehman et al. 2006) and have been shown to lead to further interior habitat degradation (Laurance et al. 2002). Whilst natural edge habitats, such as those along waterways, can be an important source for food, protection, sociality, and may support a high diversity of terrestrial and arboreal mammals (Ayres and Clutton-Brock 1992; Matsuda et al. 2009a), edge effects due to human activities may impact population abundance and community structure more than total fragment area does (Didham and Ewers 2012). Although some species may increase their habitat use along human-made edges (e.g. predators), as edges can improve the food

resources available, many more species may decrease their use due to increased predation risk (Brodie et al. 2015).

Most non-human primate species are found in tropical regions (Chapman and Peres 2001), and many of them are vulnerable to extinction due to the modifications in the forests they rely on (Estrada et al. 2017). This results in isolated primate populations living in low-quality habitats (Cowlishaw 1999), and forces many species to adapt to novel conditions, such as changes in food quality and environmental elements, reduced habitat area, and increased exposure to humans (Murcia 1995; Chapman et al. 2006a; González-Zamora et al. 2011).

Globally, Asia combines some of the highest primate diversity and fastest rates of tropical forest loss (Gaveau et al. 2014; Irwin 2016). As a consequence, Asia is the second only to Madagascar in its percentage of threatened primate species and those with declining populations (Estrada et al. 2017). In Southeast Asia, primates have largely been affected by habitat loss and fragmentation due to human activities such as logging and the expansion of oil palm (*Elaeis guineensis*) (Turner and Foster 2008; de Almeida-Rocha et al. 2017). Indonesia and Malaysia hold more than 80% of the remaining primary forest in Southeast Asia (Fitzherbert et al. 2008), but also produced 86% of the world's palm oil by 2013 (Rifai et al. 2015). Up until the 1980's, the main driver of forest loss was commercial logging, but then it switched to agricultural plantations (McMorrow and Talip 2001; Gaveau et al. 2016). After the decline of available land for oil palm trees in Peninsular Malaysia, there was an expansion of oil palm plantations in Malaysian Borneo (Hai et al. 2001). From 1973-2015, Sabah had lost 1.9 Mha (32%) of its forest cover, 65% of which had been converted to oil palm plantations during that time (Gaveau et al. 2016). By 2001 most of the suitable soils had already been planted with oil palm in Sabah, but continued to expand in vast areas

of marginal suitability (Hai et al. 2001). By 2015, 12.5% of Borneo and 24% of Sabah's land area was covered in industrial-scale oil palm plantations (Gaveau et al. 2016).

## 1.2   Study subjects

Proboscis monkeys (*Nasalis larvatus*) are endemic to the island of Borneo, and live in riparian, mangrove and swamp forests (Meijaard and Nijman 2000a; Sha et al. 2008. These are amongst the most threatened of all habitat types in Borneo, largely due to the clearing of forest for agriculture, aquaculture, and logging (Rautner et al. 2005), which may subsequently be restricting the ranging and dispersal patterns of proboscis monkeys. As a result of habitat loss, proboscis monkeys are listed as Endangered (A2bc) on the IUCN Red List, with a declining population trend (Meijaard et al. 2008). Proboscis monkey population estimates have increased in recent years, but it is thought to be due to more extensive surveys and improved methodology rather than an actual increase in population size (Bernard and Zulhazman 2006; Sha et al. 2008; Stark et al. 2012; Matsuda et al. *in press*). Only ~15% from an estimated population size of 6,000 live in totally protected areas in Sabah (Sha et al. 2008).

Proboscis monkeys live in either stable one-male or all male (or non-breeding) social groups (Bennett and Sebastian 1988; Boonratana 2000). Multiple groups can form a second level of social organisation, called a band, that travel together for many days, and sleep in close proximity to each other before separating back into smaller stable family units (Bennett and Sebastian 1988; Yeager 1991). Proboscis monkeys are sexually dimorphic, with adult males weighing around 20-25 kg, more than double that of the females. They are colobine monkeys, feeding mostly on young leaves, unripe fruits and seeds, typically consuming the most abundant plant species in their habitat (Yeager 1989; Matsuda et al. 2009b). Proboscis monkeys are able to cope with the high levels of leaves in their diet due to a foregut-fermentation process. Regurgitation

and remastication (i.e. rumination) has also been observed in wild proboscis monkeys and is thought to aid further in the digestion process (Matsuda et al. 2011a).

Due to the water-logged habitat that proboscis monkeys are often found in, it has been more difficult for researchers to continuously follow and observe groups than for other colobine species (Bennett 1986; Newton 1992; Fuentes 1996; Li et al. 2000; Teichroeb et al. 2012). The majority of studies on proboscis monkeys and their basic ecology have been restricted to riverbank observations (Murai 2004; Bernard et al. 2010; Feilen and Marshall 2017; Thiry et al. 2016). Groups are thought to travel no more than half a day's journey from the river, up to 800 m from the riverbank (Matsuda et al. 2009a), but relatively little is known about how they use these inland habitats.

Proboscis monkeys are able to live in disturbed or secondary forest, but avoid severely disturbed areas, such as oil palm plantations, agricultural areas, and areas of extensive grasslands and human settlements (Salter et al. 1985; Boonratana 2000; Bernard and Zulhazman 2006). Riparian forests are not used evenly throughout the species range (Matsuda et al. 2009a), with a preference for taller forests and areas with greater tree coverage (Boonratana 2000). The extent to which proboscis monkeys visit the forest floor appears to vary, with some studies concluding that they rarely travel to the ground (Salter et al. 1985), whilst others have observed them travelling, socialising and resting on the forest floor in secondary forest (Salgado-Lynn 2010, B. Goossens *unpublished data)*.

Proboscis monkey home ranges are estimated to be 137-260 ha in swamp and riparian forests (Salter et al. 1985; Yeager 1989; Boonratana 2000; Matsuda et al. 2009a), and 300-900 ha in mangrove forests (Bennett and Sebastian 1988; Boonratana 2000; Onuma 2002). However, as it has been difficult to continuously follow proboscis monkeys, home range and population sizes have been largely extrapolated using

riverbank observations. Only three studies have been able to calculate ranging patterns based on actual tracking through the forest, each focussing on a single group or a solitary individual (Boonratana 2000; Onuma 2002; Matsuda et al. 2009a). Following the release of a proboscis monkey caught in a fishing net, a female was tracked for 12 days over a 2-month period using radio-telemetry and triangulation; the female was only directly observed five times (Onuma 2002). The other studies were along a tributary in the riparian forest of the Kinabatangan floodplain, tracking the group by foot for 93 (Boonratana 2000) to 161 days of full follows (Matsuda et al. 2009a).

## 1.3   Study area: the Lower Kinabatangan Floodplain

### 1.3.1   Geography

The Lower Kinabatangan Floodplain is located in eastern Sabah, Malaysian Borneo (approximate range: 5°'18'N to 5°42'N and 117°54' to 118°33'E) (Fig. 1.1). The climate is humid tropical, with an average annual rainfall of approximately 3,000 mm (Chapter 5). Mean temperatures range from 23°C to 36°C across the year (Chapter 5). The Kinabatangan River is the longest river in Sabah, flowing 560 km to the east coast of Sabah, and draining a catchment of 1,680,000 ha (Estes et al. 2012). Active and ancient oxbow lakes are scattered throughout the floodplain, and it is considered among the most productive types of wetlands and one of the most significant in Sabah (Davison 2006). It comprises riparian, seasonally flooded/inundated, swamp, dry dipterocarp, estuary nipa palm, and mangrove forests (Estes et al. 2012). The area is characterised by seasonal and occasionally severe flooding (Davison 2006).

Within the floodplain is the Lower Kinabatangan Wildlife Sanctuary (LKWS), consisting of 10 forest blocks (or lots) totalling 27,000 ha and ranging in size from 870 ha to 7,420 ha (Ancrenaz et al. 2004). The broad disturbance levels for the LKWS lots include undisturbed (~5,000 ha), disturbed (~23,000 ha) and heavily disturbed forests (4,200

ha) (Ancrenaz et al. 2004). The lots extend along ~150 km of the Kinabatangan River and are interspersed with patches of Virgin Jungle Reserves (VJR, 8,900 ha) and ~10,000 ha of state and private land (Ancrenaz et al. 2004; Estes et al. 2012). Despite this, the lots and forest reserves are not well connected, sometimes only through narrow strips of highly degraded forest, or are completely isolated (Abram et al. 2014). Although the severity of disturbance varies in the privately owned forest, it is still considered a viable habitat for wildlife (Ancrenaz et al. 2004).
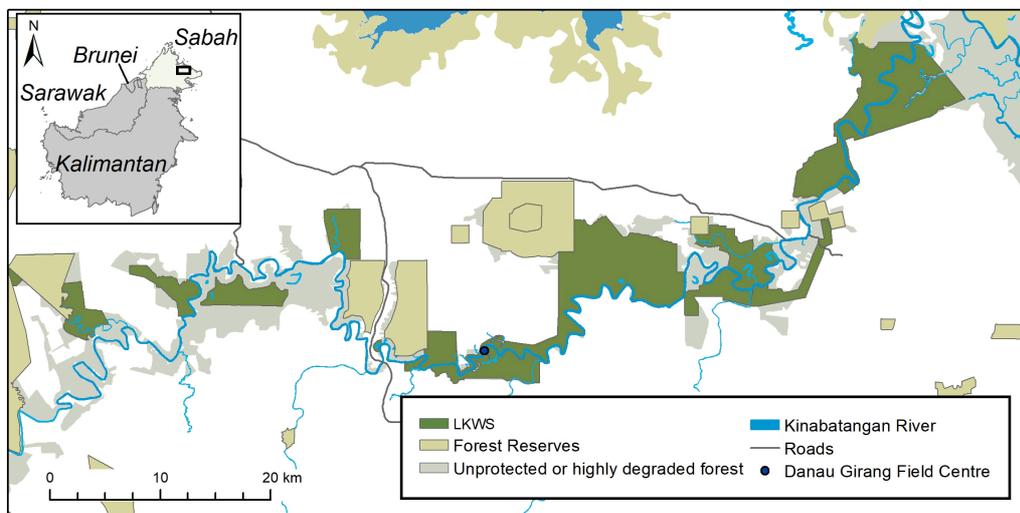


Figure 1.1 Map of the protected and unprotected forests in the Lower Kinabatangan Floodplain, and field station (Danau Girang Field Centre) in Sabah, Malaysian Borneo.

*1.3.2   Wildlife*

Besides containing one of the largest protected populations of proboscis monkeys remaining in Borneo (approximately one-third of Sabah's population), the Kinabatangan Floodplain is home to long-tailed and pig-tailed macaques (*Macaca fascicularis* and *M. nemestrina*), Philippine slow lorises (*Nycticebus menagensis*), Western tarsier (*Cephlopachus bancanus*), and silvered langurs (*Trachypithecus cristata*). Along with proboscis monkeys, four additional primate species which are endemic to Borneo are found in the floodplain: Bornean orang-utans (*Pongo pygmaeus*), Bornean gibbons (*Hylobates muelleri*), maroon langurs (*Presbytis rubicanda*)*,* and Hose's langurs (*P. hosei*). Other large mammals in the region include

Bornean forest elephants (*Elephas maximus borneensis*), Sunda clouded leopards (*Neofelis diardi*), and Malayan sun bears (*Helarctos malayanus*).

### 1.3.3 Threats in the Kinabatangan

The Kinabatangan floodplain has sustained large-scale commercial logging since the 1950's (Lackman-Ancrenaz et al. 2001), and by 2000 contained 28% of the total planted area of oil palm in Sabah (Hai et al. 2001). Forest clearance for oil palm plantations in the 1990's resulted in the conversion of most privately owned property in the area to commercial agricultural land (Lackman-Ancrenaz et al. 2001). By the 2000's, the expansion of oil palm started to slow down, although >9,000 ha of forest was still converted, mainly to oil palm, between 2005 and 2014 (Matsuda et al. *in press*). Almost half of the floodplain is covered by oil palm, most of which is at the commercial scale (Abram et al. 2014). Although a 20 m riparian corridor along the Kinabatangan River is required by law to maintain a continuous habitat for wildlife, the reserves are being encroached by oil palm, and in reality, the depth and even presence of riparian forest corridors varies. Almost all of the remaining forest in the Kinabatangan floodplain has been selectively logged at least once over the past century (Ancrenaz et al. 2004). The degradation levels vary throughout the floodplain, most likely due to factors such as extent of selective logging within existing forests and time since last logging (Chapman et al. 2006b), although these details are not readily or consistently available for the Kinabatangan.

Due to their charismatic appearance and endemism, proboscis monkeys are one of the major attractions that bring tourists to Borneo (Sha et al. 2008; Leasor and Macgregor 2014). Tourists are attracted to Sabah because of its natural values and wildlife (Chan and Baum 2007), and because of the ease of accessibility relative to other parts of Borneo. Tourism is one of the main sources of income in Malaysia, and wildlife tourism in particular is becoming an increasingly important industry in terms of job opportunities

and infrastructure development in Malaysia (Kunjuraman and Hussin 2016; Newsome et al. 2017). In the course of only six years, tourist expenditure had increased from MYR36.3 to MYR82.1 billion up to 2016, and is projected to increase to MYR168 billion by 2020 (Kunjuraman and Hussin 2016; Tourism Malaysia 2018). Areas that bring in large number of tourists for wildlife viewing, such as the Kinabatangan, have been designated by the government as nature tourist zones in Sabah, as they have significant socioeconomic value (Bagul 2009; Newsome et al. 2017). Therefore the protection of proboscis monkeys, along with many other wildlife species, and their habitat, are important for the financial wellbeing of the local people and the overall revenue of the State of Sabah.

The Kinabatangan floodplain is a prime area to examine the impact of forest loss on the movement and forest use of primates. Selective logging and land conversion for agriculture or settlements within the Kinabatangan floodplain has left the remaining forest blocks along the river in a variety of sizes, shapes and levels of disturbance. There are extensive sections of forest within proboscis monkeys' ranges that do not extend far enough inland to surpass the median distance to which edge effects can be detected (Broadbent et al. 2008). The variation in the shape and width of the remaining forest makes it important to understand the mechanisms of survival of proboscis monkeys in an human-mediated landscape. In areas such as the Kinabatangan floodplain, where oil palm plantations form part of the landscape matrix, plantations can act as a barrier to animal movement and tend to support fewer forest species than other agricultural options (Fitzherbert et al. 2008). For the effective conservation management of a species, there is a need to understand which factors affect the persistence of a population in a disturbed forest environment (Fahrig 2001).

## 1.4 Thesis overview

The overall aim of this study was to obtain a more accurate depiction of the habitat use and ranging patterns of proboscis monkeys in a degraded forest landscape. Differences in long-term ranging patterns across gradients of forest block sizes and disturbance levels were expected, as were daily and seasonal variations in movement and sleeping site selection. Proboscis monkeys were expected to show a preference for forest edges, due to the potential for increased food quality and availability found in areas exposed to sunlight, but those along rivers would be preferred over those bordering oil palm plantations. Structural forest characteristics were expected to be important in the habitat use of proboscis monkeys, but seasonal changes in potential food availability would be also be a large determinant in movement patterns and sleeping site selection. The use of high-importance areas (e.g. areas with potential food sources or safe resting locations) within their home ranges was expected to increase when in smaller or more disturbed forests, indicating potential over-exploitation of resources. Alternatively, individuals in more disturbed forest may exhibit larger home ranges in order to obtain sufficient resources.

Due to the complexities of primate ecology in disturbed and decreasing forest environments, **Chapter 2** reviews some of the issues surrounding habitat loss and fragmentation, how these impact primates, and advances in the tools used to study habitat use. Although direct observations are possible for proboscis monkeys in some habitat types, GPS tracking technology has untapped potential beyond being used as a resource for tracking cryptic or shy species (Fedigan et al. 1988; Markham and Altmann 2008), as it can be used to track multiple individuals in greater detail with minimal biases throughout their range. By deploying satellite tracking devices on proboscis monkeys for the first time, **Chapter 3** explores the most commonly used home range estimators in primatology and identifies the strengths and weaknesses of each one. A version of Chapter 3 has been published in PLoS ONE (Stark et al.

2017a). Based on the home range estimator that seemed most suitable for the current data in Chapter 3, **Chapter 4** examines resource utilisation within the home ranges of proboscis monkeys. To do so, habitat variables were derived from a high-resolution light detection and ranging (LiDAR) dataset, and resource use differences were examined for overall utilisation, along with the frequency and duration that different parts of the home range were used. **Chapter 5** looks at daily and monthly proboscis monkey movement patterns in relation to changing environmental conditions and phenology. Movement patterns are examined inside and outside areas identified as high use from Chapter 4. In addition, Chapter 5 also tests whether proboscis monkey movement patterns change in proximity to different forest edges. **Chapter 6** presents a case study highlighting the role that satellite tracking data and visually striking remote sensing habitat data (from an unmanned aerial vehicle) can have in calling governments and other organisations to action. A version of Chapter 6 has been published in Remote Sensing in Ecology and Conservation (Stark et al. 2017b). In the General Discussion (**Chapter 7**), the major findings from each chapter are assessed, and the results of the thesis are discussed in terms of how they can help determine appropriate guidelines and inform conservation management plans. Each chapter is self-contained, and therefore some repetition is necessary.

# Chapter 2  The ecology of primates in changing forest habitats

Largely due to human and agricultural expansion, natural habitats are being modified and the species living within those habitats must adjust in order to survive (Fahrig 2003; Arroyo-Rodríguez et al. 2013). Habitat change can include loss (conversion from suitable to unsuitable habitat types), fragmentation (the breaking apart of habitat remnants), and degradation (negative changes in the local characteristics of the habitat) (Irwin 2016). In this review, habitat change will be explored in the context of primate responses. After a brief discussion of some important topics often associated with modified habitats (edges and corridors), the ways in which primates respond to modified landscapes will be reviewed, followed by how advances in analyses or technology can be used to understand how land use changes have influenced primate movement or predict how movement may respond to habitat change in the future.

## 2.1  Forest loss in the tropics

Forests are being cleared at vast rates across the tropics (Hansen et al. 2013). The natural extent of earth's tropical forests has declined by an estimated 40%, with the remaining tropical forest estimated to contain between 50 and 90% of all terrestrial species (Shvidenko et al. 2005). Losses are driven by clearing land for farming, settlements, aquaculture, timber, and large-scale agriculture (i.e. converted into oil palm and pulpwood plantations), and degrades many pristine areas (Chapman and Peres 2001). Around 28% of the world's tropical forests have some form of protection, 13% of which are located in Asia (Nelson and Chomitz 2011). Despite protection status, forest loss continues to occur within protected areas, albeit at slower rates (Curran et al. 2004; Gaveau et al. 2009; Ferraro et al. 2013). Protected areas have become increasingly isolated, and buffer zones are being degraded (Curran et al. 2004). Between 1980 and 2000 more wood had been harvested from Borneo than Africa and the Amazon combined (Curran et al. 2004), and by 2015, Borneo had lost

62% of its old-growth forest (Gaveau et al. 2016). Areas set aside for protection in Indonesian Borneo are being distributed and cleared for timber concessions and plantations, and mines are polluting the rivers (Meijaard and Nijman 2000a; Jepson and Noord 2002). Indonesia and Malaysia hold more than 80% of the remaining primary forest in Southeast Asia (Fitzherbert et al. 2008), but also produced 86% of the world's palm oil by 2013 (Rifai et al. 2015). The economic value of large-scale agriculture for tropical countries, in particular, oil palm, suggests that the demand is not about to decline (Hai et al. 2001).

Habitat is a species-specific term, which includes the range of environments suitable for a given species (Hall et al. 1997). It usually refers to broad vegetation types (i.e. tropical rain forest) and is a gradient of quality, not a binary suitable/unsuitable variable (Arroyo-Rodríguez and Mandujano 2009). Globally, habitat loss is considered the most important factor in declining biodiversity and threatening ecological processes (Fahrig 2003; Arroyo-Rodríguez et al. 2013). Only half of the 60 protected areas of tropical forest reviewed by Laurance et al. (2012) were considered capable of maintaining the needs of the species within their boundaries. Direct measures of biodiversity, such as species richness, population abundance and distribution, and genetic diversity are negatively affected by habitat loss, whilst indirect measures also show negative responses, including reduced population growth rates, breeding success or trophic chain length (Fahrig 2003).

Beyond the effect of simply reducing the area available, the impact of habitat loss can be intensified by fragmentation (Arroyo-Rodríguez et al. 2013). Through an increase in the number and isolation of habitat fragments, and a decrease of size, fragmentation increases the extent of edge habitats and exposes the forest boundaries to novel conditions (Ewers and Didham 2006; Arroyo-Rodríguez et al. 2013). The complex series of co-occurring events of habitat loss and fragmentation makes it difficult to

differentiate the impacts on biodiversity, such as whether habitat loss alone or the effects caused by fragmentation per se, are more important factors in the fate of a species (Fahrig 2003). Beyond the area of habitat, there are more than 40 measurements that have been used to try to understand the complicated effects of fragmentation. These measurements include: number of fragments, fragment density, total edge, edge density, landscape shape index, and largest patch index (Fahrig 2003; Arroyo-Rodríguez et al. 2013). However, the net effects of fragmentation per se tend to be weaker and more difficult to predict than habitat loss. Being both species and analysis dependant, the effects can be positive or negative (Fahrig 2003; Ewers and Didham 2006; St-Laurent et al. 2009; Arroyo-Rodríguez et al. 2013).

### 2.1.1 Edge effects

Edge habitats occur naturally in a range of environments, such as rivers, lakes, and grasslands. They are important habitats for foraging, protection from predators and for social activities, and are often areas of high biodiversity for frogs, birds, butterflies, and mammals (Ayres and Clutton-Brock 1992; Laurance et al. 2002; Matsuda et al. 2011b; Scriven et al. 2018). Forest edge habitats may be gradual transitions between habitat types, but they can also be abrupt edges between relatively undisturbed forest and agricultural land (Naughton-Treves 1998; Chapman et al. 2006a).

Habitat loss from human activities is resulting in non-natural forest edges becoming more prevalent throughout the tropics (Harper et al. 2005). Edges are the most drastically altered zone of remaining forests (Laurance and Yensen 1991), and changes in forest edges have been shown to lead to further interior habitat degradation (Laurance et al. 2002). Soft-edges, such as tree-felling gaps, have less dramatic effects, but can still create a change extending up to 100 m from the site (Pereira Jr et al. 2002; Asner et al. 2004), whereas more abrupt edges can cause effects as far in as 5 km (Murcia 1995; Curran et al. 1999; Broadbent et al. 2008). Negative edge effects

include structural damage, and increased seedling and tree mortality (Nascimento and Laurance 2004; Harper et al. 2005; Arroyo-Rodríguez and Mandujano 2006). Other impacts include changes in plant and animal community composition and diversity (Broadbent et al. 2008), and altered microclimates (Williams-Linera et al. 1998). Depending on the species of interest, these are not necessarily negative, and responses can be site-specific (Harper et al. 2005). In a review of the effect edges have on forest structure and composition, Harper et al. (2005) found that older edges tended to have fewer canopy trees, less canopy cover, more snags and logs, increased understory tree density and less secondary tree recruitment than interior forest. Newly-made edges followed similar trends, but also showed an increase in tree mortality, secondary recruitment, tree growth rates, and greater individual species abundance than interior forests (Harper et al. 2005). Changes in the physical environment, particularly the microclimate, begin immediately after the edge has been created (Broadbent et al. 2008).

The varying response that wildlife display to edge effects within the same study site are due to differences in life-history strategies and habitat requirements (Ewers and Didham 2006). Mammal prey species, for example, such as sambar deer (*Rusa unicolor*) and muntjac (*Tragulus kanchil* and *T. napu*), have been observed avoiding areas up to 2-4 km from edges caused by logging events, whereas in contrast, Sunda clouded leopards (*Neofelis diardi*) increased their habitat use near these edges (Brodie et al. 2015). It is therefore essential to understand these species-specific responses to edge habitats for the effective management of the positive or negative impacts of habitat loss (Campbell et al. 2011; Didham and Ewers 2012).

### 2.1.2 Habitat corridors

Urbanisation and human activities are increasingly fragmenting landscapes and creating barriers, preventing animals from freely moving throughout their habitat (Beier

and Noss 1998). Habitat corridors provide a way of improving an animal's ability to move from one place to another, and have the ability to enhance the population viability of many species (Noss 1987; Hess and Fischer 2001). In a review by Beir and Noss (1998), corridor use provided benefits to, and was used by, numerous species. However, corridors are not utilised similarly by all species and can be split into six functional uses: habitat, conduit, barrier, filter, source or sink (see review by Hess and Fischer 2001). Even in areas where two species follow similar dietary and social patterns, one species may readily use habitat corridors, while another may not (Beier and Noss 1998; Laurance and Laurance 1999). Importantly, finding individuals inside corridors does not necessarily mean that the corridor is assisting in the movement among fragments, or the survival of the population (Hess and Fischer 2001). For example, corridors may act as a sink (i.e. when mortality exceeds reproduction) if the increased edge associated with the corridor intensifies an animal's risk of predation (Hess and Fischer 2001).

Traditionally it has been suggested that habitat restoration programmes should focus on connecting isolated forest fragments through corridors. However, because corridors typically increase the proportion of edge habitats and therefore increase the amount of forest experiencing edge effects, Ewers and Didham (2007) suggested instead to focus on enlarging disconnected core areas in complex fragment shapes (i.e. areas that are not already experiencing edge effects). Alternative considerations such as this may be important when determining appropriate areas, and methods, for habitat restoration, as well as when considering the ability of corridors to re-link forest fragments. Due to the financial costs of establishing new corridors and the difficulties in obtaining sufficient funds for conservation projects, a corridor project must be carefully planned to perform a well-defined function, as the corridors are only of value if animals use them (Beier and Noss 1998; Hess and Fischer 2001).

It is important to recognise that due to the current global levels of habitat disturbance, much of the research in wildlife ecology is conducted in areas already affected, in one way or another, by habitat loss, human encroachment, fragmentation or forest degradation. It is therefore imperative to gain a proper understanding of the roles habitat disturbance is having on an ecosystem and how organisms use their altered or fragmented landscape, to determine the effectiveness of further conservation measures, including curbing human activities and incorporating habitat restoration programs (Mbora and Meikle 2004).

## 2.2 Primates in a modified habitat

As more than half the world's primates species are vulnerable to extinction due to habitat modification, and three-quarters are experiencing population declines (Estrada et al. 2017), most studies on wild primates must incorporate a conservation aspect due to the potential effects of habitat loss, fragmentation, or degradation (Cowlishaw 1999; Carretero-Pinzon et al. 2016; Irwin 2016). Arboreal primate groups or populations can become isolated due to an inability to cross non-forested areas (Chiarello and De Melo 2001). Primate species respond to fragmentation or other human disturbances (e.g., wildfires, logging, hunting) according to differences in their ecology (Michalski and Peres 2005; de Almeida-Rocha et al. 2017). However, the impact of habitat fragmentation on primates is a complicated topic, occasionally leading to conflicting conclusions that are difficult to interpret (see review by Arroyo-Rodríguez and Mandujano 2009). Of more than 40 measures that can be used to describe landscape fragmentation, most studies in primatology investigate just one (generally fragment size) and occasionally one or two additional variables (see review by Arroyo-Rodríguez et al. 2013). The complication lies in the difficulty in identifying the relative importance of fragmentation and habitat loss on the persistence of primate populations, as the two processes can occur simultaneously and their relative impacts may vary depending on the extent of habitat loss (Arroyo-Rodríguez and Benítez-Malvido 2008). However,

once the remaining habitat falls below a certain (species-specific) threshold, the survival probability of primate populations drops significantly (Arroyo-Rodríguez and Benítez-Malvido 2008).

Effects of habitat loss, fragmentation and declining habitat quality have been documented on many aspects of primate ecology, from the entire primate community (e.g. species and genetic diversity), down to individual health (e.g. gastrointestinal parasites, Gillespie et al. 2005; Snaith et al. 2008). It is a complicated topic that requires consideration of the interactions between biological traits and environmental factors of the primate, or habitat, in question. Biological traits include dietary requirements, social system, demography, territoriality, and behavioural adaptability. The external or environmental pressures facing a particular species, or habitat, includes spatial and temporal aspects of disturbance events (fragmentation or habitat loss, degree of isolation, time since event), the presence or absence of hunting pressure, and variation in seasonality (Chapman et al. 2006b). The interaction between these multiple factors along with continually changing environments can result in some conflicting results. However, it is important to monitor as many of these factors as possible, in order to track and identify responses to the changing environment over time.

### 2.2.1   Diversity & density

Primate species richness and abundance tend to decrease as fragment size decreases (Chapman et al. 2003; Wieczkowski 2004; da Silva et al. 2015). When a forest is fragmented, the habitat quality is altered due to changes in the composition and plant structure of the forest over time, and thereby changing the carrying capacity of the forest (Arroyo-Rodríguez and Mandujano 2006). For example, due to an increase in edges created by fragmentation, large canopy trees can experience increased rates of tree mortality, which subsequently reduces important food sources, whereas fragment

isolation can modify the dispersal or predation rates of seeds (Arroyo-Rodríguez and Mandujano 2006). The distance to the nearest forest patch or the amount of growth surrounding a fragment also plays an important role in predicting primate species richness (Boyle 2008).

The temporal dimension of habitat loss or fragmentation is an important factor to consider when interpreting changes in primate density. Primates are often found at higher densities in newly fragmented forests than in older fragments, but after some time, a decline in population density may be seen, which could result from factors such as hunting, disease, genetic inbreeding, or a loss in food resources due to initial over-exploitation and intra- and interspecific competition (Link et al. 2010). However, a population decrease may not always occur; although changes in the habitat may lower recruitment, it rarely reduces survival (Chapman et al. 2006b). In relatively small forest patches (<50 km$^2$), primate densities may increase, attributed to a lack of large predators (Harcourt and Doherty 2005), density compensation (Peres and Dolmon 2000), or the adaptability of many primates (González-Solís et al. 2001). For example, Boyle (2008) found a higher density of two saki monkey species (Northern bearded saki monkey *Chiropotes sagulatus* and white-faced saki monkey *Pithecia pithecia*) in smaller fragments, although these species had been completely absent from fragments immediately following the isolation event and took up to 20 years before the saki monkeys had recolonised.

Diversity also applies at the genetic level. The ability of primates to respond to their changing environment in the short-term is likely based on the genetic diversity of a population (Salgado Lynn et al. 2016), but some species may be more vulnerable than others to genetic erosion due to habitat change (Mbora and McPeek 2015). Small and isolated populations are more at risk of experiencing deleterious effects than larger populations because of the reduction or loss of gene flow (Oklander et al. 2010).

Without sufficient levels of gene flow, mutations can be amplified and can eventually result in extinction (see review by Frankham 2015). Habitat loss and fragmentation have been shown to have negative effects on the genetic diversity in primate populations, in historical or the relatively recent past, due to human colonisation and climate change (Perrier's sifaka *Propithecus perrieri* and Tattersall's sifaka *P. tattersalli*, see Salmona et al. 2017), creation of small habitat-gaps and roads (white-headed langur *Trachypithecus leucocephalus*, see Wang et al. 2017) or other human activities (Udzungwa red colobus monkey *Piliocolobus gordonorum,* see Ruiz-Lopez et al. 2016). The genetic diversity of a population can also be used to identify how and when populations responded to fragmentation events in the past (Grauer's gorilla *Gorilla beringei graueri*, see Baas et al. 2018), and emphasises the importance of connecting habitats and allowing smaller populations to expand.

*2.2.2   Diet*
It has been suggested that species' ecological traits can predict which species would be able to persist in fragmented habitats (Boyle 2008). Diet can be an effective predictor of vulnerability to habitat modification, as folivores are generally expected to be less selective in their diet by exploiting more widespread and reliable food sources than frugivores. In a survey of six primate species in the Amazon, large folivorous-frugivorous primates (red howler monkeys *Alouatta seniculus*) followed the predictions of persistence due to diet preference and were found in all fragment sizes (Boyle 2008). In contrast, the three frugivorous species were more sensitive to fragmentation, and were not widely found (black spider monkeys *Ateles paniscus*, Northern bearded saki monkeys and white-faced saki monkeys), possibly due to the preferred food resources being patchier and unevenly distributed throughout the landscape. However, once the make-up of their diets was examined more closely, the frugivorous species with higher reliance on seeds (saki monkeys) were more persistent than the species relying on just the fruit (black spider monkeys), which, besides a few opportunistic

sightings in a single fragment, had not been seen in the area for 30 years (Boyle 2008). This work suggests that the fundamental differences in diet, such as a species' degree of frugivory or folivory can help predict the persistence of a species (Boyle 2008).

Changes in canopy cover can reduce the quantity and quality of available habitat for primates (Medley 1993; Estrada and Coates-Estrada 1996; Wieczkowski 2004). Colobines may be especially vulnerable to the effects of forest loss, fragmentation and the modification of remaining forest habitat (Anderson et al. 2007), largely due to their highly arboreal nature and dependence on leaves, seeds and unripe fruit (Mbora and McPeek 2015). On the other hand, because young leaf production can increase following forest disturbance, and young leaves have a higher nutritional value than mature leaves (Johns and Skorupa 1987; Mbora and Meikle 2004), folivorous primates have been observed to feed more in fragmented than continuous forest (Onderdonk and Chapman 2000; Stevenson et al. 2015). For example, the probability of Tana River red colobus monkeys (*P. rufomitratus*) inhabiting forests was positively correlated with the relative amount of forest edge, the canopy tree species composition, and the basal area of food trees (Mbora and Meikle 2004).

### 2.2.3 Demography and social structure

Habitat modification can affect the size and composition of primate social units, in part due to the change in food availability and quality (Gogarten et al. 2015). For example, Boyle (2008) found that the number of Northern bearded saki monkeys in a group increased with fragment size. Larger forest fragments may also support groups having more immature individuals and a higher birth rate, as seen with lion-tailed macaques (*Macaca silenus*) (Umapathy and Kumar 2000). Along with changes to the number of individuals belonging to the social unit, group structure can also be altered, introducing additional pressures to the already complex structure of primate groups. Umpathy and Kumar (2000) found that lion-tailed macaque groups, which normally have a single

adult male and a single sub-adult male, were more likely to have >1 adult male in smaller fragments. Chapman et al. (2006b) also found that Uganda red colobus (*P. tephrosceles*) and black and white colobus (*Colobus guereza*) groups in previously-logged forests tended to have smaller group sizes than groups in unlogged forest, independent of forest area. In the same landscape, the variation observed in how group size within and between species adjusts in response to habitat change may also indicate a state of non-equilibrium, as seen in the primate community in Kibale, Uganda (Gogarten et al. 2015).

Habitat loss or fragmentation leads to additional forest impacts besides the actual removal of trees. Remaining forests become more easily accessible, resulting in increased human activities such as hunting for food and pets. Initial overcrowding of wildlife following clear-cutting events can be exploited by for easy hunting opportunities (Peres 2001). These activities can cause directional shifts in abundance, primate species composition, and sex ratios (e.g., Peres 2001; Rode et al. 2006; Pyritz et al. 2010; Stevenson 2016). Some primates can be particularly sensitive to hunting due to their life cycle and reproductive rates. In Mexico, hunters often target adult female spider monkeys (*Ateles* sp.) due to their large body size (Duarte-Quiroga and Estrada 2003). This species has a relatively long life-cycle and slow reproductive rates, which – coupled with the possibility of hunters capturing the female's offspring for the exotic pet trade – makes it difficult for the spider monkey population to recover from short-term declines (Cowlishaw and Dunbar 2000; Duarte-Quiroga and Estrada 2003; Link et al. 2010). Furthermore, if a forest decreases beyond a certain size or becomes isolated from surrounding habitats, preferred target species can be hunted to local extinction even when hunting pressure is light (Wright et al. 2000). Finally, along with reducing the abundance of wildlife, poaching can have long-term effects on a forest's plant composition through the removal of game species which may be responsible for the dispersal, germination, or predation of particular plant species (Wright et al. 2000).

## 2.2.4   Primate health

Although most studies of habitat loss and fragmentation focus primarily on species diversity, or the demographics and population viability of a single species, primate health has become a topic of increasing interest, including host-parasite dynamics in fragmented habitats, at both population and individual levels. Parasite infection is a common and normal occurrence in wild primate populations, but human impacts may alter the natural host-parasite relationship, including transmission rates, ranges and virulence (Gillespie et al. 2005; Snaith et al. 2008). Such changes in infection may result from factors including altered primate behaviour and increased proximity to human settlements.

The change in landscape characteristics can influence the frequency and nature of contact between primate hosts and parasites (McCallum and Dobson 2002; Gillespie and Chapman 2007). Groups that travel further within a small home range may have increased parasite infections compared to species that travel less each day and have a larger range (Nunn and Dokey 2006). By increasing the intensity with which primates use their habitat, forest loss and fragmentation may replicate the patterns of range use usually described in the context of territory defence (Nunn and Dokey 2006). This in turn may increase gastrointestinal parasite richness, as animals may not be able to avoid recently used sleeping sites, increasing susceptibility to infection (Hausfater and Meade 1982; McCallum and Dobson 2002; Gillespie and Chapman 2007). With evidence that some gastrointestinal parasites can reduce host fecundity and survival at high loads, and that stress may increase the susceptibility of infection, parasite loads may act as an indication of forest-quality (Wright et al. 2009). Once a primate population is pushed beyond the forest's carrying capacity, they can become nutritionally stressed, making them more susceptible to parasites (Gillespie and Chapman 2007). Alternatively, primates associated with forest-agricultural edges can improve their nutritional status by their increased access to food available from crops (Hockings et al. 2009; Cancelliere et al. 2018). These well-fed groups may be in better

physical condition than forest dwelling ones and are therefore more able to fight off infection (Chapman et al. 2006a).

Habitat loss or fragmentation may alter an animal's parasite load and transmission rate due to increased proximity to humans. For example, the prevalence of parasitic nematodes in colobine species in Kibale, Uganda (red colobus and black-and-white colobus) was strongly influenced by habitat degradation and human presence (Gillespie and Chapman 2006). Ursine colobus monkeys (*C. vellerosus*) that spent more time near human settlements had a higher prevalence of *Isospora* sp. resembling the human strain, suggesting possible anthropozoonotic and/or zoonotic transmission between humans and colobines (Teichroeb et al. 2009). Finally, the increased proximity of primates to human settlements can also increase zoonotic transmission. For example, long- and pig-tailed macaques (*M. fascicularis* and *M. nemestrina*) act as natural carriers of the zoonotic malaria species, *Plasmodium knowlesi* (see Fornace et al. 2016). However, due to the rapid loss of forest in their range in Malaysian Borneo, *P. knowlesi* has become the most common source of human malaria in the region (Fornace et al. 2016). An increased parasite incidence in humans has been attributed to increased forest accessibility for people, and by forest loss concentrating wildlife closer to villages (Galinsky and Barnwell 2009; Gómez et al. 2013; Stark et al. *unpublished manuscript)*.

### 2.2.5 Ranging behaviour

The home range is the area an animal regularly uses for feeding, sleeping, finding mates, or raising young (Burt 1943). Primates tend to move directly between known resources patches rather than chance encounters with food sources (Milton and May 1976). They display a strong degree of site fidelity in space-use over time, which is partly due to familiarity with a known area (Ramos-Fernández et al. 2013). However, when a forest is being cleared, primates have to re-adjust their home range, and can

go through a period of fluctuation as they establish a new home range (e.g., western lowland gorillas *Gorilla gorilla gorilla*, see Arnhem et al. 2008; howler monkeys *Alouatta spp.*, see Fortes et al. 2014; long-tailed macaques, Stark et al. *unpublished manuscript*). Frugivorous primates typically occupy larger home ranges relative to their body weight than folivores, which is attributed to the clumped distribution of fruiting trees in the highly heterogeneous plant species composition of typical tropical forests (Milton and May 1976). However, when habitat loss concentrates the primate population in close proximity to humans (e.g., urban development, tourism), these ranging patterns may change; long-tailed macaques and Barbary macaques (*M. sylvanus*) with regular access to human food resources through provisioning or crop raiding tend to have smaller home ranges and shorter daily movements than those that have less access (Klegarth et al. 2017).

Despite the adaptability some primates show by altering certain behaviours, other behaviours may be less adaptable. For example, within small forest fragments, Northern bearded saki monkeys were able to alter the tree species they fed on, but were not able to move between fragments requiring terrestrial travel; travel became possible when tall secondary growth connected the fragments (Boyle 2008). However, some species that are primarily or preferentially arboreal have been able to adapt to travelling on the ground between fragments, although this may expose them to additional risks, such as crossing roads, or increased predation risk (lion-tailed macaques, Menon and Poirier 1996; Bornean orangutan *Pongo pygmeaus,* Ancrenaz et al. 2014).

Home range area can be impacted by forest size (Cristóbal-Azkarate and Arroyo-Rodríguez 2007). Studies on the folivorous howler monkeys (*Allouata palliata* and *A. seniculus)* found that home range areas were positively related to forest size (Cristóbal-Azkarate and Arroyo-Rodríguez 2007; Stevenson et al. 2015). Northern

bearded saki monkeys living in small fragments (1 ha, 10 ha and 100 ha) had smaller home ranges which they used more uniformly than groups living in continuous forest (Boyle et al. 2009). Groups in the smaller fragments moved in a more circular motion (i.e. their daily start and end points were closer together than in the larger fragments), whereas the groups in larger fragments moved between food patches throughout the area, generally travelling in more straight-line movements (Boyle et al. 2009). Furthermore, the groups in continuous forest revisited the same tree on the same day 2% of the time, whilst re-visitation rates increased to 6% in the 100 ha fragments, to 16% in the 10 ha and 54% in the 1 ha fragment (Boyle et al. 2009).

Daily path length increases in poorer quality habitats, with a greater impact on frugivores and omnivores (Di Fiore 2003). Boyle and Smith (2010) found that groups of Northern bearded saki monkeys travelled shorter daily distances and ranged over smaller areas in smaller fragments. Although time spent travelling decreased and resting increased in smaller habitats, there was no difference in time spent feeding or in the food types consumed (flowers, leaves, insects). However, although there was a decrease in time spent travelling in smaller habitats, saki monkeys travelled greater distances relative to fragment size than those in larger fragments (Boyle et al. 2009).

### 2.2.6 Importance of understanding how primates respond in a changing habitat

Although many primates can survive in disturbed forests, there is a threshold at which the forest is no longer able to support them (Irwin 2016). As forests continue to decline and landscapes become more fragmented, it is important that population thresholds are estimated, and the ecosystem is monitored. To respond appropriately to the increased levels of fragmentation or habitat modification, there is a need to understand the effect of connectivity on the population. The size of a fragment cannot be the sole criterion in conservation land management plans. Secondary growth forest surrounding the area, as well as the diet and adaptability of primates in the area, all need to be

considered as important factors in developing effective management strategies (Boyle et al. 2009; Bryant et al. 2017). Detailed studies on the spatial requirements of primates are needed to predict how animals will react to habitat disturbance (Anderson et al. 2007; Pyritz et al. 2010; Bryant et al. 2017). Understanding the effects and the underlying causes of habitat disturbance can also reveal how forest size and shape, isolation or connectivity affect the quality and quantity of resources for primates in fragmented or disturbed landscapes (Arroyo-Rodríguez and Mandujano 2009; Ni et al. 2018).

## 2.3   Advancements in the study of home range

There has been a growing recognition of the need to understand and predict how changes in movement play a role in driving processes such as disease transmission, or the persistence of populations or species in light of global environmental changes (Nathan et al. 2008). Incorporating human habitat use and land use changes into the study of movement ecology can increase the understanding of the causes, mechanisms and consequences of altered movement patterns to improve management and restoration of degraded landscapes (Nathan et al. 2008). How humans perceive or record an animal's home range is only an estimate of the true range. There are many different methods used to estimate home ranges, and the most common purpose of doing so is to assess the area used, often including a measure of the relative use of different parts within the home range (Fieberg and Börger 2012). However, how this is achieved varies in terms of mathematical complexity, statistical assumptions, and degree of realism, and is continuously evolving as new technologies (e.g. GPS collars) change the data that are available (Kie et al. 2010; Walter et al. 2011).

The performance of different home range estimators has been compared in several ways, using both real and simulated data (e.g., Seaman and Powell 1996; Horne and

Garton 2006; Pebsworth et al. 2012; Lyons et al. 2013; Chapter 3). One of the benefits of using simulated distributions is that the "true" home ranges are known and can be designed to represent different types of ranging behaviour (e.g., denning, migrations, geographical barriers) (Worton 1995; Getz and Wilmers 2004; Fieberg 2007; Lyons et al. 2013). Using simulated distributions, the deviation of the simulated data from the true distribution can be used to select the best fitting model (Horne and Garton 2006). It is important to note that there will not be one model that fits all distributions. Instead, these comparisons are useful to explain the errors associated with the models, as well as to help determine which model is most appropriate, based on the data available or the research question posited.

### 2.3.1 Traditional approaches to estimating the home range

An animal's home range is commonly used to investigate the interaction between a species and its environment (Getz and Wilmers 2004). The most straightforward technique for estimating home range is by delineating the outer boundary of an animal's movement using the minimum convex polygon method (MCP). The MCP is the smallest polygon in which no internal angle is greater than 180° and typically contains all known locations of the animal (Burgman and Fox 2003). MCP is one of the most widely used methods for calculating home range areas, as there is a notion that it is easily comparable among studies (Sekercioglu et al. 2007). However, it is also widely accepted that MCPs do not fit most animal movement data well, especially when the home range is a complex or an irregular shape (Burgman and Fox 2003; Börger et al. 2006). MCP is sensitive to sample size and outliers, resulting in estimates that may have unpredictable biases, such as a change in the estimated area of -10% to +400% as sampling effort increases (Ostro et al. 1999; Börger et al. 2006). Even removing the outermost locations (i.e. exploratory movements) does not eliminate this bias (Burgman and Fox 2003). Recent studies tend to use MCPs only to assist with

comparisons to previous studies (e.g., Grueter et al. 2009; Asensio et al. 2011; Sawyer 2012; Gehrt et al. 2013; Quintana-Morales et al. 2017).

### 2.3.2 Development of utilisation distribution methods

Utilisation distributions (UD) expand on the idea of demarcating the boundary of a home range by measuring how intensively an animal uses different areas within its range (Getz and Wilmers 2004; Gitzen et al. 2006). The basic UD method is the grid-cell method (GCM), whereby a grid is laid over the area covered by the animal and counting the number of times each cell is entered (Ostro et al. 1999; Grueter et al. 2009; Ren et al. 2009a); the cell dimensions should be selected based on biological parameters, such as the group spread. It has been well established that GCM underestimate (Grueter et al. 2009) or overestimate (Lehmann and Boesch 2003) the home range area depending on the cell size selected. GCM may be best used in conjunction with other methods as it is better suited to explore habitat use and core areas than for calculating overall home range size (Harris et al. 1990; Sawyer 2012).

With the advancement of satellite tracking devices, it is now possible to collect larger datasets and record locations at more consistent and shorter intervals. This has led to the development of more advanced analytical techniques (Table 2.1). The study objectives or the dataset available should be used to determine the suitability of different analytical methods (Henson et al. 2006). There are two general approaches for calculating UDs: location-based methods, which examine the location of each point regardless of their sequence in time, and movement-based methods, which incorporate time between points into the models (Walter et al. 2011). Location and movement-based models should not be seen as different methods to produce similar outputs, but are dependent on the study objectives. The former is more appropriate when focusing on resident or seasonal habitat use, the latter intended more in documenting paths followed and used by animals (Walter et al. 2011).

Table 2.1    Examples of the commonly used location-based and movement-based home range methods. * refers to methods used in Chapter 3.

| Model | Parameters | Output | Concept | Issues | Ref |
|---|---|---|---|---|---|
| **Location-based methods** | | | | | |
| Minimum convex polygon | --- | Outline | Delineates outer boundary of points; easily comparable between studies | Over-estimates HR size; sensitive to sample size and outliers; no indication of use intensities | 1 |
| Grid cell method* | cell dimension | Frequency | Sum of cells entered estimates home range size, number of times entered each cell estimates utilisation; cell size should correspond to typical spread of the group | Not suited for calculating overall home range size; can underestimate if animals are not intensively followed | 2,3 |
| Kernel density estimator | smoothing bandwidth (i.e. href (fixed or adaptive), hlscv) | UD | Unimodal; second bi-variate normal or Epanechnikov; requires points to be independent | Overshoots the data equal to the bandwidth value regardless of point density; issues in point independence, clustered data, sample size and habitat conditions (i.e. distinct barriers) | 4 |
| Local convex hull (LoCoH) | | | Forms arise directly out of the data (not from a single parameter function); can identify true/hard boundaries | Thresholds for parameters manually defined; requires *a priori* knowledge of area for barriers; does not model spatial uncertainty well | |
| fixed k | k-1 (k = nearest neighbour) | UD | Number of nearest neighbours (k) | Tends to over-fit data, resulting in an underestimate of the space required | 5 |
| fixed r | radius around root point | UD | Uses a fixed radius from the root points | Functions similar a non-parametric kernel methods, taking the size from the radius | 6 |
| adaptive* | sum of distances of points ≤ a | UD | Maximum number of nearest neighbours so that the sum of their distance is less than or equal to this parameter | Tends to over-fit data, resulting in an underestimate of the space required | 6 |
| **Movement-based methods** | | | | | |
| Time LoCoH* | same as LoCoH + *s*-value | UD | Time-scaled distance factor selects nearest neighbour based on an animal's maximum speed | Tends to over-fit data, resulting in an underestimate of the space required; does not model spatial uncertainty well | 7 |
| Biased random bridges (BRB or MKDE)* | $T_{max}$, $h_{min}$, $L_{min}$ | UD | Considers tracks rather than GPS fixes; incorporates drift; also produces intensity and recursion distribution; incorporates barriers, activity and habitat data | Lack of standardised procedure for setting parameter values; requires *a priori* knowledge of area for barriers | 8,9 |

(1) Mohr 1947; (2) White & Garrot 1990; (3) Grueter et al. 2009; (4) Worton 1995; (5) Getz & Wilmers 2004; (6) Getz et al. 2007;
(7) Lyons et al. 2013; (8) Benhamou & Cornelius 2010;(9) Benhamou 2011

### *2.3.3 Location-based methods*

Location-based kernel density estimates (KDE) are one of the preferred methods for UD estimation, and describe the density probability of positional fixes across the home range (Marzluff et al. 2004). A kernel is placed over each location point, and the density of intersecting kernels is summed at each point (Seaman and Powell 1996). The width of the kernel is called bandwidth (*h*) and determines the resolution of the UD (Seaman and Powell 1996). The bandwidth (or smoothing parameter) selection is the most important factor in a KDE, and selecting the appropriate value has been a main topic of debate (e.g., Seaman and Powell 1996; Getz and Wilmers 2004; Gitzen et al. 2006; Walter et al. 2011; Pebsworth et al. 2012). Bandwidths can either be a fixed value for all observations or adaptive and vary depending on the number of nearby locations (Walter et al. 2011). The appropriate bandwidth varies depending on the dataset (Walter et al. 2011), making home range estimates sensitive to the bandwidth selected (Pebsworth et al. 2012).

Many requirements of classical KDEs are violated due to the high temporal resolution data that GPS technology can provide due to regularly sampled non-independent points, and clustered location data (Walter et al. 2011; Lyons et al. 2013). They are unable to handle large clustered data well and perform poorly when they are fit to distributions that have distinct landscape boundaries, such as rivers (Getz and Wilmers 2004). It has been suggested that KDE may not be effective as a conservation tool in areas of high human pressure because it lacks the specificity required to assess habitat suitability and habitat selection at small scales (Riley et al. 2003), and because they perform poorly at excluding unused areas which are near areas of high importance (Ryan et al. 2006).

A solution to overcome the assumptions of KDEs is the local convex hull kernel method (LoCoH) (Getz et al. 2007). Unlike classical KDEs, LoCoH takes its form directly from

the data; there is no need to specify the functional form of the kernel, and therefore the data can be connected based on true boundaries (Getz et al. 2007). LoCoH is superior to classical KDEs in many instances (Getz and Wilmers 2004; Niemi et al. 2012; Sawyer 2012; Gehrt et al. 2013; Ramos-Fernández et al. 2013). The LoCoH estimate takes its form from one of three algorithms that constructs small convex hulls around each point and then merges the hulls incrementally to form density isopleths (Getz et al. 2007). Fixed-*r* LoCoH constructs hulls using all points within a defined radius around each point (Getz et al. 2007), and fixed-*k* LoCoH uses a fixed number of neighbours (*k*-1) around each point (Getz and Wilmers 2004). Adaptive LoCoH applies the hulls to the maximum number of nearest neighbours such that the sum of their distance is less than or equal to a defined distance, *a* (Getz et al. 2007). The recommended value of *a* is generally the maximum distance between any two points in the dataset (Getz et al. 2007). LoCoH is currently considered to be one of the best methods for identifying and excluding unused areas within a home range, and therefore may be most suitable for animals living in highly fragmented habitats or landscapes with human-made barriers to movement (Getz and Wilmers 2004), but there have been few applications to primate home ranging besides for home range estimator comparisons (Pebsworth et al. 2012; Sawyer 2012; Bryant et al. 2017; but see Coleman and Hill 2014).

### 2.3.4   Movement-based methods

In response to data with high temporal resolution, analyses were developed to handle serially correlated points by incorporating the time taken by the animals to get to their next destination (Horne et al. 2007; Keating and Cherry 2009; Benhamou and Cornélis 2010; Benhamou 2011). Adaptive T-LoCoH is an extension to the location-based adaptive LoCoH which incorporates time (Lyons et al. 2013). The algorithm for creating convex hulls around each point includes a time-scaled distance factor to select the nearest neighbours based on the maximum speed of the animal. However, as with the

location-based LoCoH methods, adaptive T-LoCoH does not incorporate fix error when constructing the hulls, and therefore tends to underestimate the home range (Pebsworth et al. 2012). Alternative movement-based methods are able to calculate density estimates by predicting the path the animal took by taking into account the time between fixes and the GPS location error (Benhamou and Cornélis 2010). The Brownian bridge movement model (BBMM) method uses the properties of a conditional random walk to construct kernel density surfaces based on the spatial uncertainty of each endpoint and assumes purely and constantly diffusive movement (Horne et al. 2007). However, with BBMM's assumption on movement, changes in diffusion based on adjusting speeds, sinuosity and memory-based reorientation caused by habitat preference are not supported (Benhamou 2011).

Biased random bridges (BRB) builds on BBMM by interpolating points between known locations based on activity data, and with the option to incorporate boundaries and/or vegetation types (Benhamou and Cornélis 2010). BRB is an advective-diffusive model that is based on frequent reorientations towards preferred areas (Benhamou 2011). The change in advection ("drift") strength is more efficient than that of pure diffusion in allowing for changes in space-use intensity (Benhamou 2011). When habitat types are incorporated in the estimate, the advection strength adjusts based on the frequency an animal reorients itself towards more attractive areas in the home range (Benhamou 2011).

To understand how an animal adapts their movement behaviour based on the temporal or spatial distribution of the resources they rely on, BRB was further developed into a more dynamic approach, by identifying areas of particular interest in terms of exploitation intensity (mean time per visit) or path recursion (visit frequencies) (Benhamou and Riotte-Lambert 2012). For example, an animal may move at a constant speed, but when it returns to certain areas, the movement slows down to

exploit the area more intensively. Although studies have demonstrated the central role of both residence time and recursion rates in home ranges (Li and Rogers 2005; Moorcroft et al. 2006; Barraquand and Benhamou 2008; Bjørneraas et al. 2012; Van Moorter et al. 2016), incorporating this aspect into the UD is relatively novel (Benhamou and Riotte-Lambert 2012; Lyons et al. 2013; Rock et al. 2016). The potential to provide researchers with a tool to study how intensively various areas are exploited, and how often the areas are revisited, could be an important contribution in understanding home range use (Benhamou and Riotte-Lambert 2012).

### 2.3.5   Remote activity

Despite the benefits that GPS collars can bring to understanding the relationship between an animal and its habitat, there can still be a large gap that cannot be filled by GPS locations alone. Due to different constraints (e.g., animal shyness, observer disturbance, logistics, accessibility), 24-h behavioural observations are not feasible (Löttker et al. 2009). In response, there has been an expansion of remote activity data collection, and many GPS collars are now capable of incorporating activity sensors (i.e. accelerometer). Markham and Altman (2008) reported that the travel rates (m/h) and activity sensor rates (head toggles/h) of chacma baboons (*Papio hamadryas ursinus*) followed a similar pattern throughout the day. Activity sensors have primarily been used to distinguish activities as either passive or active (Adrados et al. 2003; Coulombe et al. 2006; Gervasi et al. 2006). However, calibrating remotely measured activity with observed behaviour can allow certain behaviour types to be differentiated, such as distinguishing resting from feeding/slow locomotion and feeding/slow locomotion from fast locomotion (red deer *Cervus elaphus*, Löttker et al. 2009). The activity sensor can introduce new information into an animal's ranging behaviour that GPS locations alone cannot. For example, being able to determine if animals travel shorter distances after restless nights (e.g. due to predators or human activity) could give new insight into how external stressors may impact the animal's health (Markham

and Altmann 2008). There is also the possibility of examining the relationship between restlessness, moon phase (predator vulnerability) and sleeping site selection with activity data (Isbell et al. 2017).

### 2.3.6 Satellite tracking and home ranging methods for primates

Many primate home range studies using traditional behavioural follows have been limited to tracking only a few groups, or for only a few consecutive days at a time (e.g., Boonratana 2000; Garber and Jelinek 2005; Biebouw 2009; Musyoki and Strum 2016; Ni et al. 2018). Home ranges can be underestimated with traditional tracking, particularly when groups are not habituated or during early stages of a study when no prior knowledge of the home range exists (Oi et al. 2016). As most of the variation observed in home range size within species is due to individual and study site differences, it is preferable to increase the number of individuals monitored rather than sampling rate per individual (Börger et al. 2006). However, this has often not been possible with traditional follows due to logistical issues, such as group habituation, size of research team or field conditions.

GPS tracking can improve the availability of unbiased, high-quality data on ranging patterns of multiple groups and enhance a researcher's ability to identify important habitat for wildlife species (Hebblewhite and Haydon 2010). However, sample size has continued to be a major constraint on the use of GPS tracking in primatology; factors such as collar costs, and the risks of capturing and handling primates, have resulted in smaller than ideal sample sizes (Markham and Altmann 2008; Ren et al. 2009a; Pebsworth et al. 2012; Oi et al. 2016). As GPS collars are still new for primatological use, studies have primarily focussed on the discussion of the technology and on a comparison of methods (Pebsworth et al. 2012; Sawyer 2012; Bryant et al. 2017; Quintana-Morales et al. 2017), rather than focussing on the relationship between the primates and their environment. Only recently have GPS collar studies with multiple

groups been applied to primate ecology besides for methodological comparisons, such as for social dynamics (golden snub-nosed monkey *Rhinopithecus roxellana*, see Qi et al. 2014), disease transmission (Verreaux's sifaka *Propithecus verauxi*, see Springer et al. 2016), nocturnal activity (vervet monkey *Chlorocebus pygerythrus* and olive baboon *Papio anubis*, see Isbell et al. 2017), and urban ranging patterns (long-tailed and pig-tailed macaques, see Klegarth et al. 2017). For GPS collars to become a powerful tool in primate conservation, there is a need for the development of a standardised sampling regime and reporting methods so meaningful comparisons can be made (Börger et al. 2006; Pebsworth et al. 2012).

## 2.4   Overall conclusions and future work

Most primates are facing some degree of disturbance or modification in their natural habitat. Despite attempts to make generalisations of how species respond to these disturbances, conclusions can be difficult due to the combination of biological and environmental factors involved. One of the main issues in studying primates in a modified habitat is based on the terminology of the research question, and therefore the definition of the process or modification being examined should be stated explicitly (Arroyo-Rodríguez and Benítez-Malvido 2008).

With the continuous development of more sophisticated statistical modelling, the variation observed between or within species, such as group size, forest size, or environmental conditions, can be controlled for and stronger predictions can be made. However, the gaps in the available or existing data can make it more difficult to produce strong predictions. As automated research tools become more affordable, it is becoming more feasible to record continuous data in order to examine long-term trends in populations and the environment (e.g., automated weather stations, aerial remote sensing tools, data-loggers). Including environmental and habitat data can be used to

help fill in the gaps of how primates use the habitat within their home range and help identify areas of importance or concern.

GPS collars can contribute to the long-term monitoring of habitat use by tracking multiple individuals or groups over extended and continuous periods of time. An increase in the number of multi-group studies in primatology can also lead to a greater understanding in the nuances between individual and species level differences in habitat use. Although there has recently been an increase in using more advanced home range estimators for primates, it is important that the correct estimator is used based on the objectives of the study, rather than what is easily comparable to other studies. However, through methodological standardisation in data collection and data sharing, it should be possible to increase replication of analyses to help facilitate and improve understanding of primate behaviour and detect trends. Given the fast-moving nature of the statistical measures in home range estimation methods, it is important for up-to-date methodological comparisons, and is especially important in areas such as primatology, where new methods have received less exposure (Chapter 3).

Primates demonstrate resilience to changes in their habitat up to a certain point (Irwin 2016), but their long lifespan and reproductive timeline can make it more difficult to observe generational changes or adaptations. However, by monitoring as many of these factors as possible, it can be possible to track and identify responses to their changing environment over time.

# Chapter 3 Evaluating methods for estimating home ranges using GPS collars: a comparison using proboscis monkeys (*Nasalis larvatus*)

## 3.0 Abstract

The development of GPS tags for tracking wildlife has revolutionised the study of animal movement ecology. Concomitantly, there have been rapid developments in methods for estimating habitat use from GPS data. In combination, these changes can create challenges in choosing the best methods for estimating home ranges. In primatology, this issue has received relatively little attention, as there have been few GPS collar-based studies to date. However, as advancing technology is making collaring studies more feasible, there is a need for the analysis to advance alongside the technology. Using a high-quality GPS collaring dataset from 10 proboscis monkeys (*Nasalis larvatus*), this study aimed to: 1) compare home range estimates from the most commonly used method in primatology, the grid-cell method, with three recent methods designed for large and/or temporally correlated GPS datasets; 2) evaluate how well these methods identify known physical barriers (e.g. rivers); and 3) test the robustness of the different methods to data containing either less frequent GPS fixes or fixes missing at random. Biased random bridges had the best overall performance, combining a high level of agreement between the raw data and estimated utilisation distribution with relatively low sensitivity to reduced fixed frequency or loss of data. It estimated the home range of proboscis monkeys to be 24-165 ha (mean 80.8 ha). The grid-cell method and approaches based on local convex hulls had some advantages including simplicity and excellent barrier identification, respectively, but lower overall performance. With the most suitable model, or combination of models, it is possible to understand more fully the patterns and potential consequences that disturbances could have on an animal, and accordingly be used to assist in the management and restoration of degraded landscapes.

## 3.1 Introduction

The development of global positioning system (GPS) tags for tracking wildlife has revolutionised the study of home ranges, habitat use and behaviour (Hebblewhite and Haydon 2010). GPS telemetry has provided the opportunity to simultaneously track multiple animals with improved locational accuracy, without the limitations associated with radio-tracking or direct human observation, such as biases due to bad weather, length of time followed, distance covered, or difficult terrain (Hebblewhite and Haydon 2010; Tomkiewicz et al. 2010). However, the larger datasets and more frequent sampling intervals compared to traditional tracking have challenged the validity and feasibility of established data analysis methods, stimulating the development of new methods to reveal movement patterns and estimate home ranges (Fieberg et al. 2010; Kie et al. 2010). These are important developments, yet relatively little guidance is available to help researchers choose between them.

Home range estimation is one of the main applications of GPS tagging data (Kie et al. 2010). An animal's home range is traditionally defined as the area used for feeding, sleeping, finding mates, and raising young (Burt 1943), but more modern definitions describe it in terms of the area across which an animal has a defined probability of occurrence during a specified window of time (Kernohan et al. 2001). Furthermore, the home range is suggested to be part of the animal's cognitive map, in which movements are planned based on the nutritional state or motivation of the animal, and may include areas which it is aware of but does not go to, due to smell, sight or hearing (Powell and Mitchell 2012). Within the home range, important information for studies of ecology and conservation includes the total area required by the study subjects, the time spent in different areas and how frequently different areas are used (Fieberg and Börger 2012). This is often displayed in terms of a utilisation distribution (UD), the relative frequency at which an animal uses different parts of its home range (Van Winkle 1975; Gitzen et al. 2006). This in turn can help to identify the core area where an animal spends most

of its time, including important feeding and resting sites (Osborn 2004; Asensio et al. 2011). Characterising these different aspects of home ranges, and understanding the processes of habitat selection, movement and activity patterns and how they respond to environmental and human-made changes, are all important for the conservation management of wild populations (Osborn 2004; Nathan et al. 2008; Mattisson et al. 2010).

Since the early use of radio-collaring for studying home ranging in the 1960's (Craighead et al. 1995), methods for analysing tracking data have continuously evolved (Table 2.1), accelerating once GPS accuracy was unblocked in the 2000s and the subsequent rapid technological developments (Hulbert and French 2001). Home range estimators vary widely in their sophistication, assumptions and the level of detail revealed, but fall into two main groups: location-based methods, which ignore temporal information, and movement-based methods, which are more recent developments that combine time and location data. Both categories include methods for estimating utilisation distributions (see Section 2.3 for more detailed background).

Location-based estimators tend to be conceptually simple and computationally efficient. The grid-cell method (GCM) is the simplest approach to estimating the utilisation distribution, in which a grid is superimposed over an area, and the number of times an animal enters each cell counted (Grueter et al. 2009; Sawyer 2012). Although GCM is useful in highlighting hotspots in utilisation patterns, its main disadvantage is in measuring overall home range size, as well as estimating range boundaries, i.e. barriers or ranges with complex boundaries (Sawyer 2012). Both GCM and location-based kernel density estimators (KDE) are widely used throughout ecological studies, but the disadvantage of these approaches is that they are sensitive to the degree of smoothing (e.g. grid cell size or kernel widths) (Kie et al. 2010). These approaches also struggle in habitats with barriers to movement or where there are abrupt changes in

habitat type (Getz and Wilmers 2004). Location-based estimators also assume that points are independent of each other - an assumption that is rarely met by the short time intervals between GPS fixes (Walter et al. 2011).

In response to the limitation of location-based methods in handling barriers and assumptions requiring GPS point independence, the local convex hull kernel method (LoCoH) was developed by Getz and Wilmers (2004). LoCoH calculates the convex hull around each GPS fix based upon its nearest neighbours, before forming density isopleths by merging hulls (Getz and Wilmers 2004; Getz et al. 2007). Neighbours can be defined in different ways, leading to different variants of LoCoH (Getz et al. 2007). Unlike traditional kernel methods, LoCoHs do not require the user to make any pre-assumptions of the functional form for the kernels, and therefore they are more successful at identifying the true boundaries as the density of data increases (Getz et al. 2007).

Temporal autocorrelation between location fixes has traditionally been considered a problem in home range analysis, often leading to large amounts of data being discarded for independent observations (Schoener 1981; Swihart and Slade 1985). By contrast, movement-based density estimates combine the location and time of a fix, as well as being able to incorporate activity data collected between fixes by the movement sensors built into most GPS collars (Horne et al. 2007; Benhamou and Cornélis 2010; Lyons et al. 2013). Two of the movement-based methods are adaptive time LoCoH (T-LoCoH) and biased random bridges (BRB). T-LoCoH adds temporal information to the basic LoCoH analysis while retaining the desirable edge-detection qualities (Lyons et al. 2013). BRB is a development on KDE by combining serially correlated GPS fixes with high-frequency activity data to estimate fine scale movements and habitat use (Benhamou and Cornélis 2010; Walter et al. 2011; Campos et al. 2014). Recognising the value of accurately identifying home range edges, BRB allows barriers to

movement (e.g. rivers) to be specified, further reducing biases associated with traditional kernel smoothing (Benhamou and Cornélis 2010).

The number of home range analysis methods that are available, combined with the rapid rate of development of these analyses, can make it difficult for researchers to choose between methods. While the research question should be the primary driver of the method selected (Fieberg and Börger 2012), a greater practical understanding of how different methods perform would aid this selection and assist comparisons amongst existing home range estimates. Within the field of conservation biology, there has been an increase in studies comparing different home range estimators with GPS collaring data (e.g., Getz et al. 2007; Campbell et al. 2012; Gehrt et al. 2013; Dürr and Ward 2014). In primatology, however, this issue has received scant consideration as advanced home range studies are still in their infancy, with few GPS-collar-based studies and the analysis often relying upon the GCM (e.g., Grueter et al. 2009; Asensio et al. 2011; Sawyer 2012; Shaffer 2013a). Using a high-quality GPS collaring dataset collected from 10 proboscis monkeys (*Nasalis larvatus*) in northern Borneo, this study aimed to: 1) compare home range estimates generated by the most commonly used estimator in primatology, the GCM, with three alternative methods designed for large and/or temporally correlated datasets (adaptive LoCoH, time LoCoH and BRB); 2) evaluate model performance with known physical barriers for a species which recurrently utilises forest edges; and 3) test which of the models is the most versatile and robust by simulating less intense sampling regimes resulting from technological limitations or failures.

## 3.2   Methods

### 3.2.1   Ethics statement

Animal handling was carried out in accordance with the current laws of Malaysia and Sabah Wildlife Department's Standard Operation Procedures on Animal Capture,

Anaesthesia and Welfare. Permission was granted by the Sabah Biodiversity Centre (permit JKM/MBS.1000-2/2 JLD.3 (73)). The work carried out during this study was in accordance with the Weatherall report (Weatherall et al. 2006), and followed the guidelines for non-human primates as described by Unwin et al. (2011). All efforts were made to ensure the welfare, and reduce the stress of the animals, with the addition of full personal protective equipment worn by all team members throughout the process to prevent human-primate disease transmission. After conducting an evaluation of the area and target individual to minimise risk to the animals, a veterinarian specialised in the capture and anaesthesia of wildlife performed the darting. Animals were anaesthetised using Zoletil 100 (Tiletamine + Zolazepam; 6-10 mg/kg), and a prophylactic dose of Alamycine LA (20 mg/kg) and Ivermectin (0.2 mg/kg) was given as a preventative measure to assist in the post-anaesthesia recovery. Anaesthesia and the vital signs were monitored throughout the procedure.

### 3.2.2   Study site and subjects
This study took place in the Lower Kinabatangan Floodplain, Sabah, Malaysian Borneo (5°18'N-5°42'N and 117°54'E-118°33'E). The floodplain consists of 42,000 ha of protected forest and approximately 10,000 ha of state and private forest (Ancrenaz et al. 2004). It is a mosaic of agricultural land and natural forest types, including dry lowland, semi-inundated, semi-swamp/grassy and swamp forests (Abram et al. 2014).

Ten proboscis monkeys were collared from different one-male social units spread along the Kinabatangan River, covering a range of habitat quality, and forest fragment sizes (Fig. 3.1). Proboscis monkeys travel as an integrated unit, so the movement of a single individual can be considered representative of the whole group (Matsuda et al. 2011b). Collaring locations were always >2 km apart, or on opposite sides of the river, to minimise potential overlap between home ranges. Seven individuals were collared within the Lower Kinabatangan Wildlife Sanctuary (LKWS), and three were collared in

partially to totally unprotected forests that connected protected forest lots. GPS collars were fitted to six males and four females (male: Lotek Biotrack GSM WildCellSD; female: e-obs UHF 1C-Light), and weighed <2% of the individual's body mass (cf. recommended 5% maximum; American Society of Mammalogist 1998). Captures were done overnight so that the collared individual could be returned to its social unit before the group began to move the following morning. Collars were fitted and active from 2011-2015 and provided data for 241 (± 33) days (Table A1.1). By equipping the males' collars with a pre-programmed automatic release mechanism after 12 or 18 months, and the females' collars with leather spacers (due to weight constraints), no recapture was necessary. Collars were programmed to record hourly positions between 05:00 and 19:00 (at least 30 minutes before sunrise/after sunset) to maximise battery life, as proboscis monkeys are sedentary after dark (Matsuda et al. 2009a).
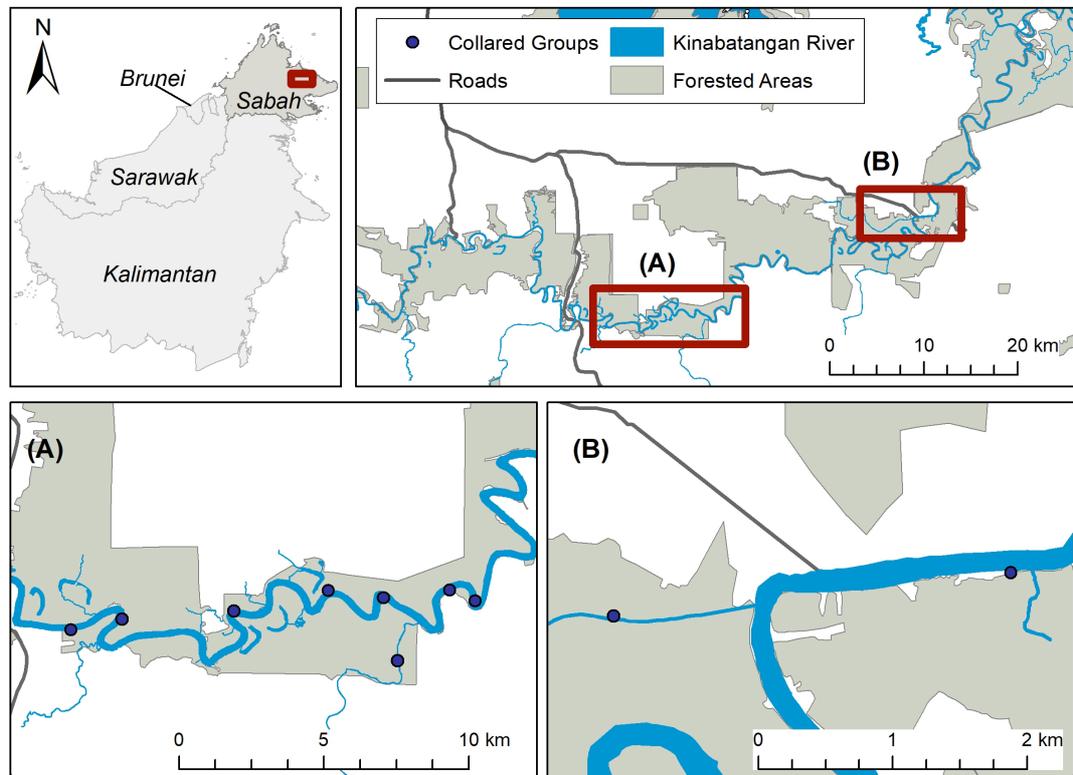


Figure 3.1 Collaring sites of 10 proboscis monkeys along the Kinabatangan River, Sabah, Malaysia.

*3.2.3   Home ranging datasets*

To improve the quality of the dataset as per Bjørneraas (2010), the GPS data were filtered prior to analysis to remove locations which were: i) fixed by fewer than four satellites; or ii) further from both the previous point and subsequent point than an animal is able to travel in the elapsed time. This distance was calculated using extensive ground follows of a single proboscis monkey group from a previous study that calculated the estimated daily path length during ground follows (Matsuda et al. 2009a). Therefore, any distance greater than half that (i.e. >400 m) between consecutive hourly points was excluded to account for GPS error. To account for pseudo-replication in the home range estimates due to the 19:00 and the subsequent 05:00 fix being taken in the same tree, all 05:00 points were removed. Compared to other studies, which have had to remove 16-26% of their points (Pebsworth et al. 2012; Markham and Altmann 2008), this study only rejected a small proportion of points (8.3%) and is therefore considered a high-quality dataset.

Many GPS collaring studies have a lower fix frequency than in the current study to maximise battery longevity when tag weight is restricted by the study species (Blackie 2010). In addition, a large proportion of GPS fixes often fail (e.g. <60% fix success rate, Johnson et al. 2002) or are rejected due to low quality, based on high dilution of precision values (Hulbert and French 2001; Bjørneraas et al. 2010; Pebsworth et al. 2012). To investigate the effects of these two factors on home range estimation, home range estimates were compared using the complete dataset to two subsets of the data that simulated lower fix frequency or higher fix error rates (Sawyer 2012). Simulation 1 removed 75% of the data to create regular 4-hour intervals between fixes to mimic the reality that many GPS tracking studies have to take less frequent fixes. Simulation 2 represented the situation where regular fixes were not always possible, or the GPS error was too high for the fix to be usable. This situation is more prevalent for smaller collars or for animals living on the forest floor (Gamo et al. 2000; Johnson et al. 2002; Lewis et al. 2007; Dürr and Ward 2014). As it is possible for multiple fixes to fail in a

day, a minimum of five fixes were randomly selected each day to represent fix success, with the maximum potential for 14 hourly fixes (see Table A1.1 for number of points used).

### 3.2.4 Home range estimations

Utilisation distributions were estimated using four approaches: i) GCM, ii) adaptive localised convex hull (*a*-LoCoH), iii) time-based adaptive localised convex hull (T-LoCoH), and iv) BRB. GCM and *a*-LoCoH are location-based estimators, whereas T-LoCoH and BRB are movement-based estimators (Table 2.1). GCM was calculated in Geospatial Modelling Environment (Beyer 2010) and ArcGIS 10 (ESRI 2011). The remaining estimators were calculated in R 3.1 (R Core Team 2015) using the packages *adehabitatHR*, *adehabitatLT* (*a*-LoCoH and BRB) (Calenge 2006) and *tlocoh* (Lyons et al. 2013). The UDs were based on the 90$^{th}$ percentile for overall home range size and 50$^{th}$ percentile for the core area (Börger et al. 2006).

GCM used a grid with 50 x 50 m cells, consistent with previous proboscis monkey studies (Boonratana 2000; Matsuda et al. 2009a). Despite the recommendation for home range estimates to exclude a proportion of outlying points, most studies continue to use 100% of the points for GCM home range estimates. However, to reduce the bias in home range estimations that include imprecise or exploratory movements, as well as to make the GCM method comparable to the other methods examined in this study, the cells consisting of 10% or less of point density per cell were eliminated to create the 90% home range, and cells with 50% or less of the point density were eliminated for the core UD estimates.

*a*-LoCoH is a development of the traditional minimum convex polygon method for calculating home ranges (Getz et al. 2007). It calculates a convex hull for every point in the dataset, based on its nearest neighbours, before merging the hulls into a set of

kernels based on the density of points (Getz et al. 2007). The nearest neighbours for each GPS fix are the sets of points whose cumulative distance to the focal fix is less than or equal to a defined threshold, *a*, resulting in areas of higher use having smaller convex hulls (Getz et al. 2007). The value of *a* was selected using the two-part method recommended by Getz et al. (2007): measure the maximum distance between two GPS fixes in the dataset as the starting value for *a*, and refine by rounding to the nearest multiple of 10 by visually assessing the maps using the "minimum spurious hole covering" technique (MSHC), which ensures the physical features that cannot form part of the home range (e.g. lakes) are excluded from the *a*-LoCoH estimate (Getz et al. 2007; Lyons et al. 2013) (Table A1.2 for the *a*-LoCoH model parameters used).

Adaptive T-LoCoH builds upon *a*-LoCoH by incorporating time into the model. A time-scaled distance factor, *s*, is used to select nearest neighbours for T-LoCoH by calculating the maximum theoretical velocity of an individual (Lyons et al. 2013). The scaling factor specifies the maximum amount of time at which spatially neighbouring, but not necessarily sequential, GPS fixes are still considered to be temporally correlated to the focal location, and therefore included as a nearest neighbour (Lyons et al. 2013). By increasing *s*, time becomes more important in defining the degree of correlation in the distance between fixes and the time between those fixes (Dürr and Ward 2014); when *s* = 0, time is not incorporated (Lyons et al. 2013). Lyons et al. (2013) recommend that the value of *s* should ensure that 40-60% of hulls are constructed using temporally correlated fixes so that both the spatial and temporal data are being considered relatively equal in the analysis; 50% was used throughout for consistency. The *a*-value was then selected using the MSHC technique (Table A1.2 for the T-LoCoH model parameters used).

BRB is a movement-based kernel method that links successive GPS fixes and then interpolates between them to develop a smoothed kernel density estimate for each interpolated location (Dürr and Ward 2014). To interpolate between locations, BRB assumes that the animal is moving towards the next location, but incorporates a random component to model deviations from the straight line path (Benhamou 2011). BRB requires three main parameter values to be set. The maximum time threshold ($T_{max}$) is the longest period between points before they are no longer considered to be autocorrelated. Autocorrelation was determined by comparing the summed squared differences in step length between successive fixes with randomly permuted values of step length using the acfdist.ltraj function in the R package *adehabitatLT* (Calenge 2006; Dray et al. 2010). For the complete dataset and Simulation 2, $T_{max}$ = 7,800 sec (2 h plus 10 min tolerance), and 29,400 sec for Simulation 1 (8 h plus 10 min tolerance) (Benhamou and Cornélis 2010). The second parameter, the minimum step length ($L_{min}$), defines a distance between successive points below which the animal is considered stationary (e.g. when feeding or resting; Benhamou and Riotte-Lambert 2012). To account for the possibility of an animal moving within a tree when foraging or from social displacements, or from possible false movements due to GPS error (average 14.3 m based on static collar tests with the collars set at a fixed location), track segments 15 m or less were assumed to be resting points ($L_{min}$ = 15). Finally, the minimum smoothing parameter ($h_{min}$) corresponds to the minimum standard deviation in relocation uncertainty (Benhamou 2011). $h_{min}$ must be large enough to encompass the range of potential locations an animal could actually occupy while being recorded at the same point, while being less than half the mean distance travelled for the time $T_{max}$ (Benhamou and Cornélis 2010). To assist in the selection of $h_{min}$, the mean cosine of relative turning angles of 0.3 was calculated to estimate the uncertainty of a location between two recorded locations (Benhamou 2004). This value suggested an intermediate selection of $h_{min}$ between the range of the observed standard deviation of relocation uncertainty (19 m) and half the mean distance travelled for time $T_{max}$ (68 m).

However, as boundary segment lengths must be greater than 3×$h_{min}$ and cannot be sharper than 90° (Benhamou 2012), $h_{min}$ was set at 25 m to account for these restrictions. See Benhamou (2004) for full details of this process. Images from Google Earth Pro (Google Earth 7.1 2014) were digitised and processed in ArcGIS 10 (ESRI 2011) to create the river barrier.

*3.2.5   Model comparisons and statistical analysis*
The home range estimates produced by the four methods were compared in two ways: i) the overall dissimilarity between the utilisation distributions, and ii) specific characteristics of the range estimates. Overall dissimilarity was assessed by calculating the Hellinger distance between each pair of home range estimates and ordinating the resulting distance matrix using principal coordinates analysis (PCoA), using the *pco* package in R (Wilson 2011; Roberts 2016). All 40 home range estimates (10 individuals x four methods) were converted to rasters on a standard grid with identical coordinate origin and resolution for a pixel-by-pixel comparison between the paired maps (Wilson 2011). The significance of differences between the methods was tested using permutational multivariate analysis of variance (perMANOVA), using the adonis function in the *vegan* package (Anderson 2001; Oksanen et al. 2017). Permutations were stratified by individual proboscis monkeys to control for individual differences and focus on the differences between the methods.

Five characteristics were used to compare home range estimates from the four methods (Table 3.1). Although an animal's 'true' home range using empirical data is unknown (as opposed to *in silico* comparisons), the relative properties of different estimators can be assessed using a range of measures. Area, boundary complexity and patchiness provided information about the basic shape of the home range. Variation in these three properties can illustrate the likelihood of estimators under- or over-fitting, and therefore can be indicative of the model's tendency to over- or

underestimate home range area, respectively. The complexity of a boundary can be used as a proxy to measure the relative goodness of fit of a home range, and may show that, due to irregular or concave boundaries created, it excludes areas which were both used and not used (Pebsworth et al. 2012). Although patches in a home range may be indicative of differences in habitat quality (McGarigal 2015) or an increase in speed through unfavourable areas to reach favoured areas, a large degree of patchiness due to over-fitting may also mean that the important pathways taken to the patches are not included. Accurate barrier detection is important for reliably delineating the edges of the home range. Methods that are unable to delineate the edges of an animal's range intrinsically are particularly susceptible to boundary bias. Quadrats that are in direct contact with the boundary are particularly susceptible, as values will be over- or under-estimated, depending on whether the quadrat lies on the unused side of the boundary, or the used side, respectively (Benhamou and Cornélis 2010). The area-under-the-curve (AUC) is a metric that has recently been used to determine the most appropriate home range estimator by assessing how well GPS fixes fit the contours of each estimator (Walter et al. 2015). AUC values measured each home range estimator's ability to discriminate between areas that had GPS fixes and those that did not (Walter et al. 2015). In effect it provided a measure of accuracy – the agreement between the observed GPS points and the modelled utilisation distribution. AUC values range between 0.5 to 1.0, with 0.5 equivalent to chance – no agreement between observed and modelled data – and a value of 1.0 indicating perfect agreement between the points and the utilisation distribution (Cumming and Cornelis 2012).

Table 3.1   Summary and methods used to calculate the physical characteristics used to compare the home range estimators.

| Home range characteristics | Justification and method |
|---|---|
| Total home range area | Calculated in ArcGIS in ha |
| Boundary complexity | Edge density (ED) ratio: ED = perimeter (m) / area (ha) (Hargis et al. 1998). Higher numbers indicate more complex boundaries, used as a proxy for how the data fit the model (i.e. by creating irregular or concave boundaries; Pebsworth et al. 2012). |
| Patchiness | The number of separate patches. Too many patches may indicate the model over-fitting (underestimating) the data and less representative towards the area actually required by the animal (Sawyer 2012). |
| Barrier detection | The percentage of the estimated home range that overlapped features known to be barriers to proboscis monkeys: large water bodies (main river and oxbow lakes) in this study. Small tributaries (<10 m wide) were not considered as true barriers, as proboscis monkeys are able to cross them easily (Matsuda et al. 2009a). |
| Area-under-the-curve (AUC) | A measure of accuracy used to assess how well GPS fixes fit the contours of each estimator, calculated using the *caTools* package in R based on Walter et al. (2015) (Tuszynski 2014). |

Differences in the five home range descriptors between the four methods were tested using generalised linear mixed models (GLMM) from the R package *lme4* (Bates et al. 2015), with estimation method as a fixed effect. The individual identification for each collared animal was treated as a random effect to account for multiple estimates of each individual's home range, and sex was included as a covariate to control for differences between males and females. The significance of terms was tested with a likelihood ratio test, comparing nested models with and without the fixed effect of interest, and Tukey tests were carried out using the *multcomp* package in R to examine pairwise differences between the four methods (Hothorn et al. 2008; Zuur et al. 2009).

The effects of reduced data quantity (Simulations 1 & 2) were assessed in two ways. First, a subsample overlap analysis was used to compare the home ranges estimated using the full data with those from the two simulations (Sawyer 2012). The percentage of the fixes from the full dataset included within the subsampled home range was calculated for both simulations, as well as the percentage of area overlapping between

the complete and simulation ranges of the same method. A higher percentage of overlap and greater inclusion of fixes indicated a more robust model (Sawyer 2012). The second approach compared home range estimates from both simulations to the estimates obtained using the full data based on the five measures (Table 3.1). GLMMs were used, with fixed effects for dataset (complete, Simulation 1 or Simulation 2) and estimation method, and a random effect for proboscis monkey individuals.

## 3.3. Results

### 3.3.1 *Method comparisons using the full dataset*
Utilisation distributions differed significantly among home range estimators ($F(3,36) = 0.45$, $p = 0.001$) and in how closely they matched the original GPS fixes (AUC; Chi-sq = 112.92, df = 3, $p<0.001$). GCMs were clearly separated from the other three methods, which were similar to one another: *a*-LoCoH and T-LoCoH models were generally concordant, while half of the BRB models overlapped the LoCoH models, and the remaining half were still closer to the LoCoH methods than to the GCMs (Fig. 3.2). GCM estimates agreed most closely with the raw GPS fixes (AUC = 0.998), followed by BRB (0.969), and the two LoCoH methods showing weaker agreement: *a*-LoCoH (0.841) and T-LoCoH (AUC = 0.807) (Fig. 3.3). All pairwise comparisons of AUC were significantly different ($p<0.05$) (see Table A2.1 for individual areas of each home range estimate method).
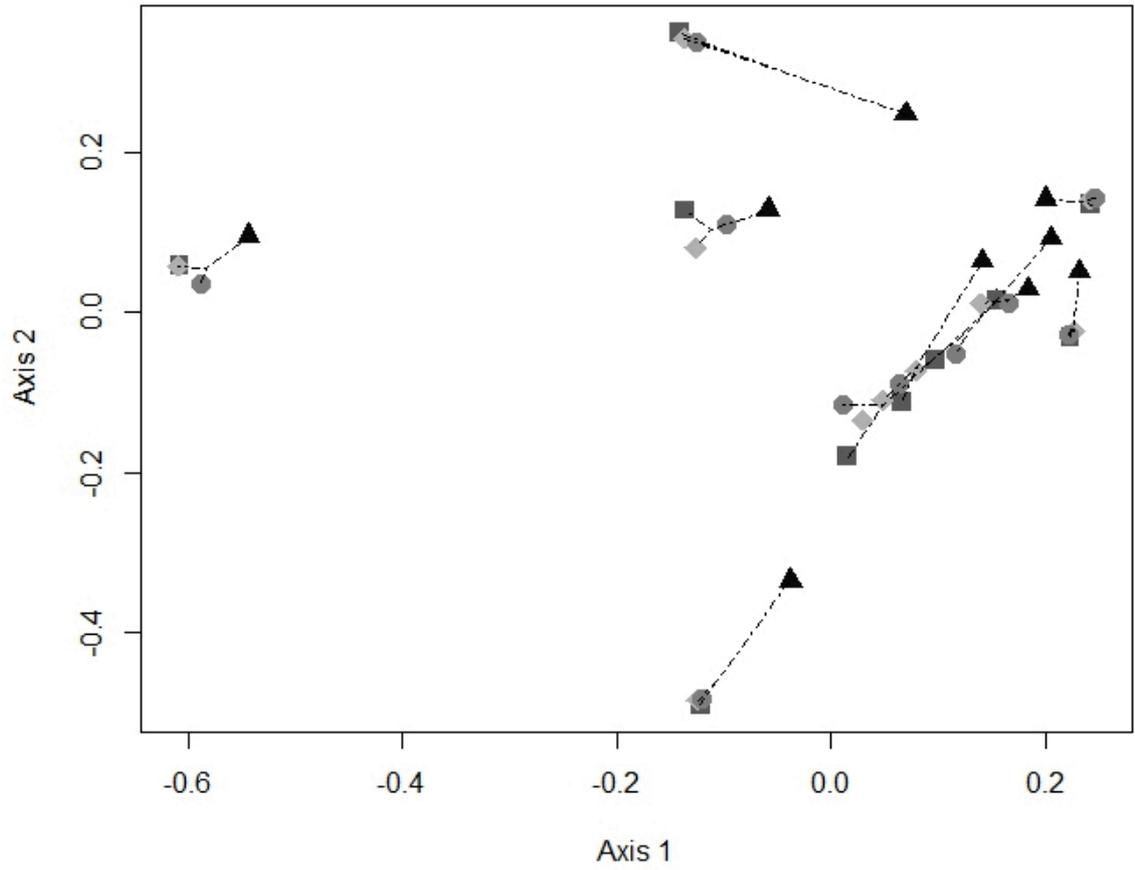
Figure 3.2   Principal coordinates plot of the home range estimators for 10 proboscis monkeys. Dotted lines indicate Hellinger distance, showing the dissimilarity between the ranges produced by four home range estimators: grid-cell method (triangle), adaptive local convex hull (square); adaptive time local convex hull (diamond), and biased random bridges (circle).
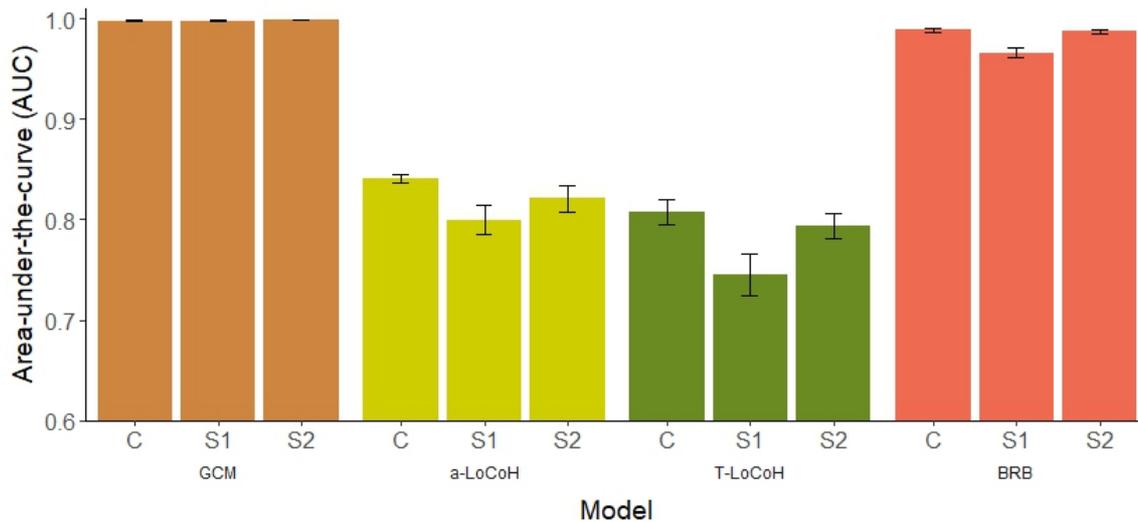
Figure 3.3 Mean (± SE, N = 10 individuals) area-under-the-curve for the home range estimators: grid-cell method (GCM; brown), adaptive local convex hull (a-LoCoH; yellow), adaptive time local convex hull (T-LoCoH; green) and biased random bridges (BRB; red), using the complete dataset (C) and the simulated scenarios, with a decreased sampling interval (S1 = fixes every 4 h), and simulating random failures (S2).

The choice of home range estimate method also significantly affected the area, boundary complexity, patchiness and edge detection accuracy of the resulting home range estimates (all p<0.001; Fig. 3.4, see Table A2.2 for detailed values and test statistics of overall and core range). GCM produced the largest, most patchy estimates, with the longest boundaries relative to area and the largest overlaps with the rivers/oxbow lakes for overall home range and core range (Fig. 3.5). It differed significantly from all other methods on these four measures (all Tukey tests p<0.05), with the exception of BRB for total area and a-LoCoH for boundary complexity of the core range. Using 100% of the points for GCM (as is commonly used in other studies) resulted in a home range estimate that was 22.1% larger, from 83.1 ha (range 35.0 – 167.3 ha) to 108.1 ha (range 41.3 – 217.0 ha).

a-LoCoH produced the smallest home range estimates and was not significantly different than T-LoCoH in producing the least patchy estimates. a-LoCoH had the least amount of overlap with the river and oxbow lakes. There was no difference in edge density between a-LoCoH, T-LoCoH and BRB in overall home range, but the core

range edge density for *a*-LoCoH was significantly higher than that of T-LoCoH and BRB. BRB produced mid-range estimates for patchiness and barrier detection for the overall range but was no different than *a*-LoCoH and T-LoCoH in its overlaps with rivers and oxbow lakes for core ranges.
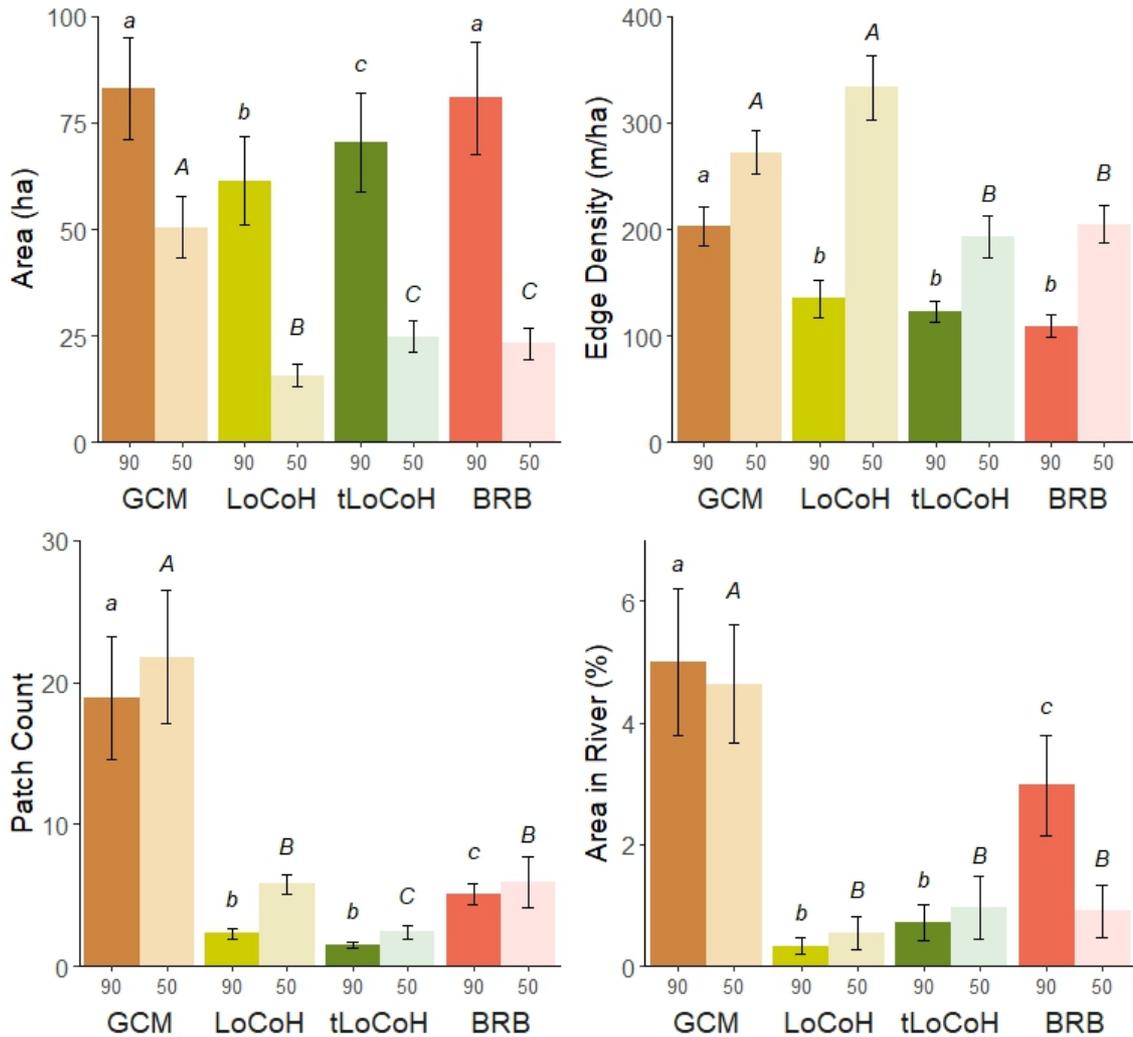


Figure 3.4  Summary of averages (± SE, N = 10 individuals) for overall (90%, dark) and core (50%, light) home range comparison variables: home range area (top left); boundary complexity (edge density; top right); patchiness (bottom left) and barrier detection (bottom right) for: grid-cell method (GCM; brown), adaptive local convex hull (*a*-LoCoH; yellow), adaptive time local convex hull (T-LoCoH; green), and biased random bridge (BRB; red).

a,b,c Pair-wise results from Tukey test; results significantly different from another (p<0.05) are indicated by a different letter, those with the same letter showed no significant difference. Lower-case letters represent overall home range differences, and upper-case letters represent core-range differences.
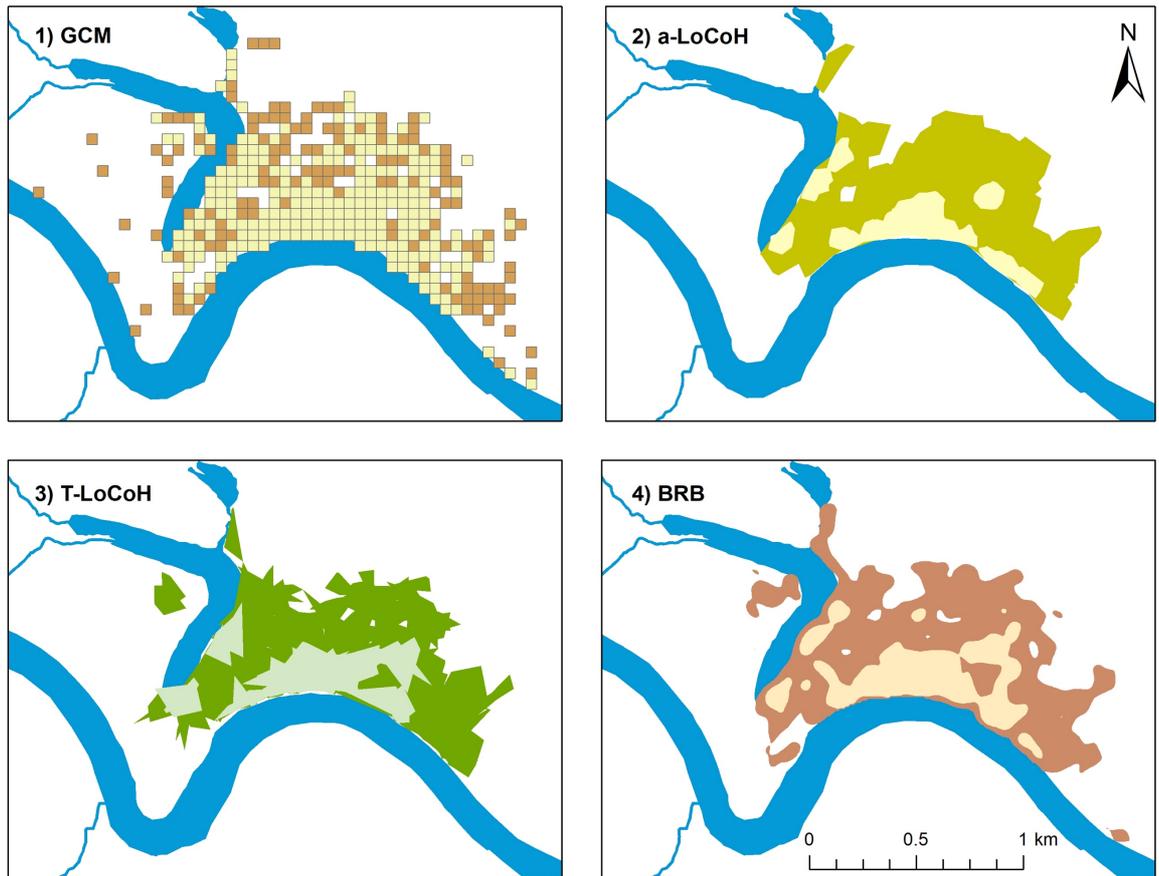
Figure 3.5  An example of the home range estimates produced for one proboscis monkey group. Home range estimator (1) grid-cell method (GCM), (2) adaptive local convex hull (*a*-LoCoH), (3) adaptive time local convex hull (T-LoCoH), and (4) biased random bridges (BRB); light colours = 50% isopleth, and dark colours = 90% isopleth. See Figure A2.1 for maps of the home range estimates of all 10 individuals.

### 3.3.2   Simulations

In the majority of cases, rarefaction of the GPS data (Simulation 1) or random selection of 5-14 points per day (Simulation 2) did not have significant effects upon the average characteristics of estimated UDs (Table 3.2, see Table A2.3 for each individual's complete and simulation home range area estimates). Differences occurred most frequently between Simulation 1 and the full data and affected GCM and BRB to a greater extent than the two LoCoH techniques. GCM was the only method to experience a significant change in the sub-sample overlap analysis, with Simulation 1 having the lowest percentage of overlap. Despite changes in area and outline, the AUC values for GCMs and BRBs showed no difference between simulations. The AUC was

the only measure by which *a*-LoCoHs and T-LoCoHs were affected, both producing smaller AUC values for Simulation 1 (Fig. 3.3). Different methods responded to the simulations in different ways. For GCM, Simulation 1 produced smaller UDs, with more complex outlines. BRB area estimates increased by a factor of 1.4 (core) and 1.5 (overall) and had smoother boundaries. Simulation 2 did not differ from the full data for either measure. Patchiness only changed for BRB with Simulation 1, decreasing the number of patches more by a factor of 2.6 (core) to 2.7 (overall) from the complete model. The area overlapping the river was not significantly affected by either simulation, despite the significant changes in home range area and boundary complexity for GCMs and BRBs (Fig. 3.6; see Table A2.4 for core range model summaries).

Table 3.2    Patch characteristics of the overall home range models: grid-cell method (GCM), adaptive local convex hull (*a*-LoCoH), adaptive time local convex hull (T-LoCoH) and biased random bridges (BRB). Simulation 1 simulated low fix rate (every 4 h) and Simulation 2 simulated fix failures. (Table A2.4 for core range model results).

| Simulation | Ave. Area (ha) | Ave. Edge Density (m/ha) | Ave. Patch Count | Area in river (%) | Point Inclusion (%) | AUC |
|---|---|---|---|---|---|---|
| *GCM: Comp.* | *83.1[a]* | *202.8[a]* | *18.9* | *5.0* | *96.3[a]* | *0.998* |
| Simulation 1 | 40.7[b] | 404.2[b] | 34.9 | 6.3 | 85.5[b] | 0.997 |
| Simulation 2 | 71.15[a] | 252.8[a] | 24.1 | 4.6 | 94.3[a] | 0.998 |
| *a-LoCoH: Comp.* | *61.4* | *134.8* | *2.3* | *0.3* | *89.8* | *0.841[a]* |
| Simulation 1 | 59.0 | 127.1 | 1.8 | 0.5 | 89.5 | 0.800[b] |
| Simulation 2 | 62.3 | 123.7 | 2.2 | 0.2 | 89.5 | 0.821[a,b] |
| *T-LoCoH: Comp.* | *70.5* | *122.5* | *1.5* | *0.7* | *89.7* | *0.807[a]* |
| Simulation 1 | 73.8 | 99.2 | 1.2 | 2.9 | 90.2 | 0.745[b] |
| Simulation 2 | 72.9 | 108.6 | 1.6 | 1.2 | 89.9 | 0.794[a] |
| *BRB: Comp.* | *80.8[a]* | *109.0[a]* | *5.1[a]* | *3.0* | *93.9* | *0.969* |
| Simulation 1 | 122.5[b] | 60.4[b] | 1.9[b] | 6.7 | 97.3 | 0.954 |
| Simulation 2 | 81.2[a] | 111.1[a] | 5.5[a] | 3.0 | 94.0 | 0.968 |
| Chi-sq value* | 123.2 | 205.7 | 213.1 | 111.6 | 98.0 | 310.1 |

a,b Pair-wise results from Tukey test; model results significantly different from another ($p<0.05$) are indicated by a different letter, those with the same letter showed no significant difference.
*Chi-square values for GLMM likelihood ratio test: for all tests, df = 11 and $p <0.001$.
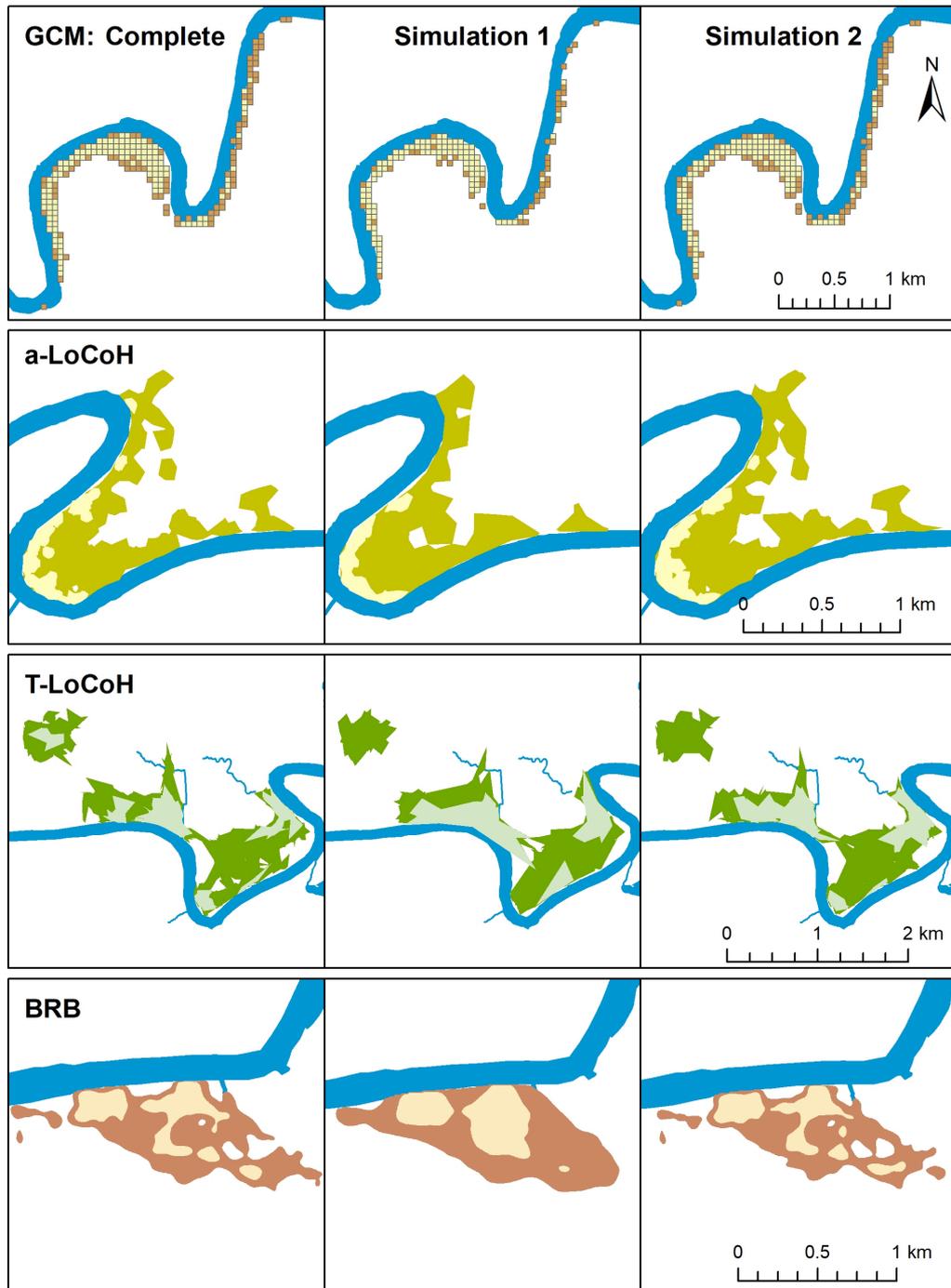
Figure 3.6   An example of selected home range estimators under different simulations: (A) grid-cell method (GCM), (B) adaptive local convex hull (*a*-LoCoH), (C) adaptive time local convex hull (T-LoCoH), and (D) biased random bridges (BRB). Simulation 1 simulated low fix rate (every 4 h) and Simulation 2 simulated fix failures (light = 50% isopleth, dark = 90% isopleth). See Figure A2.1 for maps of the home range estimates of all 10 individuals.

## 3.4   Discussion

Considering the advances in methods for home range estimation over recent years, there have been relatively few studies examining the suitability of new methods for primate ecology or conservation using multiple individuals. This study compared the most widely used approach in primatology (GCM) against several recently developed methods, and showed that the home range estimates produced by GCM were distinctly dissimilar from the others, even when only using 90% of the points instead of the standard 100%. For the physical characteristics, both LoCoHs were particularly robust to variations in sampling intensity and were the best methods for detecting barriers. Next to GCM, BRB estimates agreed most closely with the raw data, even when sampling intensity varied. Despite BRBs similarity to GCM in terms of area and AUC values, the Hellinger distances were more similar to the LoCoH methods and produced intermediate results between GCM and LoCoHs. The results demonstrate that the choice of home range estimator can have important impacts on the conclusions drawn from a study, and could be important considerations in selecting a method for home range estimation (Table 3.3). Some of the limitations to the study are considered before discussing the results in greater detail and concluding with some recommendations for future studies.

Table 3.3    Summary of the strengths and weaknesses of the home range estimators examined in this study: grid-cell method (GCM), adaptive local convex hull (*a*-LoCoH), adaptive time local convex hull (T-LoCoH) and biased random bridges (BRB).

| Method | Strengths | Weaknesses | Requirements | Suitability |
|---|---|---|---|---|
| GCM | • Comparable to other studies<br>• Identifies areas of importance<br>• High AUC<br>• Computationally simple | • Sensitive to sample size<br>• Cannot handle barriers well<br>• Largely biased by cell size selected<br>• Interpretation is sensitive to intervals displayed<br>• Time not a factor | • Knowledge of group spread, locational accuracy<br>• Use <100% points (i.e. 90%) | • Supplement other estimators to look at finer detail in high use areas |
| *a*-LoCoH & T-LoCoH | • Identifies complex barriers or inaccessible areas<br>• Incorporates time (T-LoCoH)<br>• Robust area estimate with changing sample size or sampling frequency | • Underestimates home range area<br>• No allowance for location uncertainties<br>• Low and variable AUC<br>• User-controlled process in selecting output | • Large dataset<br>• High temporal correlation (T-LoCoH)<br>• Knowledge of natural barriers | • Conservation planning to identify barriers or predator avoidance<br>• Range overlap between groups/species<br>• Core areas along sharp barriers |
| BRB | • Incorporates time<br>• High AUC<br>• Robust area estimates with fix failures<br>• Accounts for location uncertainties<br>• Area robust in variation of parameters selected ($T_{max}$ and $L_{min}$) | • Reduced barrier detection as barrier complexity increases<br>• Cannot detect behavioural or biological barriers<br>• Sensitive to decreased sampling frequency | • Species-specific knowledge, locational accuracy<br>• High temporal correlation<br>• Knowledge of natural barriers<br>• At least 200 locations | • Area estimates<br>• Home range for species living along definite habitat edges<br>• Studies with less precise records and more irregular fix success |

There are three main limitations to this study. The first is that it used a single species in one location, and so it is not possible to assess how different environments or home ranging behaviours might affect the conclusions. Nevertheless, the comparison is valuable alongside other studies comparing home range methods in an increasing diversity of single species (e.g., blacktip reef sharks *Carcharhinus melanopterus,* see Papastamatiou et al. 2009; grizzly bears *Ursus arctos horribilis*, see Steiniger et al. 2010; chacma baboons *Papio hamadryas ursinus*, see Pebsworth et al. 2012; domestic dogs *Canis familiaris*, see Dürr and Ward 2014). Furthermore, proboscis monkeys are a good model species for home ranging comparisons as they naturally occur in habitats that have sharp barriers (water bodies) against which to test the edge-finding ability of different range estimators and, as one of the largest monkey species, are able to wear GPS collars that can collect high-quality data over longer periods of time. This made it possible to use subsets of the data to simulate other tracking scenarios.

The second limitation is that the "true" home range of proboscis monkeys, as it is with mammals in general, is unknown. While it is possible to compare different methods and simulations in terms of their relative performance, there is no way to know the absolute accuracy of the proboscis monkey home range estimates. Powell and Mitchell (2012) suggest that because a mammal's home range is part of their cognitive map, which is constantly updating, home range estimates can only be defined for a specific point in time. Instead, utilisation distribution models can be used to predict areas in which the animal is likely to be at a point in time (Powell and Mitchell 2012). Simulation studies in the literature overcome this problem by using artificial tracking data, in which the true distribution is known in order to determine the method able to predict the UD most accurately (e.g., Millspaugh et al. 2006; Lichti and Swihart 2011), but few studies take these simulations a step further to real applications, using data with limitations such as GPS fix failure. Comparing the results from real scenarios with those from simulations

provides greater insight into the differences between methods.

The final limitation is that this is not an exhaustive comparison of home range estimators. The number of techniques is continuously developing, all of which have a wide range of parameters that need to be optimised based on the specific study or dataset. It is, however, a realistic application for studies that are restricted in the number of units or animals that can be tracked, or by the size of the study subject and therefore the performance of the GPS tracker. The methods compared here represent both location and movement-based methods, and are some of the key methods developed specifically for GPS data.

### 3.4.1  Model performance

Although it is now relied upon less in other ecological fields, GCM is still used in primate studies, as it is computationally simple and easily comparable between studies and sites. Overall, it showed the closest agreement between GPS fixes and the estimated home range but was the most sensitive to changes in sample size and produced estimates that were distinct from the other three methods (Fig. 3.2). These findings agree with previous studies showing that GCM will produce gross underestimates of home ranges if the subjects are not followed intensively (Grueter et al. 2009). GCM is therefore unsuitable for studies with longer time intervals between fixes, or random (time) sampling, such as sign surveys (Kenward 2001; Grueter et al. 2009; Sawyer 2012). Using the full dataset, GCM and BRB estimates of the home range area were similar, but the area of GCM estimates declined substantially in the simulations. It is important to note that if using 100% of the points, as is standard practice for GCM, the difference in home range area between GCM and BRB would no longer be similar, as the GCM area increased by almost a quarter. The close relationship between sample size and area was also evident with the unchanging AUC value.

The two LoCoH methods were the most robust to changes in sample size for range area and shape but produced the lowest and most variable AUC values. *a*-LoCoH produced significantly higher AUC values than T-LoCoH, which may be due to the additional parameter of T-LoCoH required to incorporate time. The overall home range areas estimated with *a*-LoCoHs and T-LoCoHs were very similar, which was expected as T-LoCoH was developed as an extension of the location-based *a*-LoCoH (Lyons et al. 2013). The area estimates were also smaller than the GCM and BRB, which is supported by simulated LoCoH studies showing the hulls created essentially 'hug' the data (Getz et al. 2007; Lyons et al. 2013). However, this also means that the LoCoH methods are not as strong at modelling spatial uncertainty associated with GPS fixes (Lyons et al. 2013). They both perform most effectively with large datasets (Niemi et al. 2012); *a*-LoCoH has been shown to converge on the true range as sample size increases (Getz et al. 2007), and is beginning to be used in primatology (Pebsworth et al. 2012; Sawyer 2012; Coleman and Hill 2014; Bryant et al. 2017).

BRB appeared to show the best overall performance, producing high and robust AUC values. BRB did not show as much sensitivity to sample size or fix frequency as GCM, which had similarly high AUC values. The positioning of BRB home ranges on the PCoA plot indicates its similarity to LoCoH models. Nevertheless, reducing the sampling frequency, and in turn, increasing $T_{max}$, results in a greater degree of smoothing and larger predicted areas for BRB (Dürr and Ward 2014). This was observed for Simulation 1, evident in the lower edge density and patchiness, and greater overlap with the river. The AUC value showed little change, however, suggesting that the model was appropriate to use with the current data. The irregular time spacing in Simulation 2, mimicking high fix failure rates, had much less effect on the BRB estimates, producing similar values to the complete dataset for all variables. This was probably because there were periods in the data with higher fix frequencies than the 4 h intervals in Simulation 1, allowing better predictions of the tracks taken

between fixes. The results from this study agree with previous findings that BRB is well-suited for studies with less precise records and more irregular fix success (Dürr and Ward 2014), which is often the case for smaller collars or for collars that have less direct exposure to satellites (e.g. terrestrial forest-dwelling animals).

### 3.4.2 Barrier detection

The ability to detect or incorporate barriers is an important function for home range estimates, as including inaccessible areas will overestimate the home range area. This is becoming increasingly important in conservation ecology: there has been a dramatic increase in the number of studies addressing fragmentation and therefore increasingly at sites that include a physical barrier, due primarily to habitat loss (e.g., Chapman and Peres 2001; Piper and Catterall 2004; Ting and Shaolin 2008; Arroyo-Rodríguez et al. 2013; Brodie et al. 2015). GCM had the weakest performance, as almost entire cells overlapped the river and oxbow lakes. Grid cells in direct contact with barriers have a large bias, as on average half the cell will be under or overestimated (Benhamou and Cornélis 2010). The amount of overlap with a barrier will be influenced by cell size and has been shown to heavily affect the estimated home range area (Ostro et al. 1999; Lehmann and Boesch 2003; Fieberg and Kochanny 2005; Grueter et al. 2009; Sawyer 2012). The choice of 50 x 50 m cell size in this study is already finer than in most primate studies (100-500 m: chimpanzees *Pan troglodytes*, see Chapman and Wrangham 1993; lowland woolly monkeys *Lagothrix lagotricha poeppigii,* see Di Fiore 2003; Bornean orangutans *Pongo pygmaeus,* see Knott et al. 2008; snub-nosed monkeys *Rhinopithecus bieti*, see Grueter et al. 2009; spider monkeys *Ateles geoffroyi,* see Asensio et al. 2011; Cross River gorilla *Gorilla gorilla diehli,* see Sawyer 2012; northern bearded sakis *Chiropotes sagulatus*, see Shaffer 2013b), so the problems of barrier overlap demonstrated here should be relatively conservative.

LoCoH methods, on the other hand, were designed to detect hard barriers or areas that seem inaccessible (Naidoo et al. 2012). This property was apparent in the current study, with LoCoH consistently showing the lowest overlap with the river and oxbow lakes. As long as the points are taken at a frequent enough rate that corresponds with the movement rates of the species in question, LoCoH is capable of identifying sharp and complex boundaries within a few meters, even when the animal is moving along that boundary (Getz et al. 2007; Lyons et al. 2013). Having fewer spatially and temporally auto-correlated points reduces the model's ability to detect important pathways taken by animals within their home range (Schweiger et al. 2015). Consequently, T-LoCoH works most efficiently with a large dataset with high temporal correlation (Lyons et al. 2013). The major strength of LoCoH in detecting barriers, such as river edges, can also be its weakness, resulting in the exclusion of areas that are actually used (Pebsworth et al. 2012).

BRB does not have the same inherent ability to detect barriers as the LoCoH methods do (Benhamou and Cornélis 2010) and therefore, unlike LoCoH, cannot identify non-geographic barriers, such as territorial barriers or predator avoidance. The mathematical requirements necessary to implement the barrier also result in some limitations to their use (Benhamou and Cornélis 2010). The barrier requirements can be difficult to satisfy when they are complex or have sharp and tight bends, as observed in several sections of the river in this study. The barrier requirements became increasingly difficult to satisfy as $T_{max}$ increased: when the bend of the river was narrower than a distance of $3*h_{min}$, a simpler barrier had to be used. Subsequently, the riverbanks within the sharpest bends could not be included, resulting in an increase in the percentage of the home range extending in the river along those areas. However, provided the data have relatively frequent fixes and the barriers are well known (as with the river here), the integrated barrier function performed comparatively well.

### 3.4.3   Practical considerations

All of the home range estimator methods considered here require choices to be made for one or more model parameter. For GCM, only the grid cell size needs to be chosen, but as discussed above, this choice can greatly affect the estimated home range area. Often there is little justification given as to the value selected. If GCM is used, biologically based information, such as typical group spread, as well as locational accuracy (i.e. GPS error) needs to be carefully considered in the selection of cell size prior to analysis. Smaller cell sizes may be better at demarcating areas of importance, and it has been suggested that GCM could be useful when examining habitat suitability and identifying important areas for resource selection (Harris et al. 1990; Doran-Sheehy et al. 2004; Page et al. 2009; Sawyer 2012).

The LoCoH methods involve selecting an *a*-value directly from the output that visibly looks best to the user. Getz et al. (2007) described the standard method of initially selecting the parameter values by using the maximum distance between points, then using the "minimum spurious hole covering" rule to refine the parameter based on *a priori* knowledge of the area. Of the three parameter options (radius, nearest neighbours or adaptive), adaptive is the least sensitive to changes in the parameter value selected (Getz et al. 2007; Niemi et al. 2012; Lyons et al. 2013). However, the final selection falls down to the user to decide which parameter value creates the most suitable looking isopleths, based only on visual aids (Lyons et al. 2013; Dürr and Ward 2014), potentially adding bias. Furthermore, LoCoH tends to over-fit the data, resulting in irregular and concave boundaries (Pebsworth et al. 2012). Over-fitting was supported in this study as indicated by the higher levels of boundary complexity than BRB, and results in an underestimation of home range area by excluding areas in which the animal actually goes (Pebsworth et al. 2012; Sawyer 2012). By not providing any buffer around the fix (i.e. to account for location uncertainties), any surrounding habitat that may be critical for the species is excluded (Sawyer 2012).

Compared to many location-based kernel density estimates, the parameters chosen for BRB are more intuitive. BRB uses species-specific knowledge as well as the information regarding the precision of the location data (Benhamou and Cornélis 2010) without the same user-defined bias that the LoCoH methods have in looking at the resulting range estimate and making it fit the expected shape. Furthermore, previous studies have shown that adjusting the values of two of the three BRB parameters ($T_{max}$ and $L_{min}$) appears to have little effect on isopleth area and shape (Dürr and Ward 2014). In studies applying BRB, a balance has to be made in selecting a smoothing value that is representative of the GPS data itself, and one that allows for implementing barriers. For species that use definite habitat edges, such as proboscis monkeys, neglecting barriers in the home range analysis could result in an important source of error.

### 3.4.4   Conclusions and recommendations

The selection of a home range estimator needs to consider a combination of the underlying research question and information already known about the species and its environment, to determine the most suitable method (Fieberg and Börger 2012). In this study of several popular home range estimators some clear differences in performance among the methods were revealed. Although GCMs produced the highest and most consistent AUC values, it performed the worst at barrier detection, generated highly fragmented home range estimates and was the most sensitive method to sample size or sampling frequency. Despite being commonly used in primatology, GCM is not recommended for determining home range boundaries, especially when animals cannot be followed intensively (Sawyer 2012), or for a species that spends a large proportion of time along areas with hard barriers, such as proboscis monkeys. However, GCM may be useful in conjunction with other methods as a simple way to identify areas of importance within the range boundary, i.e. as a simple way of estimating the UD. *a*-LoCoH and T-LoCoH were the most robust models to variations

in sample size and fix frequency but had the lowest AUC values and the most variation in AUC values for the simulations. They tended to underestimate the range area, and therefore may not be suitable when looking to conserve an area for a species. Between the location-based and movement-based LoCoH methods, *a*-LoCoH only slightly outperformed T-LoCoH regarding AUC values. However, the incorporation of time in T-LoCoH makes it more biologically relevant in utilisation distribution modelling and therefore is preferred over the location-based method if the dataset has frequent and regular GPS fixes. The inclusion of time (T-LoCoH and BRB) allows for a more dynamic approach of UDs by further analysis into how often an area is visited, the time spent in those areas and the time between visits (Benhamou and Riotte-Lambert 2012; Lyons et al. 2013; Chapters 4 and 5). The additional information that the movement-based methods provide can shed more light on the habitat requirements of an animal, particularly when it comes to conservation planning. Moreover, although LoCoH may not be the most effective method for determining the total area an animal requires, it can also be useful for conservation planning by detecting unused areas within a range or potential restrictions to movement, such as human-made barriers or avoidance of predators (Pebsworth et al. 2012; Sawyer 2012; Gehrt et al. 2013), identifying range overlap between species or groups (Gehrt et al. 2013; Schweiger et al. 2015), or for identifying core ranges along sharp boundaries (Naidoo et al. 2012).

With the increasing fragmentation of habitats across the globe, incorporating boundaries in home range analysis is becoming more relevant in more studies. By including the barrier feature, BRB seems to be the most suitable overall method for determining the home range of an animal with relatively frequent points (<4 h) and identifying pathways or routes that are important in the connectivity of an animal's ranging behaviour. Where the nature of barriers is uncertain *a priori* or could follow complex landscape features, or when fixes are at a relatively low frequency, LoCoH methods could complement BRB.

By using the most suitable model, or combination of models, it is possible to understand more fully the patterns, causes, and potential consequences that disturbances could have on an animal, which can then be used to assist in the management and restoration of degraded landscapes (Nathan et al. 2008). Proboscis monkey ranging behaviour is poorly known, with only two previous estimates, both of which were limited to a single group (Boonratana 2000; Matsuda et al. 2009a). By using 100% GCM, the home range estimate averaged 108 ha (41-217 ha) compares to previous estimates using the same method, of 138 ha (Matsuda et al. 2009a) to 221 ha (Boonratana 2000). By using GPS collars on multiple proboscis monkey groups, this study showed that BRB was the best-performing home range estimator according to the parameters defined. As GCM tends to over-estimate home range size (as discussed above), the value of home range size of proboscis monkeys in a riparian habitat is smaller using BRB, ranging from 24 to 165 ha, with a mean of 81 ha. The BRB should be considered the most representative estimates of proboscis monkey home range to date. Further work using BRB will allow the movement patterns and habitat use within the home ranges to be quantified, alongside the factors affecting the selected range size and variation between the different ranges, contributing further towards the conservation of this endangered primate species.

# Chapter 4 Resource utilisation by proboscis monkeys in a degraded forest landscape

## 4.0 Abstract

Conversion of tropical forest to large-scale agriculture is a major concern for a wide range of species, as forest is reduced to smaller fragments in an agricultural matrix. To support conservation efforts in the remaining forest, understanding how species use the landscape is important to define minimum habitat requirements and develop quantitative targets for habitat protection. Apart from an association with rivers, little is known about proboscis monkey (*Nasalis larvatus*) habitat requirements and how forest disturbance impacts their ranging patterns and resource use. Using a combination of 20 LiDAR-derived habitat variables to describe forest structure, GIS analysis of landscape structure (e.g. forest area, proximity to forest edge) and GPS-collar tracking data from 10 proboscis monkeys, this study 1) identified core and peripheral areas of each individual's home range, along with areas used frequently (recursion) or for long periods at a time (intensity); and 2) estimated the diurnal resource utilisation preferences within their home ranges in forests of the Kinabatangan floodplain in Sabah, Malaysian Borneo. There was little difference in the overall habitat characteristics of the forests. High intensity patches tended to be smaller and distributed around the periphery of the home range, whereas high recursion patches tended to be concentrated in one main area. Resource utilisation functions indicated a significant preference for proximity to water and forest with a taller mean canopy height. Further analysis with generalised additive models revealed that proboscis monkeys most heavily used areas with mean tree heights in the range of 20-25 m, close to rivers (<200 m) or further away from oil palm plantations (>2 km). The results suggest that proboscis monkeys may have relatively general habitat preferences based upon canopy structure, but leave the possibility that they may respond to structure over shorter timescales. Although reclaiming and protecting forests unsuitable for oil palm are important actions towards the conservation of proboscis monkeys, the amount of

forest based on proximity to edge type needs to be included as a priority when developing management strategies in Borneo.

## 4.1 Introduction

As humans impact natural systems through land cover change, climate change and the introduction of invasive species (Bellard et al. 2014), it is important to understand key components of animal ecology, such as home ranging patterns and resource use, and how changing habitats may alter these components. Habitat loss, degradation, or fragmentation can prevent animals from moving freely between foraging, breeding or refuge areas (Niemelä 1999), cause shifts in home ranges (Clarke et al. 2002), encourage avoidance behaviours in ranging patterns (Kinnaird et al. 2003), or ultimately cause species extinction (Irwin 2016). Movement is a response to the environmental conditions experienced by the animal (Van Moorter et al. 2016), resulting in the animal's adaptive and uneven use of its environment. Importantly, areas visited frequently may not be the same as areas that are visited for long periods (Van Moorter et al. 2016). For example, a waterhole may be visited often, but only for a short period of time (Benhamou and Riotte-Lambert 2012). On the other hand, areas used for long periods of time may indicate an important food source or a suitable place for resting which is safe from predation. Therefore, the amount of space an animal uses tends to be more limited than what would be expected based on its locomotive capabilities (Börger et al. 2008). A better understanding of an animal's ecology can be obtained by looking at these more detailed spatial and temporal facets of movement behaviour.

Utilisation distribution (UD) models are often used to explore the ranging behaviours of animals (Benhamou and Riotte-Lambert 2012; Section 2.3.2 and Section 3.1). UDs estimate the relative frequency at which an animal uses different parts of its home range, typically over a period of months (Van Winkle 1975; Gitzen et al. 2006).

Recently, Benhamou and Riotte-Lambert (2012) went further, splitting UDs into their two basic components to explore some of the dynamics involved in animal movement choices: 1) an intensity distribution (ID), the mean residence time in a given area per visit, and 2) a recursion distribution (RD), the frequency with which areas are visited. It is generally assumed that recursion should not happen without resources at least partially recovering, and therefore longer and more complex recursion paths (e.g. more resource sites arranged in a complicated spatial configuration) can occur in areas with slower recovery rates (Berger-Tal and Bar-David 2015). If recovery were fast or resources were evenly distributed, then there would be little need for recursive movement, and the best strategy would be to stay in close vicinity of said resource. Therefore, for recursion behaviours to occur, there needs to be some degree of predictability and heterogeneity in the habitat, alongside higher level capabilities from the animal (Berger-Tal and Bar-David 2015); hence recursion tends to be observed more frequently among particular taxa, such as primates (Janson and Byrne 2007; Reyna-Hurtado et al. 2017).

Once high use areas in an animal's range have been identified (overall high utilisation, intensity or recursion), a logical next step is to determine which environmental features are associated with those areas (Papworth et al. 2012). Depending on the ecological needs of a species, the ranging patterns may be more restricted or patchy (i.e. specialist species) or more uniform (i.e. generalists). Such resource use studies can help to define minimum habitat requirements and can be used to develop quantitative targets for habitat protection (Garabedian et al. 2017). Traditionally, habitat descriptions have relied upon ground surveys, a labour-intensive method, especially over large spatial scales. More recently, remote sensing has become a widely used tool to derive ecologically relevant forest vegetation characteristics over local and regional scales, and has been shown to do so more efficiently than extensive ground

surveys, while still being able to detect subtle differences in the vegetation profiles (Bässler et al. 2011).

Light detection and ranging (LiDAR) is an active remote sensing tool that provides fine-scale 3D data on the habitat structure of an area and allows for accurate quantification and contiguous measurements of a landscape (Davies and Asner 2014). As well as being used to derive habitat maps, LiDAR has been used to model habitat suitability for forest species (Ackers et al. 2015; Singh et al. 2018), map local-scale habitat quality (Rechsteiner et al. 2017), show the effect animals may have on their landscape (Asner and Levick 2012), and explore how species movement is affected by vegetation structure (Loarie et al. 2013; Zellweger et al. 2014; McLean et al. 2016; Davies et al. 2017; Evans et al. 2018). Combining remotely sensed habitat data with animal satellite tracking can highlight the home range nuances of a species without observer bias and increase the amount of information obtainable in logistically remote areas or in challenging terrain (Chabot and Bird 2015; Schweiger et al. 2015). Having fine-scale habitat data and high resolution GPS data allows for microhabitat use on a scale that has been largely untapped in primate studies, apart from the recent use of these data to compare canopy structure preferences in daily path movements between mantled howler monkeys (*Alouatta palliata*), black-handed spider monkeys (*Ateles geoffroyi*) and white-faced capuchin monkeys (*Cebus* capucinus) (McLean et al. 2016), and on the collective movement behaviour in olive baboons (*Papio abunis*, see Strandburg-Peshkin et al. 2017).

The island of Borneo is ranked among the most vulnerable biodiversity hotspots, in part due to the number of endemic species vulnerable to climate change (Bellard et al. 2014). In the past 40 years, Borneo has experienced forest conversion rate almost twice as fast as the rest of the world's humid tropical forests (Gaveau et al. 2014). Proboscis monkeys (*Nasalis larvatus*), classified as Endangered (Meijaard et al. 2008),

are endemic to Borneo and a focal species in attracting tourism to the island (Leasor and Macgregor 2014). Proboscis monkeys are generally considered to be associated with forest close to rivers, swamps, lakes and mangroves, and the combination of this association with the difficulties of surveying in the forest interior, have led to the majority of research being restricted to boat-based surveys (e.g., Yeager and Blondal 1990; Goossens et al. 2002; Sha et al. 2008; Matsuda et al. *in press*). However, this approach to studying the species may reinforce this apparent link, which has relatively little evidence to underpin it. Besides three published studies, two on the basic ranging behavioural observations in the forest of single groups (Boonratana 2000; Matsuda et al. 2009a), and one on determining the most suitable home range estimator with using GPS collars (Chapter 3: Stark et al. 2017a), little is known on how proboscis monkeys utilise the forest within their range and the structural or physical habitat characteristics associated with habitat selection.

In the Malaysian state of Sabah, only 15% of proboscis monkeys live in totally protected forests (Sha et al. 2008), and despite laws, conversion or clearing of the riparian reserves which support them is still occurring (Chapter 6). Proboscis monkeys do well in secondary forests and along forest edges because of the high levels of young leaf growth, and hence high-quality foods (Ganzhorn 1995; Matsuda et al. 2013). However, unlike many of the other diurnal primates in Sabah (e.g., long-tailed macaque *Macaca fascicularis,* pig-tailed macaque *M. nemestrina,* Bornean orangutan *Pongo pygmaeus,* maroon langur *Presbytis rubicunda, pers. obs.*), proboscis monkeys appear restricted to forested areas, as they avoid entering severely disturbed areas such as oil palm plantations, extensive grasslands and human settlements (Salter and MacKenzie 1985; Bernard and Zulhazman 2006). Hence, to inform land change policy for the survival of one of Sabah's most charismatic species, it is vital to identify the resources important to proboscis monkeys and how the proximity of human-made edges (i.e. plantations) or limited forest availability may impact their ranging and

resource use.

To date, there have been very few published studies in primatology that have used LiDAR and GPS collars together to examine an animal's resource use (but see McLean et al. 2016), and no studies examining proboscis monkey resource use based on ranging behaviour. This chapter aims to address this gap, looking at how overall utilisation of forest areas, along with its intensity and recursion components, is related to forest and landscape structure (using LiDAR and GIS-derived variables respectively). It has three specific aims. The first was to identify a subset of LiDAR variables that capture the main sources of variation in habitat structure. Well over 50 LiDAR-based variables have been used in recent studies of forest structure, and it is likely that there is a high degree of redundancy amongst them, comparable to the numerous metrics devised in other fields such as hydrology (Olden and Poff 2003). The second aim was to use the recursion and intensity components of proboscis monkeys' home ranges to explore how forest size and disturbance may influence the use of these 'high importance' areas. More overlap between high intensity and high recursion areas was predicted in smaller or more disturbed forests, whereas there would be greater separation between them in larger or less disturbed forests. Finally, using the subset of LiDAR-derived variables and proximity to forest edges, this study also aims to determine individual and population-level resource preferences for proboscis monkeys. Increased use (intensity and recursion) was expected to be associated with taller trees, fewer canopy gaps and proximity to forest edges and be more weakly related to edges bordering plantations than rivers.

## 4.2   Methods

### 4.2.1   Proboscis monkey collaring
Between 2011 and 2015, 10 proboscis monkeys were collared from different one-male social units along the Lower Kinabatangan Floodplain in Sabah, Malaysian Borneo

(5°18'N-5°42'N and 117°54'E-118°33'E) (Fig. 4.1). Group size and composition were not consistently available or reliable, as the groups in this study were not habituated, but ranged between 10-20 individuals. The floodplain consists of the Lower Kinabatangan Wildlife Sanctuary (LKWS), Virgin Jungle Reserves, and privately owned (unprotected) land (Ancrenaz et al. 2004). To satisfy assumptions of independence, collaring locations were >2 km apart, or on opposite sides of the river, minimising potential overlap between home ranges. Collars provided data for 241 (± 33) days (Table A1.1) and were programmed to record hourly positions between 05:00 and 19:00. See Section 3.2.2 for more collaring details. Based on the criteria described in section 3.2.3, the GPS data were filtered, and to account for pseudo-replication of the 19:00 and the subsequent 05:00 fix being in the same tree, the 05:00 points were removed. Proboscis monkey groups travel as a cohesive unit (Matsuda 2009a), and therefore, the locations of the collared individual were considered representative of the group as a whole (Campos et al. 2014).
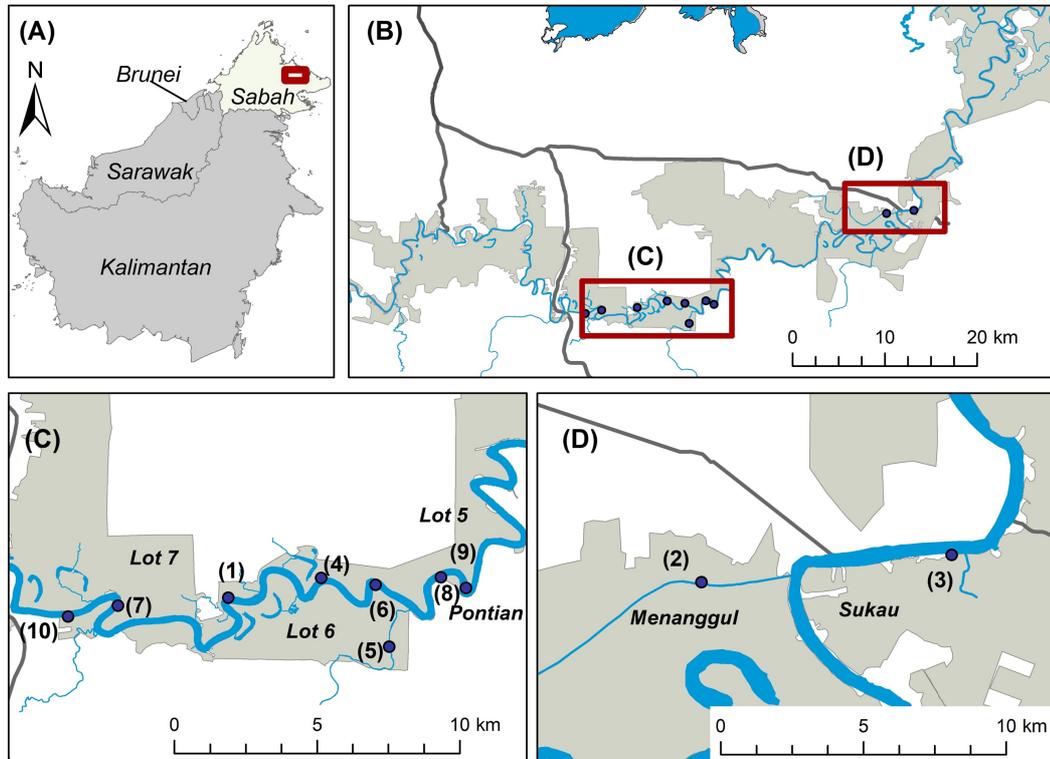


Figure 4.1   Forest block names and collaring sites (points) of 10 proboscis monkeys (C = eight upstream groups; D = two downstream groups) along the Kinabatangan River (B) in Sabah, Malaysian Borneo (A); number refers to Group ID.

### 4.2.2   *LiDAR-derived habitat data*

High-resolution LiDAR data were used to quantify forest structure. The study area was mapped over two consecutive days in April 2016 by the Carnegie Airborne Observatory-3, which acquired three-dimensional structural information of aboveground vegetation using a custom-built LiDAR subsystem on-board the CAO-3 aircraft (Asner et al. 2012; Asner et al. 2018). The CAO data were collected from 3,600 m above ground level, using a scan angle of 36º and a side overlap of 30% (see Asner et al. 2018 for detailed flight and processing settings). There was an average point density of 3.20 laser shots per square meter and the horizontal and vertical error estimates were 16 cm and 7 cm root-mean-square error, respectively (Davies et al. 2017). The 3D locations of laser returns were used to produce a "cloud" of LiDAR data, a large number of geo-referenced point elevation estimates. The points that penetrated the canopy and reached the ground surface were used to produce a raster digital terrain model (DTM). The first-return points (the first pulses to detect the top of canopy or bare ground) were used to produce a digital surface model (DSM). The vertical difference between the DTM and DSM produced the digital canopy model (DCM), which was the basis for deriving the outer-canopy measurements. The vertical distribution of vegetation layers was created by binning all the returns between the DSM and DTM into 1-m vertical resolution layers and dividing that by the total number of LiDAR points in that column, providing the percentage of vegetation in each 1-m height category (Davies et al. 2017).

A wide range of structural parameters have been used to describe LiDAR data (e.g., see reviews by Wulder et al. 2008; McRoberts et al. 2010; Davies and Asner 2014), many of which are closely related mathematically, and therefore many parameters are likely to have a high degree of redundancy. Potential structural parameters were selected using a systematic review of the literature from 2010 to 2017 in the ISI Web of Knowledge using the terms "lidar", "light detection and ranging", or "airborne laser scanning" and "forest", "canopy" or "vegetation". From the 970 peer-reviewed articles

found, 20 of the most commonly used parameters using outer canopy height models (from first returns) and internal forest heights (all returns) were selected (Table 4.1; see Appendix 3.1 for methods used to calculate parameters). The structural parameters included in this study covered the three main forest descriptors used in the literature: 1) the horizontal distribution of the outer canopy (variation in top-of-canopy heights), 2) canopy features (crown islands, cover and gaps) and, 3) the internal distribution vegetation layers (vertical distribution of the LiDAR points below the main canopy).

To remove the influence of large numbers of ground and low vegetation points, returns below 1 m were discarded (Vaughn et al. 2014). A range of different moving window sizes have been used in the literature to calculate the different LiDAR variables, smoothing local forest features to different degrees (Vaughn et al. 2014). Although larger windows tend to produce more stable estimates, they are not able to capture fine-scale structure (Vaughn et al. 2014). Due to the heterogeneity and distinct edges present in the study site, as well as to be able to distinguish small-scale differences in animal movement, a 10-m window was selected to calculate the habitat metrics (Davies et al. 2017). To avoid issues of edge effect in the focal statistics analysis, moving window calculations were conducted over the entire study area, rather than separately within each home range. Habitat variables were transformed to improve normality where necessary. Using R 3.1 (R Core Team 2015), principal component analysis (PCA) was used to resolve the relationships between the LiDAR variables and to select a subset of distinct variables for use in further analysis by selecting one variable to represent each principal component (PC). The number of principal components to use was determined from a combination of the relative variance explained, based on the scree plot, and whether each PC had a clear interpretation. The LiDAR variable with the highest or second highest loading coefficient was selected to represent its corresponding PC, the choice based on the potential ecological relevance to proboscis monkeys.

Table 4.1    LiDAR-derived habitat parameters calculated to use in the principal component analysis to examine the relationship between one another, see Appendix 3.1 for methods used for detailed metric calculations.

| | Parameter | Description | Reference example |
|---|---|---|---|
| *Canopy Features (10 x 10 m moving window)* | | | |
| HMEAN | Mean canopy height | Canopy height in a 10 x 10 m area | Nieschulze et al. 2012 |
| HMAX | Maximum | Maximum tree height in a 10 x 10 m area | Nieschulze et al. 2012 |
| HMODE | Mode | Most common canopy height in 10 x 10 m area | Sexton et al. 2009 |
| HMED | Median | Midpoint of canopy heights in 10 x 10 m area | Sexton et al. 2009 |
| HSD | Standard Deviation | Measure of canopy height heterogeneity in a 10 x 10 m area | Nieschulze et al. 2012 |
| HSKEW | Skewness | *same as HSD | Zhao et al. 2012 |
| HKURT | Kurtosis | *same as HSD | Zhao et al. 2012 |
| HCOV | Coefficient of variation | *same as HSD | Zhao et al. 2012 |
| HQM | Quadratic Mean | *same as HSD | Zhao et al. 2012 |
| HIQR | Interquartile Range | *same as HSD | Vaughn et al. 2014 |
| *Crown (10 x 10 m moving window)* | | | |
| CC10 | Canopy Cover: 10m | Proportion of area occupied by vegetation above 10 m over a 10 x 10 m area | Thiry et al. 2016; Davies et al. 2017 |
| CIA | Crown Island Area | Outer-canopy topography, when pixel is higher than global 2/3 of q(h)0.99 | Nieschulze et al. 2012 |
| *Canopy Gaps (gap area ≥12m2 in 3 x 3 m moving window)* | | | |
| GBRO | Brokaw's Gap Index | Proportion of returns that reach down to an average height ≤2 m | Kellner & Asner 2009; Brokaw 1982 |
| GADP | Adaptive median Index | Proportion of returns less than the median height within a local neighbourhood minus the corresponding interquartile distance | Nieschulze et al. 2012, Davies et al. 2017 |
| Vertical Canopy | | | |
| VCD | Canopy Density | Percentage of returns above 3 m | Vogeler et al. 2014 |
| VUD | Understory Density | Percentage of returns between 1 - 3 m | Vogeler et al. 2014 |
| VDR | Vertical Distribution Ratio | Median canopy height from the top of canopy height and dividing it by the canopy height | Goetz et al 2007 |
| VCL | Canopy Layering | Number of vertical vegetation layers present between the forest floor and top of canopy | Davies et al. 2017 |
| VDI | Diversity Index | Shannon-Diversity index but for height categories | Listopad et al. 2015 |
| VEI | Evenness Index | Pielou's Evenness Index, variation of height categories | Listopad et al. 2015 |

### 4.2.3   Utilisation distributions

Proboscis monkey ranging patterns were analysed using biased random bridges (BRB), a movement-based density estimate (Benhamou and Cornélis 2010), as described in Section 2.3.4. See Section 3.2.4 for a description of parameters used for the BRB method. Along with the overall utilisation distribution estimate, BRB was used to divide the UD its two components, the intensity (ID) and recursion distributions (RD) (Benhamou and Riotte-Lambert 2012). The smoothing parameter (*hmin*) was set at 25

m (Section 3.2.4), and as recommended by Benhamou and Riotte-Lamert (2012), was calculated within a circle radius of 75 m (3*hmin*) – i.e. all points within 75 m were considered to be a single location for calculating ID, and a new visit if the animal returned to the same area more than 4 hours after moving more than 75 m away from the area (Benhamou and Riotte-Lambert 2012). Hereafter, the term BRB will be used to collectively refer to the three types of estimates specifically calculated using the BRB technique, and the estimates will be referred to separately as UD, ID and RD. For subsequent analysis, the use values were rescaled to 1 (lowest use) and 99 (highest use) for each of the BRBs (Marzluff et al. 2004).

The outputs of the BRB utilisation distribution are referred to hereafter as the home range (HR, 90th percentile) and core range (CR, 50th percentile) (Börger et al. 2006). The high intensity areas (CID) refer to the 30th percentile from intensity distribution, and highly frequented areas (CRD) refer to 30th percentile from recursion distribution (Benhamou and Riotte-Lambert 2012). High use areas refer to high intensity and highly frequented areas combined.

### 4.2.4   Additional habitat characteristics

Along with the LiDAR-derived forest characteristics, additional variables were derived to quantify proximity to edges, potential human disturbance and forest area. Images from Google Earth Pro (Google Earth 7.1 2014) were digitised and processed in ArcGIS 10 (ESRI 2011) to create water and plantation shapefiles; plantation boundaries were modified where necessary using LiDAR data. For the within-home range scale, pixels in the BRBs were assigned values in ArcGIS 10 based on their proximity (Euclidean distance) to i) water (main river, oxbow lakes, and major tributaries), and ii) to oil palm plantations. Proximity was only considered when on the same side of the river as the BRB.

The home ranges were split into high and low potential disturbance using the classification from Ancrenaz et al. (2004), based on tree density, canopy connectivity and density of old logging roads; small-scale illegal activities were not included as these were considered to occur uniformly throughout the study site. A substantial change in disturbance level was not expected since the original classification, particularly within the protected forest of LKWS. The ranges in unprotected forests were classified as highly disturbed and were not expected to become less disturbed since classification, as logging events have continued to be observed (Chapter 6). Based on Ancrenaz et al. (2004), Groups 1, 2, 3, 7 and 8 were within high disturbance forest and Groups 4, 5, 6, 9 and 10 were in less disturbed forest.

The area of forest available to each proboscis monkey group was calculated from GIS shapefiles. As the furthest GPS collar fix was ~1.8 km from the river, the area available was considered to be the extent of contiguous forest within which the individual's home range was centred, including all forest up to 2 km inland from the main river and extending in all directions until barriers to movement were reached (e.g., major tributaries, lakes, roads, or plantations). It did not account for other factors that may prevent proboscis monkeys from moving around freely, such as social restrictions from other groups or species. This, however, was not expected to have a significant impact on ranging behaviour, as up to 100% territory overlap has been observed between proboscis monkey groups in riparian forest (Boonratana 2000), and proboscis monkeys are often observed in proximity of other primate species (*pers. obs.*).

To see if the six forest blocks that supported the collared proboscis monkey groups were structurally distinguishable from each other (Fig. 4.1), the four LiDAR-derived habitat variables selected from the original PCA, as well as proximity to water and proximity to plantations, were used in a second PCA using 500 random points, minimum 10 m between point, per forest block. The overlap in structure between

blocks was assessed by fitting 95% confidence ellipses, assuming a multivariate normal distribution, around each forest block using the stat_ellipse function in *ggplot2* (Wikham 2009; Fox and Weisberg 2011).

### 4.2.5   Resource use

The resource utilisation function (RUF) is a multiple regression technique that models resource selection by relating UDs to groups of continuous or categorical habitat variables (Marzluff et al. 2004). RUFs were estimated to quantify differences in proboscis monkey resource use between the UD, ID and RD in R using the contributed package *ruf* (Handcock 2015). The BRB utilisation probabilities were log-transformed and the smoothed habitat variables (see section 4.2.2) were used to satisfy the requirements put forth by Hooten et al. (2013). RUFs were fit for individual proboscis monkeys using the subset of LiDAR habitat variables selected from the PCA, distance from water (main river, oxbow lakes and major tributaries) and distance from plantations. The RUFs were fit using a Matern correlation function to account for the spatial autocorrelation of UD estimates among adjacent pixels (Marzluff et al. 2004). Following the recommendations of Marzluff et al. (2004), the initial value for the range of spatial dependence (measured in m) was set as the bandwidth used for the BRB method, and the smoothness of each UD surface as 1.5.

As the home range of each animal must be considered as an independent measure for RUF calculations, the RUFs were modelled separately for each individual and the results from each animal were averaged to produce a population-level model; only the population-level model was used for the subsequent analyses  (Marzluff et al. 2004). To calculate the variance for each habitat variable of the population-level model, the individual unstandardised standard errors were averaged, according to Marzluff et al. (2004; equation 2). This variance quantifies the uncertainty in the average value of each coefficient but does not include inter-animal variation (Long et al. 2009). Variation

of inter-animal variation was also calculated as the standard error of the unstandardized resource coefficients. One-sample t-tests were used to test whether the mean resource coefficient estimate for each variable differed significantly from zero for the population-level model (Marzluff et al. 2004). Average standardised coefficients were then calculated, and the absolute value of the averaged standardised coefficients were used to rank the relative importance of each habitat variable for the different BRB models.

Although RUF yields inferences about habitat selection using UDs, it assumes linear relationships between habitat variables and resource selection. Consequently, generalised additive models (GAM) were run in R with the package *mgcv* (Wood 2011) to detect possible non-linear trends in habitat selection. Using the same response variables as in the RUF, the GAMs modelled the six habitat variables using regression splines, with the extent of smoothing estimated via cross-validation (Wood 2011). This was treated as an exploratory analysis, so no attempt was made to adjust for spatial autocorrelation: hence, p-values were not reported.

It was assumed that the natural changes in the forest structure and composition between the time of field data collection and LiDAR-data acquisition (1 – 5.5 years) had a minimal effect on changes in habitat use (Vierling et al. 2014). However, between the end of the collaring period and LiDAR data acquisition, areas of forest within three proboscis monkey home ranges had been clear-felled (see Chapter 6 for a case study on one individual). The parts of the home ranges that overlapped with the cleared forest areas (as well as 10 m buffers around the clearings) were thus removed from the resource use analysis: 14-16 ha removed from the range of Group 02 (9.6-9.9% of total BRB size), 26-28 ha from Group 03 (26.3-26.8%), and 6-9 ha removed from Group 04 (3.6-5.0%). Additionally, a small area was also removed for the GAM analysis where the ranges of Groups 1 and 7 spatially (not temporally) overlapped (35.18 ha).

## 4.3   Results

*4.3.1   LiDAR-derived habitat variables*
There was a high degree of redundancy among the LiDAR-derived habitat variables, with the first PC explaining nearly 50% of the variance across the 20 variables (see Table A3.1 for PCA results). Four PCs were selected in total, explaining 78.5% of the variance. PC1 represented overall canopy height, with large loading coefficients for variables including HMEAN, HMAX, HMODE, HMEAN, whereas PC2 represented variance in canopy height (HSD, HSKEW, HKURT, HCOV). PC3 represented internal vegetation structure, with increasing PC3 values indicative of greater canopy density and evenness, at the expense of the understory vegetation (positive loading for VEI, VCD; negative for GBRO, VUD). PC4 represented canopy gaps. The variables selected to represent the four aspects of forest structure revealed by the PCA were mean canopy height (HMEAN; PC1), top of canopy variation (HSD; PC2), evenness index (VEI; PC3), and the adaptive median gap index (GADP; PC4) (Table A3.1).

The six forest blocks that supported the 10 home ranges had very similar habitat characteristics. Lot 7 tended to extend furthest from water, whilst Pontian had a higher gap index than the other forest blocks. Aside from those differences, there were almost complete overlaps in the structural and landscape characteristics between most of the forest blocks (Fig. 4.2).
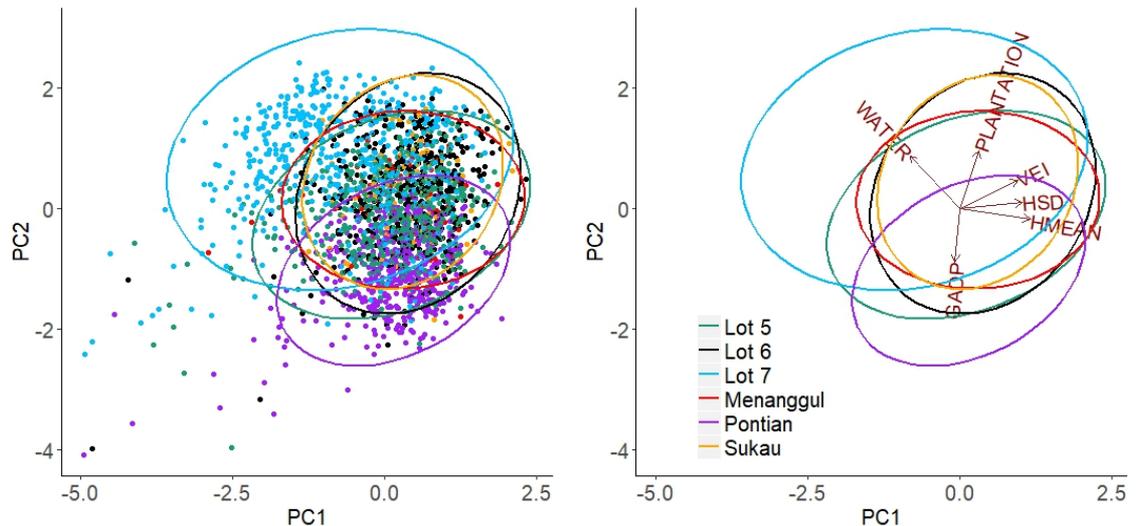
Figure 4.2  Biplot of the LiDAR-derived structural parameters (mean canopy height (HMEAN), standard deviation of top of canopy height (HSD), adaptive median gap index (GADP), vertical evenness index (VEI)), distance to water (WATER) and distance to plantation (PLANTATION) for the different forest blocks that the collared proboscis monkeys were found.

### 4.3.2   Description of the BRB distributions

The BRBs showed a marked difference between the intensity and recursion distributions (Table 4.2, Fig. 4.3). The basic UDs were presented in Chapter 3. Proboscis monkey home ranges contained an average (± SE, N = 10) of 23 (± 3) high intensity and 5 (± 1) high recursion patches used per group. The high intensity patches within the proboscis monkey home ranges were highly fragmented and had an average area of 0.8 (± 0.04) ha. There was a tendency for the high intensity areas to be distributed along the periphery of the home range, not just along the river, but also along edges inland (Fig. 4.3). There were very few groups that had high intensity areas within the middle of their range. The highly frequented areas tended to be concentrated in one main area within each HR, with an average patch size of 4.4 (± 1.0) ha. Despite the scattered distribution and small patch sizes, the high intensity patches covered more overall area than the high recursion patches. More disturbed forests had nearly significantly smaller high-intensity patches (two-sample t-test, p = 0.05), whereas highly frequented patches did not change in size (p = 0.52). The average patch size of high use areas did not change regarding to the amount of forest available (high intensity: p = 0.2, $R^2$ = 0.19, df = 8; high recursion: p = 0.1, $R^2$ = 0.26, df = 8). Almost a quarter

(22.2%) of the sleeping sites were within high recursion patches, whereas 42.8% were within the high intensity patches.

Table 4.2  Overall area and patch descriptors of the biased random bridges (BRB) outputs of 10 proboscis monkey groups: HR = home range (90%) utilisation distribution, Core = 50% utilisation distribution, ID = core (30%) intensity distribution, RD = core (30%) recursion distribution.

| Group ID | Available forest (ha) | Area (ha) | | | | # Patches | | Average Patch Size (ha) | |
|---|---|---|---|---|---|---|---|---|---|
| | | HR | CR | ID | RD | ID | RD | ID (SE) | RD (SE) |
| 1* | 991 | 165 | 46 | 37 | 28 | 36 | 12 | 0.96 (0.22) | 2.14 (0.95) |
| 2* | 2415 | 63 | 18 | 18 | 10 | 18 | 1 | 0.92 (0.19) | 9.66 (-) |
| 3* | 1635 | 50 | 15 | 10 | 8 | 11 | 5 | 0.90 (0.41) | 1.64 (1.36) |
| 4 | 1037 | 92 | 25 | 21 | 13 | 38 | 8 | 0.55 (0.09) | 1.67 (1.00) |
| 5 | 1713 | 83 | 30 | 14 | 14 | 16 | 3 | 0.76 (0.20) | 4.82 (4.45) |
| 6 | 1713 | 67 | 21 | 17 | 11 | 23 | 1 | 0.70 (0.16) | 10.69 (-) |
| 7* | 991 | 93 | 19 | 26 | 12 | 33 | 3 | 0.70 (0.16) | 3.92 (3.73) |
| 8* | 64 | 44 | 13 | 24 | 7 | 13 | 2 | 0.71 (0.16) | 3.43 (3.37) |
| 9 | 1037 | 127 | 38 | 23 | 20 | 30 | 11 | 0.68 (0.13) | 1.69 (1.13) |
| 10 | 125 | 24 | 9 | 9 | 5 | 13 | 1 | 0.69 (0.23) | 4.59 (-) |

*classified as high disturbance
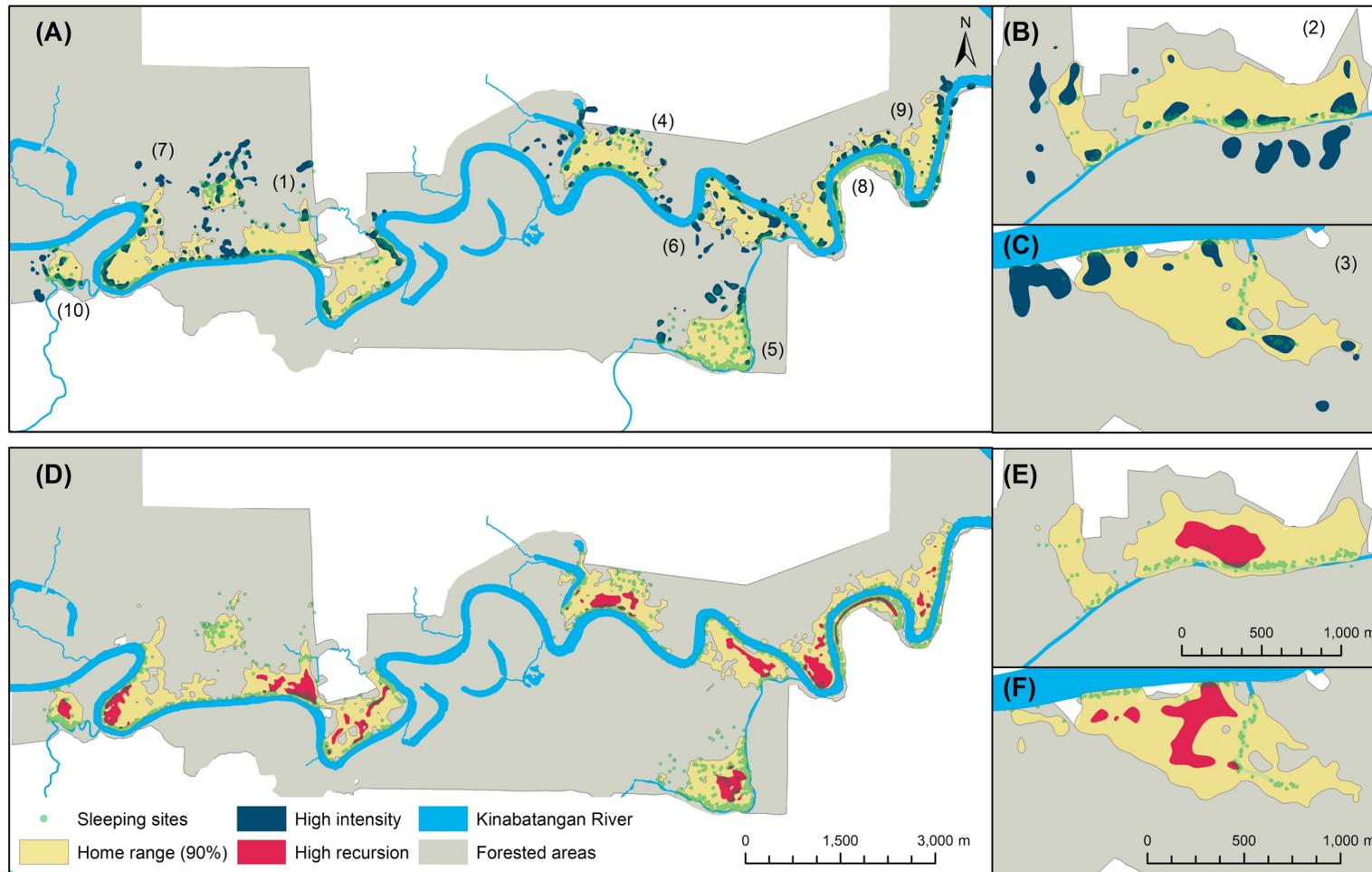
Figure 4.3    The 30th percentiles for the intensity distribution (A - C) and recursion distribution (D - F), superimposed on the overall 90% utilisation distribution for proboscis monkeys in the Lower Kinabatangan Floodplain. Light green indicates sleeping sites, and the number refers to Group ID, as listed in Table 4.2 and 4.3. Panels A & D show the upstream groups and B/E & C/F show the downstream groups.

Highly frequented areas tended to be closer to water than high intensity areas (average CID: 211 (± 38) m, CRD: 132 (± 31) m), whereas there was no difference in distance to plantation edges (average CID: 715 (± 59) m, CRD: 735 (± 62) m). There was no relationship observed between proximity of high intensity and highly frequented patches to water or plantations when more or less forest was available ($p = 0.1 - 0.9$, $R^2 = 0.0009 - 0.05$). Disturbance level also did not show a relationship with proximity to river (two-sample t-tests, $p = 0.3 - 0.9$). There was little evidence that the area of forest available to a group or the level of human disturbance affected the size of the home range, high ID or RD areas (available forest: all $p>0.2$, $df = 8$; disturbance level: two-sample t-tests, p-values = 0.4-0.5).

High intensity patches comprised of larger proportion of the home range when less forest was available ($p = 0.04$, $R^2 = 0.40$, $df = 8$; Table 4.3). Despite this, there was no relationship in the amount of spatial overlap between high intensity areas and HR ($p = 0.9$, $R^2 = 0.003$), indicating the increase of ID patches was occurring outside the HR area. There were no relationships between them, and the area of forest available (all $p>0.6$). The high recursion areas wholly overlapped with the 90% home range, whereas only an average of 59% (30.5 – 92.9%) of the high intensity areas overlapped with the HR, indicative of relatively rare, but prolonged visits to areas outside the HR. The average percentage of area overlapping between ID and RD patches was 7% (range: 0.24 – 13.6%) and was not affected by forest available or disturbance level. Disturbance levels also did not affect the amount of spatial overlap between HR and the high use areas (p-values = 0.4 – 0.8).

Table 4.3   Overlapping and patch area ratios of the biased random bridges (BRB) outputs of 10 proboscis monkey groups: HR = home range (90%) utilisation distribution, Core = 50% utilisation distribution, ID = core (30%) intensity distribution, and RD = core (30%) recursion. Patch area ratio represents the similarity in area between the total area of the two BRB output types being compared (Type1:Type2).

| Group ID | Available forest (ha) | Overlapping Area (ha) | | | Patch area ratio (ha:ha) | | |
|:---:|:---:|:---:|:---:|:---:|:---:|:---:|:---:|
| | | HR-ID | HR-RD | ID-RD | ID:HR | RD:HR | RD:ID |
| 1* | 991 | 24 | 28 | 5 | 0.22 | 0.17 | 0.76 |
| 2* | 2415 | 7 | 10 | 1 | 0.28 | 0.15 | 0.54 |
| 3* | 1635 | 7 | 8 | 2 | 0.20 | 0.16 | 0.83 |
| 4 | 1037 | 14 | 13 | 2 | 0.23 | 0.15 | 0.64 |
| 5 | 1713 | 5 | 14 | 0 | 0.16 | 0.17 | 1.06 |
| 6 | 1713 | 14 | 11 | 3 | 0.26 | 0.16 | 0.61 |
| 7* | 991 | 16 | 12 | 4 | 0.28 | 0.13 | 0.46 |
| 8* | 64 | 7 | 7 | 1 | 0.55 | 0.15 | 0.28 |
| 9 | 1037 | 21 | 20 | 3 | 0.18 | 0.16 | 0.87 |
| 10 | 125 | 4 | 5 | 1 | 0.37 | 0.19 | 0.51 |

*classified as high disturbance

### 4.3.3   Resource utilisation functions

Mean canopy height and distance to water were both significantly related to all three BRB components (UD, ID, RD) at the population-level (one sample t-tests, N = 10, all p≤0.001). The evenness index was significant only for RD (one sample t-test, N = 10, p<0.05) (Fig. 4.4), whilst the coefficients for the remaining variables did not differ from zero overall (all p>0.05). Being close to the water was the strongest relationship for all BRBs, with a slightly larger effect size for ID than RD. Increased utilisation of areas with higher canopies was the second most important relationship, and had a similar effect size for both ID and RD. More frequently visited areas (RD) were those with greater internal vegetation evenness (VEI), but the effect size was much smaller than for distance to water or canopy height (Fig. 4.4).
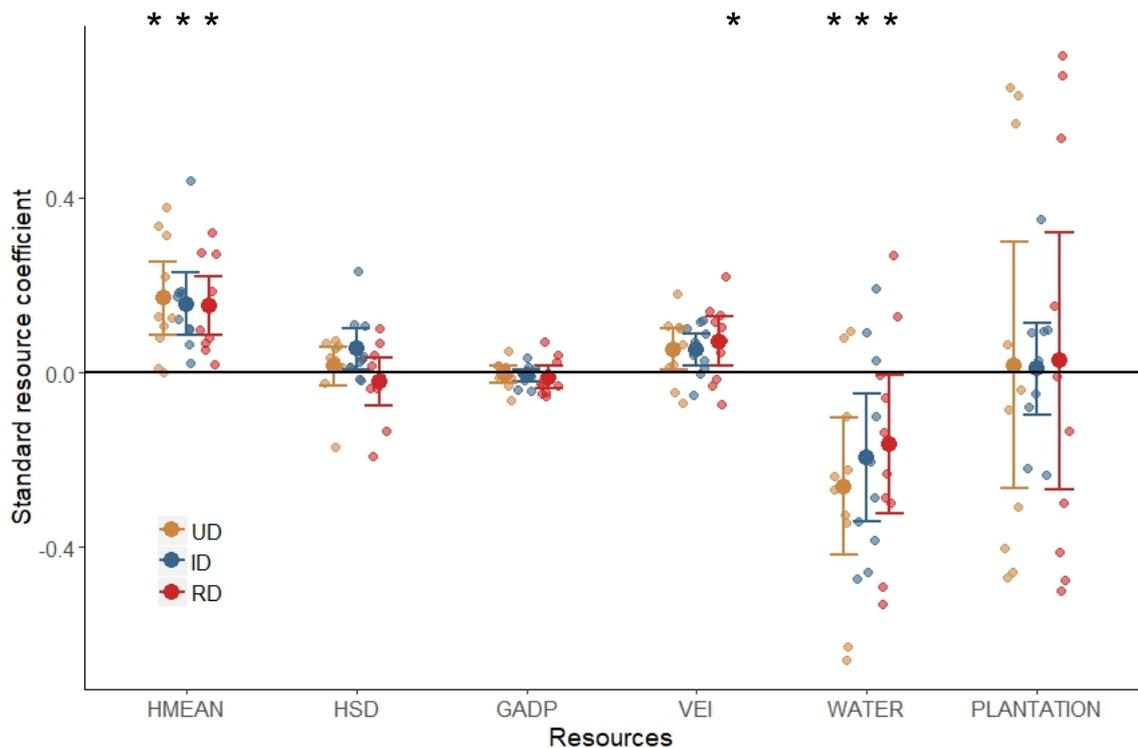
Figure 4.4 Standardised resource utilisation coefficients (ß), including population-level (mean ß; large dots) and individual (small dots) coefficients for utilisation (UD; orange), intensity (ID; blue) and recursion (RD; red) distribution models. Positive coefficients indicate increased utilisation towards larger values of measurement, and negative coefficients indicate increased utilisation towards smaller values. Standard error bars show inter-individual variation. Asterisks indicate resources that were significantly utilised. HMEAN = mean top-of-canopy height; HSD = standard deviation of top-of-canopy height; GADP = adaptive median gap index; VEI = vertical evenness index; WATER = distance to water; and PLANTATION = distance to plantation.

At the individual level, there was a great deal of variation in the importance of the different variables, both in selection strength and sign (Fig. 4.4), particularly between ID and RD. A taller mean canopy height was the only variable consistently preferred by all individuals; the remainder had a mixture of some individuals selecting higher values and some selecting lower values (Table 4.4). Except for Groups 4 and 8, all groups had at least one resource where the sign of resource utilisation switched between the intensity and recursion models.

Table 4.4    Population-level unstandardised resource coefficients (mean ß) and directionality of RUF coefficients for each proboscis monkey for BRB intensity (ID) and recursion (RD) distribution models. Positive values indicate selection towards larger values of measurement, and negative values indicate selection towards smaller. Standard errors were calculated as per Marzluff et al. (2004) equation 2, and do not account for inter-individual differences; red colour highlights change in directionality. HMEAN = mean canopy height; HSD = standard deviation of top of canopy height; GADP = adaptive median gap index; VEI = vertical evenness index; water = distance to water; and plantation = distance to plantation.

| Group ID | HMEAN | | HSD | | VEI | | GADP | | Water | | Plantation | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | ID | RD | ID | RD | ID | RD | ID | RD | ID | RD | ID | RD |
| Mean β (SE) | 0.035 (0.005) | 0.030 (0.005) | 0.073 (0.058) | -0.007 (0.063) | 0.53 (0.25) | 0.65 (0.27) | -0.045 (0.11) | -0.017 (0.11) | -0.038 (0.005) | -0.023 (0.005) | -0.0002 (0.0001) | -0.001 (0.0001) |
| 1 | + | + | + | + | + | + | - | - | **+** | **-** | **+** | **-** |
| 2 | + | + | **+** | - | + | + | - | - | - | - | - | - |
| 3 | + | + | + | + | + | + | **+** | **-** | - | - | + | + |
| 4 | + | + | + | + | - | - | + | + | - | - | - | - |
| 5 | + | + | **+** | - | + | + | - | - | + | + | **+** | **-** |
| 6 | + | + | - | - | + | + | **-** | **+** | - | - | - | - |
| 7 | + | + | **+** | - | + | + | - | - | - | - | + | + |
| 8 | + | + | + | + | - | - | + | + | - | - | + | + |
| 9 | + | + | **+** | - | + | + | - | - | - | - | + | + |
| 10 | + | + | - | - | **+** | **-** | - | - | + | + | - | - |

There was no significant relationship between the amount of available forest and any of the six resource utilisation coefficients for the ID (linear regression, all p = 0.1 – 0.9), whereas for RD, there was only a significant increase in selection for areas with greater internal vegetation evenness (p = 0.038, $R^2$ = 0.43; all other p-values>0.1). There was no clear evidence that resource selection was affected by disturbance: there was a suggestion that areas with greater top-of-canopy variation were selected more strongly in disturbed forest for the ID models (p = 0.056), but there were no other near-significant differences in RUF standardised coefficients values for disturbance levels (two-sample t-test, all p-values>0.1).

GAMs broadly agreed with the population-level RUF results, whilst providing additional insights into the non-linear relationships between the BRB components and the habitat variables (Fig. 4.5). Consistent with the population-level RUF, BRBs increased with canopy height, but, in forests with average canopy heights ranging from 1 to 58.9 m, peaked at 20-23 m before either showing a steady decline (UD and RD) or plateauing

(ID). Also supporting the RUF, the GAM indicated a high preference for being close to water for the BRBs, suggesting a peak of use around 50-100 m from water. Additionally, the GAM detected a second peak around 1200 m, which was particularly prominent in the ID model. Although top-of-canopy variation was not significant in the RUF, the GAM followed the same general relationship; there was higher use of areas with less top-of-canopy variation for RD, and the opposite for ID. Similar to the RUF, RD showed higher use of areas with more internal vegetation evenness. There was a lower likelihood of detection in areas with more gaps for ID, and only a very slight selection towards more gaps for RD. There was clear non-linearity in the relationship with distance from plantation. Both ID and RD increased in areas between 200 and 2000 m from plantations (Fig. 4.5). There were two notable spikes – the first, small one around 200 m from plantations, and the second major increase after 2000 m.

Predictions from the ID and RD GAMs highlighted that areas of high intensity use by proboscis monkeys were close to rivers, with a few important areas far inland as well (Fig. 4.6). High recursion areas had many similarities but extended deeper into the forest than high intensity areas.
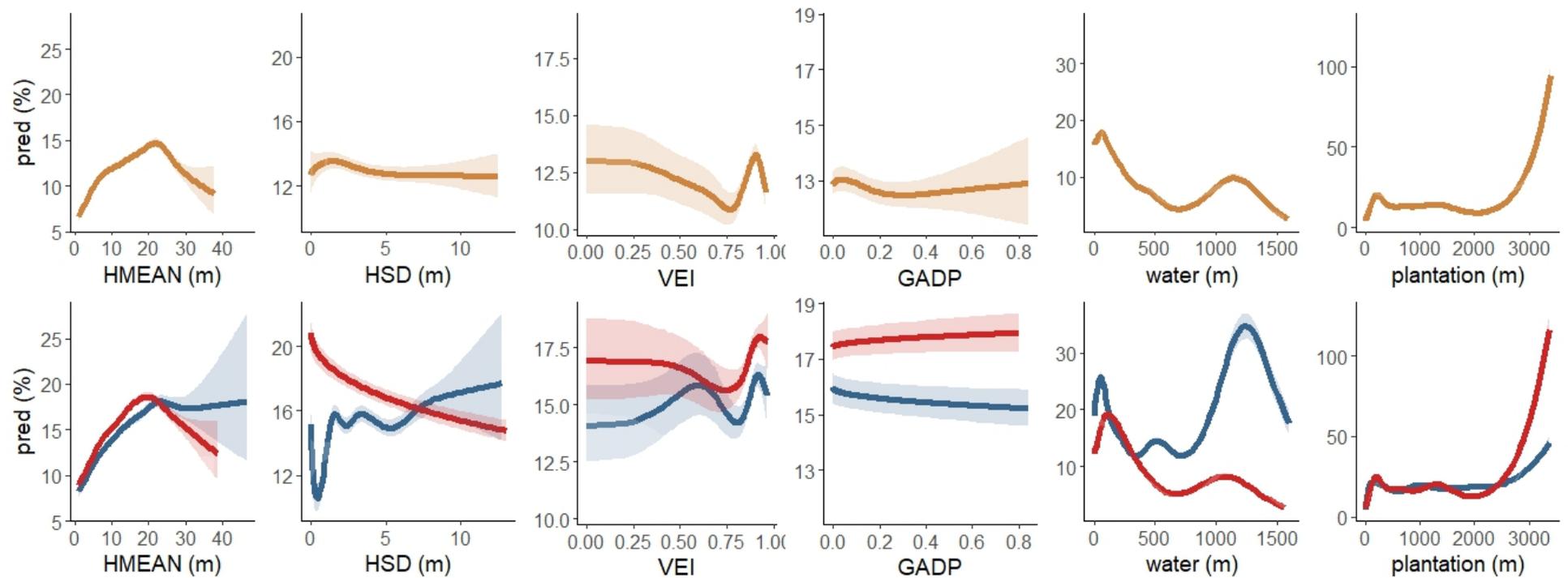
Figure 4.5  Generalised additive model and 95% confidence intervals (shaded area around fitted line) in resource use for proboscis monkey groups (N = 10) relative to habitat variables (HMEAN = mean canopy height; HSD = standard deviation of top of canopy height; GADP = adaptive median gap index; VEI = vertical evenness index; water = distance to water; and plantation = distance to plantation). Models are based on 99% utilisation (orange), intensity (blue) and recursion (red) distributions using the biased random bridges method.
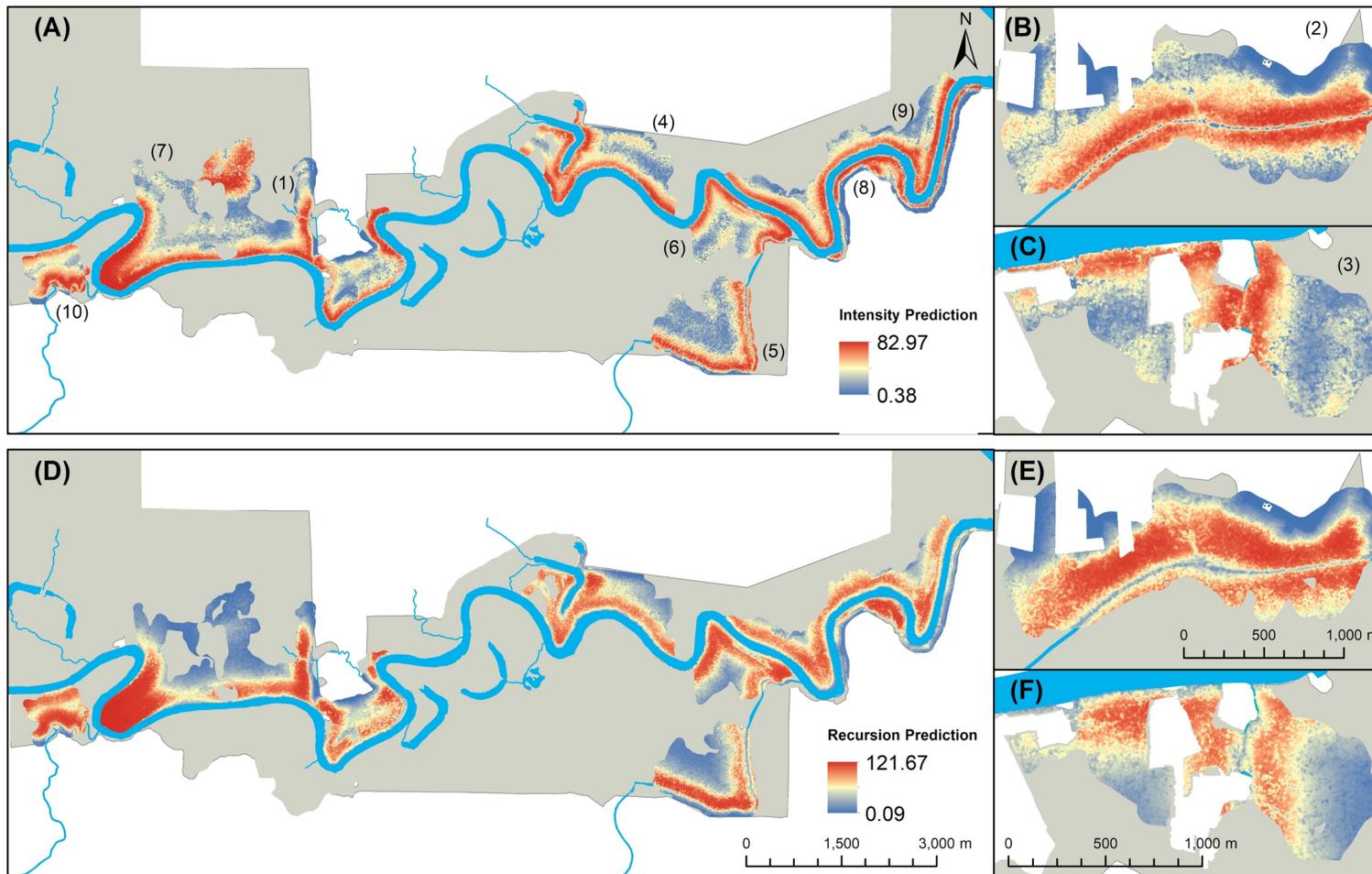
Figure 4.6   Predicted resource use map from the generalised additive model for proboscis monkeys' intensity distribution (A - C) and recursion distribution (D - F) in the Lower Kinabatangan Floodplain; red = higher resource use, blue = less resource use. Panels A & D show the eight upstream groups and B/E & C/F show the two downstream groups; the numbers refer to Group ID.

## 4.4 Discussion

Resource utilisation is useful to incorporate when developing conservation management strategies for a species (Garabedian et al. 2017). By studying the habitat and resource use of proboscis monkeys for the first time with GPS collars, multiple groups were assessed without observer bias or bias from boat-based surveys. Proboscis monkeys in this study showed a preference for areas with high mean canopy (optimal height 20-25 m), close proximity to rivers (<110-200 m), or far from plantations (>2000 m). Furthermore, this study provided tentative support for the idea that proboscis monkey ranging behaviours may be more to the range of disturbance observed in the remaining fragments of the Lower Kinabatangan forest than anticipated. Disturbance appeared to have little effect on ranging behaviour (size, overlap, distance of high use areas from edges) or resource use, apart from having smaller high intensity patches and using areas with greater top-of-canopy variation in more disturbed areas for the intensity distribution. Forest area also appeared to have little effect on ranging behaviour, except that highly frequented areas in bigger forests had more even internal vegetation. The total size of area for ID and HR also became more similar when less forest is available.

### 4.4.1 Intensity and recursion resource utilisation

Although the high recursion patches overlapped entirely with the home range, only an average of 70% of the high intensity areas did (range: 30.5-91.9%). Large numbers of patches in some ranges were rarely visited but were used for a long time when they were, possibly due to unfavourable habitats, seasonal food availability, or resource recovery. It was expected that areas that are most suitable will be used intensely and returned to frequently (Van Moorter et al. 2016). The overlap between high intensity and high recursion patches ranged from 0.2% to 13.6%, however there was no relationship with the amount of forest or disturbance.

Areas that contain important food sources for short amounts of time result in animals only using those areas when that particular food is in season. Even though daily path lengths have been shown to increase in times of increased fruit availability (Chapter 5), seasonal changes in step length are not likely to be represented in a UD. As proboscis monkeys are consistently eating young leaves, which are highly abundant in secondary and disturbed forests throughout the year (Matsuda et al. 2009b), it is less likely that proboscis monkeys are travelling to specific areas outside their main home range because of young leaves. However, fruit availability changes seasonally, and proboscis monkeys may be feeding intensively during periods of high fruit availability and then must wait until the resource has recovered before returning, which may have been longer than the study period. Alternatively, due to the abundance of young leaves in secondary forests, there may be less pressure for proboscis monkeys to frequently return to specific areas, as they would be able to find enough food throughout the range. For example, Group 8 had a much larger area of high intensity use relative to home range area than all the other individuals, (Group 8: 55%, mean of other groups: 24%) whereas the recursion rates did not differ (Group 8: 16%, mean of other groups: 16%). The discrepancy in the amount of habitat available and the amount of habitat required runs the risk of overexploiting their habitat as an area may be unable recover after use, as was observed with a population of proboscis monkeys in Indonesian Borneo (Meijaard and Nijman 2000b).

Whether proboscis monkeys use high intensity areas based on seasonal fruit availability or to allow young leaves to recover, their ranging patterns show an ability to create a cognitive map, whereby they can travel efficiently between food patches, including those on the periphery of their main ranging area (Janson and Byrne 2007). Seasonality, resource availability and resource recovery are important factors that need to be considered in primate ranging behaviour (Matsuda et al. 2009a; Campos et al. 2014; Berger-Tal and Bar-David 2015). The time between visits, the duration of

visits and how visits correspond with seasonal or food availability is examined in Chapter 5, to further investigate the drivers of proboscis monkey habitat use.

### 4.4.2  Resource utilisation using LiDAR

The LiDAR-derived habitat variables used in this study explained only a small aspect of proboscis monkeys' resource use. There are several possible explanations for this. One option is that proboscis monkeys are relatively insensitive to forest structure. When food is widely available, the structural differences within a forest can become less important in the habitat use of a species, and therefore, there is less predictability in habitat use based on structural features (McLean et al. 2016). Although proboscis monkeys have been referred to as specialists due to their digestive system (Yeager et al. 1997), the way they use their habitat appears more generalised than expected. The variation in individual resource utilisation and little response to disturbance levels or amount of forest available may be consistent with a previous study, which showed that although proboscis monkeys are selective towards eating young leaves, they are consuming the young leaves from all the common plant species (Matsuda et al. 2013).

An alternative explanation is that the LiDAR variables selected for this study may have overlooked ecologically important features for proboscis monkeys. Theoretically there can be an infinite number of possible metrics derived from a LiDAR dataset (Zhao et al. 2011), but within this infinite selection, there needs to be a balance of selecting metrics with high explanatory power that also represent different aspects of the habitat that are ecologically relevant to the species in question. The PCA of the 20 LiDAR variables highlighted the potential redundancy issue – the first PC alone explained half of the variation amongst all 20 variables. Furthermore, if the variables were not calculated in the way that the animals relate to, then responses to habitat structure might not be observed. For example, gaps in the canopy were expected to be important for proboscis monkeys because gaps naturally promote tree growth and food production

(Ganzhorn 1995), and gap specialist plant species generally have a higher nutritional value than shade-tolerant ones (Coley 1987). Despite the adaptive gap index being the only LiDAR-derived variable distinguishing one forest block from the other five, there was no evidence that it was related to proboscis monkeys' resource use. It may be that the way in which gaps were quantified (e.g. spatial resolution) was a poor match to how the animals respond, and calculating proximity to gaps rather than only the presence of gaps may have revealed a more important relationship. However, it may simply be that proboscis monkeys show little response to gaps, which may be more likely in the Kinabatangan where most of the forest has been logged to some degree over the past century (Ancrenaz et al. 2004), leading to frequent canopy gaps throughout the area that could make avoidance or attraction to gaps less evident.

### 4.4.3 Social responses to resource utilisation
As the LiDAR-derived habitat variables were largely unable to distinguish forest blocks from each other, the individual differences in ranging patterns suggest that other factors influenced movement, such as social (e.g. intergroup encounters, demography, group size) or ecological factors (e.g., food availability, resource recovery) (Doran-Sheehy et al. 2004). Although home range size and resource requirements can vary based on differences in individual body size or dietary considerations due to age and sex (Webb et al. 2011; Campos et al. 2014), it was not expected that this would account for the variation seen between individuals in this study, because the locations of the collared individual were considered representative of the group that travels as a cohesive unit (Campos et al. 2014, Matsuda et al. 2009a).

The effects of disturbance (e.g. logging) can be difficult to quantify for primates. Pre- and post-disturbance data, time since disturbance, and scale of disturbance are all factors that need to be considered when trying to draw conclusions about its effect on a species (Chapman 2006b). Rather than adjusting feeding time or ranging behaviour,

colobines have been observed to reduce group size in response to habitat disturbance, which therefore reduce feeding competition (black-and-white colobus *Colobus guereza* and Uganda red colobus *Piliocolobus tephrosceles*, see Onderdonk and Chapman 2000; Chapman et al. 2006b). This has recently been observed for proboscis monkeys in the Lower Kinabatangan Floodplain, where group size has significantly decreased since 2004, even though there was no significant change in population size (Matsuda et al. *in press*). The large-scale forest loss and major selective logging events began to decelerate in the Kinabatangan by the early 2000's (Gaveau et al. 2014; Matsuda et al. *in press*). Adjustments to their social unit over the past decade in response to the large-scale forest loss prior to 2004 would therefore not be detectable by LiDAR or ranging data and could give the appearance of a more generalised resource use pattern. Unfortunately, as the groups in this study were not habituated, group size and composition were not consistently available or reliable, and therefore could not be included in the anlaysis.

### 4.4.4   Resource utilisation at forest edges

By averaging individual RUF coefficients to create the population-level model of proboscis monkey resource use, few significant patterns emerged. Apart from mean canopy height, the sign of the resource utilisation coefficients for the other variables varied among individuals, although the signs for recursion and intensity were usually the same within individuals, with only the magnitude of the coefficient changing. Moreover, because of nonlinear changes in species' response to changes in their environment (Garabedian et al. 2017), some patterns were not detectable with the RUF. For example, there was no significant association with use depending on proximity to plantations with the RUF, whereas the GAM detected a pattern that could be important for informing conservation management plans. Since the GAM followed the general relationships highlighted with the RUF and because of the ecological

relevance of the non-linear trends, the discussion will be primarily based on the patterns detected from the GAM.

As the largest monkeys in Borneo, proboscis monkeys are limited to habitats that can support their large body size along with a relatively high density of individuals (Matsuda et al. 2013). Nutrient-rich conditions found in floodplains tend to have higher quality food plants than areas further from floodwater, i.e. leaves rich in minerals and protein, and low in fibre (crude ash) (Matsuda et al. 2013; Thiry et al. *in review*). These conditions are expected to promote greater use of areas close to rivers and lakes, as seen in the current study, with high use patches on average less than 200 m from forest-water edges. The other major peak in proximity to water was for areas 1-1.2 km from rivers and lakes (mainly associated with Group 1, Figs 4.1 and 4.6), which was not identified by the linear RUF analysis. This area was inundated forest that consisted primarily of a single tree species (*Mallotus muticus*, *pers. obs.*), an extremely abundant plant species which proboscis monkeys prefer to feed on (Matsuda et al. 2013).

Proboscis monkeys' preference for eating young leaves (Yeager et al. 1997; Matsuda et al. 2009b) means that they can thrive in secondary forests, or forests with moderate levels of disturbance. Such forests often have higher food quality (protein-fibre ratio), fruit production and overall food availability than primary forests, largely due to increased sun exposure (Ganzhorn 1995; Matsuda et al. 2013). Edge habitats in particular often provide these benefits, but proboscis monkeys used forest in close proximity to river and plantation edges in different ways. Both edge types share features such as protection from predation by being on an edge (Matsuda et al. 2009c), and increased plant growth (Ganzhorn 1995; Kuijper et al. 2009). However, proboscis monkeys rarely used areas less than 140-220 m from plantations. Plantation edges may have increased noise disturbance, due to machinery, people, or dogs (*pers. obs.*). Although hunting in Lower Kinabatangan Wildlife Sanctuary is prohibited (Sabah

Wildlife Department 1997), plantation workers erect platforms in trees along the plantation-forest boundary and shoot at night as the animals come into the plantation to forage or hunt (*pers. obs.*). Finally, proboscis monkeys' main predator, the Sunda clouded leopard (*Neofelis diardi*), often hunts near forest-plantation boundaries (Brodie et al. 2015). Therefore, maintaining safe distances from plantation edges may represent a compromise for proboscis monkeys, being close enough to benefit from the dietary advantage, whilst restricting the increased risk of being seen or disturbed.

### 4.4.5   Conservation implications

The degraded forests of the Lower Kinabatangan Floodplain are home to one of the largest known populations of proboscis monkeys in Borneo (Meijaard and Nijman 2000a; Sha et al. 2008; Stark 2009). As detected in other colobines in degraded habitats (Chapman et al. 2006b), proboscis monkeys in the Kinabatangan are forming smaller groups (Matsuda et al. *in press*). Combined with the findings from this study that there was no clear relationship between ranging and disturbance level or forest availability, this suggests that proboscis monkeys may be responding to changes in their habitat by reducing their group size to lessen the feeding-competition within the group, rather than changing their ranging behaviour (Snaith and Chapman 2007).

Proboscis monkeys appeared to have more general habitat preferences than expected, although this leaves the possibility that they may respond to structure over shorter timescales (e.g. days-weeks) or to plant species composition. However, through providing an unbiased confirmation of the importance of riparian forests to proboscis monkeys, this study stresses the necessity of maintaining a wide riparian reserve. Although the habitat use peaked around 60-110 m from rivers and lakes, areas reaching as far inland as 1.2 km were important habitats, compared to the legal minimum of conserving 20 m of forest along the main river and 3 m along tributaries (State of Sabah 1998). Based on the prediction maps, an area of at least 200-300 m

along the river is required. However, by restricting areas to this minimum width, there is the risk of over-exploitation of food resources and reducing habitat quality, as there may not be enough habitat to allow an area to recover before a group returns to feed there again (Meijaard and Nijman 2000b). Furthermore, despite the potential for forest-plantation boundaries to have suitable environmental conditions (e.g., food availability, protection from predation), this study shows that areas less than 250 m from plantations are undesirable to proboscis monkeys and they are not used to the same extent that water edges are. It will be important to maintain a balance between the amount of forest preserved along a river without it being too close to plantation on the other side.

The protection of low-elevation habitat, which includes that of proboscis monkeys, is an on-going issue in Sabah (Chapter 6), as well as the rest of Borneo (Struebig et al. 2015). Privately owned forests continue to be cleared, and the protection of riparian reserves is not being enforced without groups or individuals calling the government to action. A quarter of potential proboscis monkey habitat is not protected in the Lower Kinabatangan Floodplain (Matsuda et al. *in press*). Within this study, three of the collared individuals were living fully outside the Lower Kinabatangan Wildlife Sanctuary or a Virgin Jungle Reserve (Groups 2, 3, and 8). From the time after the collaring period ended, to the time that the LiDAR data were collected, forest had been cleared from Group 2 and 3's range (section 4.2.4). A fourth group (Group 4) had ranged into an unprotected forest during the collaring period before 4-6 ha of their range was cleared a few weeks later. Although 85% of the unprotected forest within proboscis monkeys' range in the Kinabatangan has been identified as unsuitable for oil palm, more than a third of it has already been allocated for that purpose (Matsuda et al. *in press*). Extending protection to include remaining forest that has been deemed unsuitable for oil palm and reclaiming land with underproductive oil palm would increase the connectivity to other forests and prevent over-exploitation of resources

(Abram et al. 2014). Conservation management strategies need to be developed that include considerations of proximity to both water and plantations, using the knowledge from this study in a way that can change the government's reactive responses of forest loss to preventative actions.

# Chapter 5 Insights into the spatio-temporal movement patterns of proboscis monkeys

## 5.0 Abstract

Advances in GPS technology have made it possible to explore primate travel patterns in great detail to reveal information on feeding strategies and habitat use. Ranging patterns are influenced by social and natural environmental factors, but human-disturbed habitats can confound these patterns by reducing the amount of available forest, altering the quality of food available or through an increase in edge habitats. Proboscis monkeys (*Nasalis larvatus*) are large colobine primates that live in habitats with a varying prevalence of disturbance and extent of forest edges (natural- and human-made). Using GPS-collar data from 10 proboscis monkeys over 241 (± 33) days, sleeping site selection and diurnal movement patterns were identified along the Kinabatangan River in Sabah, Malaysian Borneo. Both diurnal movements and sleeping site selection were influenced by environmental and landscape factors. Seasonality, rainfall and distance to forest edges influenced daily movement patterns, whereas sleeping site selection moved further inland during times of low rain, high maximum temperatures or during brighter moon phases, potentially to avoid disturbance. The adaptable nature of proboscis monkeys has allowed them to survive thus far in a habitat with unpredictable seasons, and which has experienced major habitat loss. However, for proboscis monkeys to continue being a focal species for tourism in Borneo, habitat protection and restorative actions must be taken alongside monitoring human behaviour to reduce the disturbances proboscis monkeys face due to their tendency to spend time along forest edges.

## 5.1 Introduction

Patterns of primate home range use and daily travel patterns can reveal much about feeding strategies, inter- and intragroup interactions or habitat suitability (Porter et al. 2007). Advances in GPS technology have made it possible to collect ranging information on multiple individuals (Chapter 4), or animals that may be shy, cryptic or difficult to follow due to the terrain or other logistical constraints (Löttker et al. 2009). Through GPS fixes and time-date information, it has become possible to infer behaviours, such as foraging strategies, or identify important areas within their habitat due to their increased utilisation of particular patches (Chapter 4). Ranging patterns are influenced by a number of factors such as group size, habitat quality and climate, which may interact to produce complex responses (Di Fiore 2003). For example, large social units may increase daily travelling efforts by moving further or faster to obtain sufficient food for the group or to prevent resource depletion (Snaith and Chapman 2005; Teichroeb and Sicotte 2009). However, the density, distribution and tolerance of neighbouring groups can restrict ranging behaviours (Palminteri et al. 2016). Additionally, primates living in lower quality habitats tend to make longer daily journeys relative to the amount of forest available (Chapman et al. 2006b; Boyle et al. 2009). Fragmented or human-disturbed habitats may be used more uniformly than continuous forest, as groups need to maximise exploitation of the forest: similar uniform use may also reflect generalist foraging (Boyle et al. 2009; Ménard et al. 2014). Finally, ranging patterns can be influenced by climatic factors that generate seasonal changes in food patch size and distribution (Hanya et al. 2013). Primates may adjust their core ranging areas based on local increases in food availability or due to patch depletion (Porter et al. 2007). Unpicking these different processes allows researchers to identify how primates use the wider landscape and can inform management strategies based on the spatial and nutritional requirements of a species. The use or avoidance of certain areas can also highlight areas of conservation importance.

Climate is considered to be a major factor driving variation in animal ranging behaviour at different temporal scales (Rivrud et al. 2010). Rainfall shows greater annual variation than temperature in the tropics, and so is often used to characterise the seasons (van Schaik and Brockman 2005; Hanya et al. 2011). The amount of rain plays a vital role in food availability, which can then influence primate movement patterns (McKey and Waterman 1982; Matsuda et al. 2009b). A greater abundance of preferred food items associated with wet seasons may lead to reduced daily ranging behaviour whilst groups exploit the food items in small areas (Matsuda et al. 2009a), or may increase ranging in order to take advantage of food resources that are more abundant during wetter seasons (Bennett 1986). Alternatively, favourable weather conditions may promote increased movement that supports a more diverse diet, such as the increased diversity of food items consumed by black colobus (*Colobus satanas*) during periods with a higher percentage of sunny weather (McKey and Waterman 1982). Besides these indirect influences of rainfall on seasonal movement, it can also have direct short-term effects within days (Rivrud et al. 2010). Heavy rain can temporarily halt a group's movement (Fuentes 1996; Ren et al. 2009b), although this may not have a direct correlation with daily travel length (Altmann and Altmann 1970).

The extent of seasonal variation in ranging behaviour varies among primate species. Proboscis monkeys (*Nasalis larvatus*), the largest of all colobine monkeys (Oates et al. 1994), generally consume high levels of leaves, and consumption of seasonal or limited foods (i.e. unripe fruits and seeds) increases at certain times of the year, which may be associated with changes in their ranging patterns during those periods (Matsuda et al. 2009a). In contrast to many other Asian colobines, proboscis monkeys feed on the fruit and seeds of dominant plant species during fruit-abundant seasons, which may alter the distance they travel between food patches during these periods (Boonratana 2000; Matsuda et al. 2009a).

Longer-term changes in ranging behaviour may be driven by habitat loss or degradation (Onderdonk and Chapman 2000; Cristóbal-Azkarate and Arroyo-Rodríguez 2007). Due to global loss and fragmentation of tropical forests, forest edges are an increasingly important influence on the daily movements of primates, as well as their overall habitat preferences (Chapter 4). As agriculture has expanded, lowland forests have become smaller and more fragmented, so that the extent of non-riparian edge habitats, such as those bordering oil palm (*Elaeis guineensis*) plantations, frequently exceed those along rivers in preferred proboscis monkey habitat (Matsuda et al. *in press*). Colobines have shown a preference for edge habitats (e.g., Mbora and Meikle 2004; Onderdonk and Chapman 2000; Chapter 4), partially because of the increased quantity and quality of food as a result of increased exposure to sunlight (Ganzhorn 1995; Gibson and Koenig 2012; Thiry et al. *in review*). Although proboscis monkeys tend to be associated with forest-river edges for sleeping, there is some evidence that they sleep along other non-riparian edges (e.g. old tractor roads) during certain times of the year (Matsuda et al. 2010). Edges tend to have a higher density of vines and other secondary vegetation that offer a more consistent food resource when fruit availability is low. Primates may also use forest-agriculture edges as a refuge when crop-raiding (Naughton-Treves et al. 1998), although there is no evidence of this for proboscis monkeys. Conversely, forest-agriculture boundaries may exhibit unfavourable conditions for primates, such as noise pollution from humans, machines or dogs (Lacerda et al. 2009; *pers. obs.*). Predation risk may also be greater (Lehman et al. 2006), such as increased exploitation of forest-agriculture boundaries by Sunda clouded leopards *Neofelis diardi*) (Brodie et al. 2015). The balance between the dietary benefits of edge habitats and the increased disturbance or predation risk near plantations, may, therefore, result in differences in movement patterns between agricultural and riparian boundaries.

Recently, greater insight into movement behaviour and habitat use has been obtained by decomposing total utilisation of an area into the frequency with which different areas are visited and the typical duration of a visit (Benhamou and Riotte-Lambert 2012; Lyons et al. 2013; Yiu et al. 2017; Chapter 4). Long duration visits to areas may indicate areas for refuge or feeding, whereas short visits may indicate transit areas or high risk areas containing desirable resources (Benhamou and Riotte-Lambert 2012). Changes in visitation rates and durations can be indicative of seasonal dependence on particular resources, such as the increased re-visitation rates by springbok (*Antidorcas marsupialis*) to perennial watering points during the dry season (Lyons et al. 2013). The time spent in an area (residence time) and frequency of visits (recursion rate) are important aspects to investigate in disturbed habitats, as resource depletion can threaten the survival of a population (Van Moorter et al. 2016). There had been an assumption that folivorous primates would not deplete food patches or experience feeding competition, but this is no longer widely accepted (Snaith and Chapman 2007). Large groups of Uganda red colobus monkeys (*Piliocolobus tephrosceles*) can deplete food patches quickly, which results in increased energy expenditure to search for food in more patches (Snaith and Chapman 2005). In extreme cases, when there is insufficient habitat available to search for food, local extinctions have been known to occur, including amongst proboscis monkeys (Meijaard and Nijman 2000b). GPS tracking data may provide insight into this, as patterns of long residence times but low recursion rates may indicate possible resource depletion, once seasonal variations in food availability are controlled for.

The current study focuses on how proboscis monkeys utilise a degraded forest landscape across timescales varying from daily, through monthly to annually. Chapter 4 studied home ranges habitat use over a period of months and started to uncover how proboscis monkeys use the landscape, revealing parts of the home ranges that were heavily used, visited at different frequencies and for different durations. However, apart

from tree height and proximity to forest edges, other canopy structure characteristics did not appear to be strongly influencing proboscis monkeys' resource use (Fig. 4.4). Over shorter timescales, the seasonal availability of food resources or resource recovery rates may play an important role in ranging behaviour. This study aims to examine changes in movement and sleeping site selection through time associated with: 1) environmental factors (i.e., phenology, rainfall, and moon phase) and 2) proximity to forest edges. A network of botanical plots was used to quantify phenology and abundance of different potential food sources (i.e., young leaves, fruit, flowers) across the study period, coupled with monthly rainfall data. Times of the year with greater fruit availability were predicted to be associated with reduced overall movement because proboscis monkeys tend to heavily exploit fruits (and seeds) in small areas, feeding on dominant plant species, and in which the distance between patches may be shorter (Matsuda et al. 2009a). The availability of young leaves and flowers was not expected to influence movement because young leaves are widely available throughout the seasons and flowers make consistently low contributions to proboscis monkey diets (Yeager 1989; Matsuda et al. 2009b; Thiry et al. *in review*). Increased rainfall was expected to reduce distance travelled and decrease path straightness (more circular) due to increased foraging in smaller areas (Matsuda et al. 2009a). Sleeping sites were expected to move further inland during times of high rain and when the moon was brighter, potentially to decrease predation risk. Path straightness and speed were expected to increase closer to plantation edges and outside of high use areas, as proboscis monkeys were expected to move more rapidly through these areas.

In a second stage, the study analyses the movement behaviour of individuals within parts of their home range identified as visited for long periods at a time or frequently visited to gain insight into the foraging strategy of proboscis monkeys (i.e. 30th percentiles of intensity and recursion distribution models identified in Chapter 4). Once

in a "profitable place" (e.g. food-abundant areas), it would be energetically preferable to spend more time there, exploiting the resources (Barraquand and Benhamou 2008). Therefore, movement was expected to become slower and more tortuous in high intensity patches. No difference was expected in high recursion patches, as they were not necessarily visited for a considerable duration. Furthermore, to reduce energy expended to move between high use areas (high intensity and high duration), movements would be more directed between patches (Van Moorter et al. 2016). Increased visitation rates and durations were expected during times of increased fruit availability, as proboscis monkeys have been shown to exploit small areas when feeding predominately on fruits (Matsuda et al. 2009a).

## 5.2 Methods

### 5.2.1 Proboscis monkey collaring data

Between 2011 and 2015, 10 proboscis monkeys were collared from different one-male social units along the Kinabatangan River (5°18'N-5°42'N and 117°54'E-118°33'E) within the Lower Kinabatangan Floodplain (Fig. 4.1). Collars provided data for 241 (± 33) days (Table A1.1) and were programmed to record hourly positions between 05:00 and 19:00 (see Section 3.2.2 for full collaring details and section 3.2.3 for pre-processing of the GPS data). The only difference from the previous chapters was that the 05:00 fixes were included in the current analysis.

### 5.2.2 Botanic data and seasonality

Daily rainfall, minimum and maximum temperatures were measured nightly at Danau Girang Field Centre (5°24'49"N, 118°2'15"E). Moon phases were extracted from moon V1.0 (Thomas 1998) and recorded on a scale of 0 to 1 (0 = new moon and 1 = full moon). Botanic plots were established to monitor the phenology and abundance of potential foods throughout the area during the study period. Random points were created using ArcGIS, at a minimum distance of 300 m apart throughout the forested

study area. A ground-survey was conducted to select suitable plots based on the main habitat type at each point, for a balanced distribution of the four main forest types: dry lowland (never or rarely inundated), semi-inundated (flooded for 3-6 months per year), semi-swamp/grassy (flooded/wet for 3-6 months) and swamp forests (flooded/wet >9 months) (Abram et al. 2014). Twenty botanic plots of 20 m x 20 m were set up in October 2011, and an additional 14 plots in May 2013 (Fig. 5.1). Each plot consisted of a single habitat type. Trees (DBH >10 cm) and large lianas (DBH >5 cm) were tagged and identified to family level, and to species when possible, by cross-referencing to pre-identified trees in established botanic plots. Photographs and samples of unknown or uncertain species were taken and identified by HUTAN/KOCP (Sukau, Sabah) or the Forest Research Centre (Sandakan, Sabah).
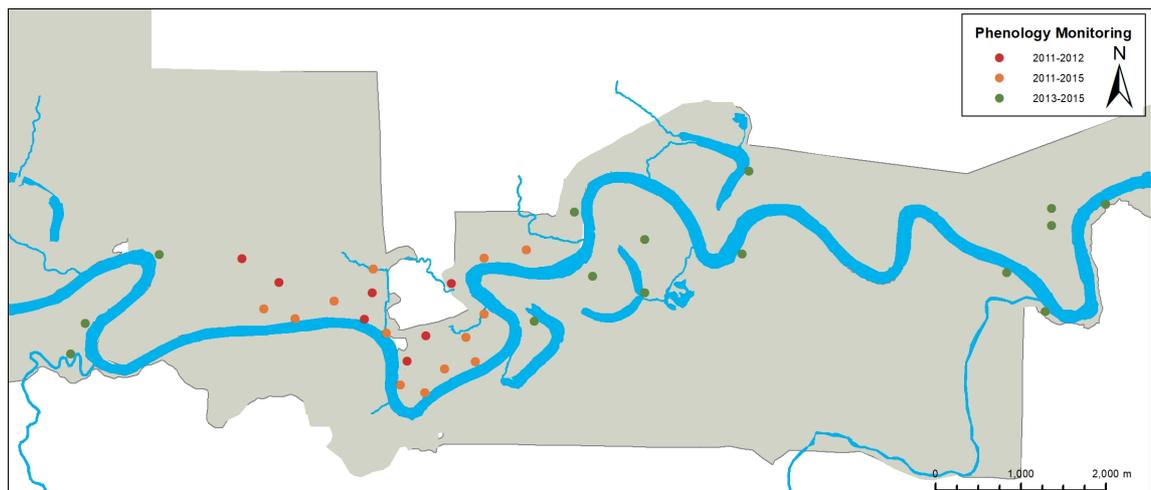


Figure 5.1    Distribution of botanic plots throughout the study area. Phenology monitoring was conducted from 2011 to 2012 and 2013 to 2015. Red dots were monitored only from 2011 to 2012, green dots were monitored from 2013 to 2015, and orange dots were monitored during both periods.

Plots were visited during the 3rd to 4th week of each month from October 2011 to September 2012 (N = 20 plots; 837 plants), and May 2013 to June 2015 (N = 24 plots, 10 original + 14 new; 626 plants). Phenology data overlapped with the tracking periods of the collared animals for the majority of the study period, except for missing phenology data during the initial two months of tracking in 2011 and from October 2012

to April 2013, and missing tracking data during the phenology periods from May to September 2013. These data were excluded from the seasonal analysis of movement patterns (section 5.2.4 GAMMs). All trees and large vines within the plots were monitored for the seasonal availability of food parts: young leaves, flowers (combined open and buds), and fruits (ripe and unripe), all of which are eaten by proboscis monkeys (Matsuda et al. 2009b). The availability of potential food parts were recorded from all plant species, as proboscis monkeys eat from the most abundant plant species within their home range (Matsuda et al. 2009b). Due to the high correlation between unripe and ripe fruits (Pearson's correlation r = 0.78, p<0.001), these plant parts were combined for the analysis. To avoid observer-dependant bias associated with abundance estimates, the presence or absence of the three plant parts was recorded for each tree in a plot rather than an abundance scale (Wartmann 2008). A simple index of potential food abundance was calculated by dividing the number of trees carrying young leaves, flowers or fruits by the total number of trees in the plot (Wartmann 2008). There generally is considered to be a high degree of intrapopulation synchrony in tropical forests (van Schaik et al. 1993). Therefore, the availability of each of the three food types was averaged across all of the botanical plots each month to represent the complete study area.

### 5.2.3 Analysis of phenology

Generalised additive mixed-effect models (GAMMs) were used to examine the seasonal variation in the availability of different plant parts (young leaves, flowers or fruit), and the role played by rainfall. Availability was square root (flowers, fruit) or modified logit transformed (young leaves) (Warton and Hui 2011). To allow for variation through the year, time (month) was modelled with a cubic cyclic smoothing spline, which is designed for analysing annual cycles (Wood 2006). Year was included in the model as an interaction term with month, to account for any general changes in phenology among years. Rainfall was modelled with a thin plate spline, restricted to

three degrees of freedom (Wood 2006). Botanic plot number was included as a random effect to account for repeated sampling through time. The degree of smoothing was determined using generalised cross validation (Wood 2006); where a linear relationship was selected, the model was refitted specifying the linear term so that the estimated coefficient was available. The models were fitted in R using the gamm function in the package *mgcv* (Wood 2011).

### 5.2.4 Movement patterns

Four variables were used to quantify diurnal movement patterns from the GPS collar data: daily path length (DPL), movement speed, straightness index (SI), and turning angles (TA). DPL and speed are descriptors of the travel effort (how far and how fast), whereas SI and TA describe how individuals move through the habitat (i.e. directed or tortuous) (Fig. 5.2). DPL was calculated in ArcGIS 10 (ESRI 2011) by measuring the cumulative sum of each step length for each day. Speed was calculated as distance travelled per time unit (m/h) with the *adehabitatLT* package in R (Calenge 2006). Straightness Index (SI) was calculated in ArcGIS with the 'Calculate Sinuosity' python tool extension. However, the terminology in this study followed the definition per Benhamou (2004), and the index was therefore referred to as the straightness index, so as not to be confused with alternative definitions for sinuosity (Benhamou 2004). The SI measured the deviation of a line from the shortest path by dividing the shortest possible path (distance between the first and last point) by the total daily path length. An index value of 1 represented a straight-line path between consecutive sleeping sites, whilst a value approaching zero indicated that a group tended to return to its starting location at the end of the day, e.g. sleeping in nearby trees on consecutive nights. For simplicity, the latter low SI values are described as 'circular' paths, although the path need not describe a perfect circle. Relative turning angles (in radians) were calculated with the *adehabitatLT* package in R (Calenge 2006) and then the absolute value of the relative turning angle was calculated for TA: a low TA represented a less

tortuous path and a high TA represented a more tortuous path. Only days with more than 10 points were used to calculate daily movement values. Monthly mean values of the four indices were calculated to match the phenology data; only months with more than 20 days were used for monthly movement analysis.
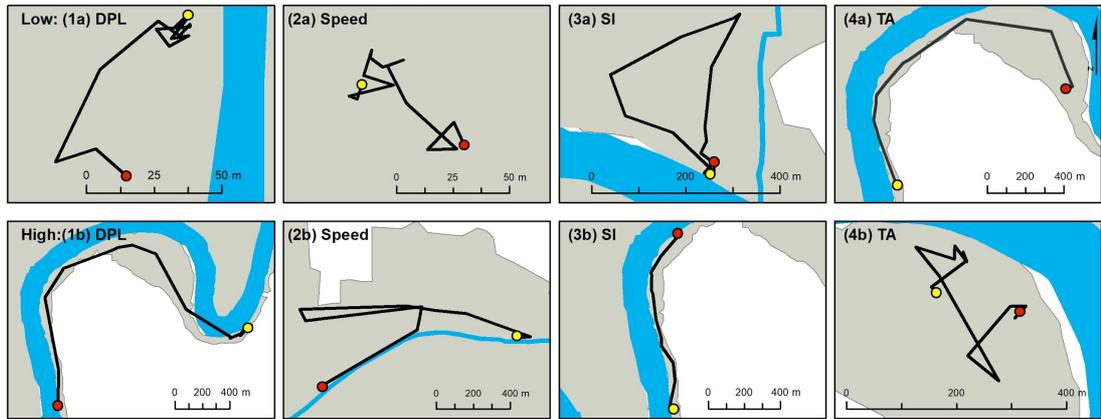


Figure 5.2   Low (a) and high (b) examples of the four movement pattern measurements used in this study: (1) daily path length (DPL), (2) speed, (3) straightness index (SI), and (4) turning angle (TA). Yellow dots indicate the daily starting point (05:00) and red dots indicate the end point (19:00). Note different scales in the different plots.

GAMMs were used to regress movement patterns onto monthly average rainfall and phenology, using individual as a random effect to account for repeated measures through time. Due to missing phenology data (section 5.2.2), only nine individuals were included in the analysis (Groups 4 excluded). Movement patterns examined were monthly average DPL, speed, SI, and TA. DPL and speed were square root transformed and SI and TA were squared. The full model contained four variables: rainfall and the monthly availability indices for young leaves, flowers and fruits. Model selection used the stepwise Akaike Information Criterion (AIC). Independent variables were removed sequentially, starting with the one that caused the largest decrease in the AIC, and stopping when further removals increased the AIC. The smoothness of the splines in the model were selected with generalised cross validation (Wood 2006) and where a linear relationship was selected for a variable in the final model, it was refitted specifying the linear term so that the estimated coefficient was available. The

fits of the models were checked using plots of the residuals. The models were fitted in R using the gamm function in the package *mgcv* (Wood 2011).

### 5.2.5 Sleeping site selection

Proboscis monkeys are generally considered to travel into the forest interior during the day before returning to river edges to sleep at night, although this has only been studied directly for a single group (Matsuda et al. 2009b). Sleeping sites were defined as the 19:00 GPS fix, and the distance to water for each sleeping point was calculated (see method in Section 4.2.4). To test whether environmental variables (moon phase, rainfall and temperature) influenced the sleeping site proximity to water, a GAMM was used, with individual as a random effect. Rainfall, minimum and maximum temperature were square-root transformed, moon phase was modified logit transformed (Warton and Hui 2011) and distance to water was log-transformed. The same model selection and fitting procedure was used as for the movement models.

### 5.2.6 Edge behaviour

To see if proboscis monkeys sleeping close to rivers travelled a characteristic distance inland each day (if available forest was not a limiting factor), the distance of the furthest GPS fix away from water was recorded for each day (hereafter MDD – maximum daily distance). Days when individuals had slept inland were excluded from the analysis. Inland days were defined as days when an animal did not return to the river to sleep or had not slept within 200 m from the river (i.e. two consecutive days where sleeping site was >200 m from water). Sleeping sites were classified as inland if they were located >200 m from water, regardless of if they were located along non-river edges (e.g., oil palm plantations, grassland edges). Density curves were separated by individual to distinguish the differences in the daily distances travelled for individuals that may have restricted ranges (i.e. bordering oil palm plantations) from those that did not. Simple linear regression models were used to test for a relationship between forest availability

or home range size (as calculated in Section 4.2.4) and MDD for each individual (N = 10).

GAMMs were used to test whether movement patterns changed in the vicinity of forest edges, both along the river and next to oil palm plantations. The distances to water and plantations were measured for each GPS fix throughout the day. Speeds and turning angles for each GPS fix were regressed onto proximity to water or plantations, with individual as a random effect. Distance to water and plantations were modelled with a thin plate spline, restricted to five degrees of freedom.

*5.2.7  High intensity and recursion areas*
Points within each area classified as a high intensity or high recursion site (30th percentile of intensity or recursion BRB distribution estimates, Benhamou and Riotte-Lambert 2012; Fig. 4.3) were counted to calculate the total number of hours spent in each ID patch per visit, as well as the average duration of visits per patch and per month. The total number of days between visits to each ID and RD patch was averaged per patch and per month. To explore how movement patterns (speed or turning angle) differed inside and outside high use areas, the average speeds and turning angles were calculated for each point inside and outside the high use patches (ID, RD, and points within both ID and RD patches). A GAMM was used to regress patch residence time (in hours) or recursion time (in days) on monthly average rainfall and the availability of different plant parts (young leaves, flowers or fruit), using individual as a random effect. Model selection used the stepwise Akaike Information Criterion (AIC) as described above.

## 5.3   Results

*5.3.1  Weather and phenology patterns*
Annual precipitation was 4159, 3467, 2756, 2647 and 1992 mm (2011-2015). April–

September tended to be drier (~195 mm per month) than October–March (~286 mm per month). Between 2011 and 2015, mean monthly minimum temperatures fluctuated between 23 – 25ºC and maximum temperatures between 28ºC and 36ºC (Fig. 5.3). Within a year, there was little variation in temperature (difference in minimum temperature within a year: <2ºC and difference in minimum temperature within a year: <6ºC), which is less than the typical daily temperature change (7ºC).
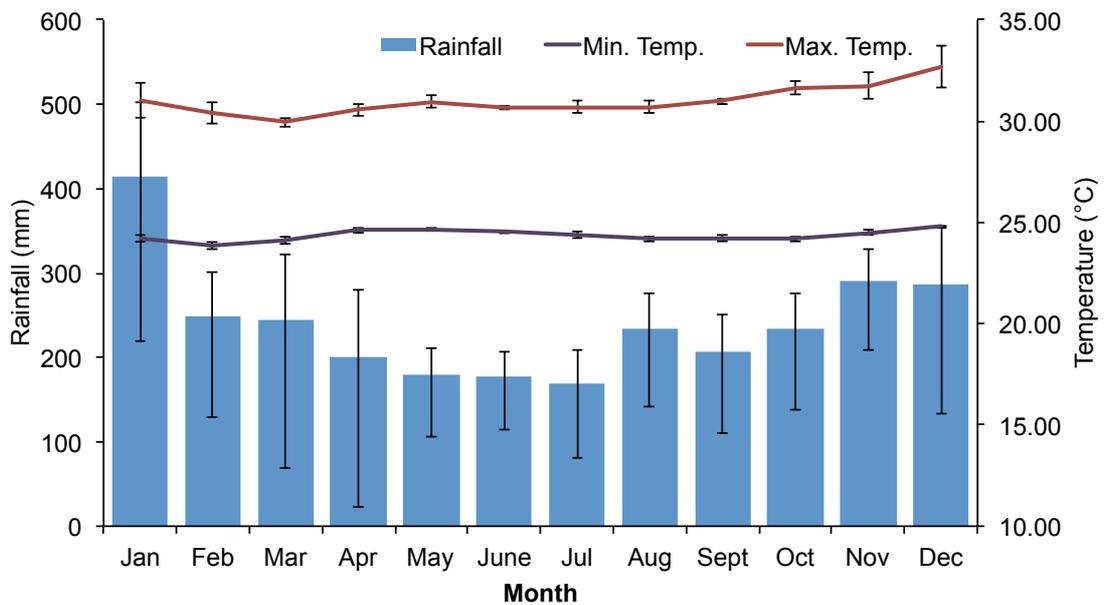


Figure 5.3   Monthly average rainfall, minimum and maximum temperatures from 2011-2015 in the Lower Kinabatangan Floodplain. Standard error bars represent monthly differences over five years.

There were 1118 plants recorded across all botanic plots over the study period, consisting of at least 148 species from 77 genera and 39 families (12 stems unable to identify to family, 17 to genus, and 29 unidentified vines). The 10 most abundant tree species recorded in the plots made up more than 50% of all the trees recorded (Table 5.1). Two species of vine (*Lophophyxis maingayi* and *Caesalphinia* sp.) were also abundant (6.2 and 5.5% of plants, respectively). These top 10 tree and top 2 vine species were all known food sources for proboscis monkeys (Thiry et al. *in review*). All plant parts showed seasonal variation in availability in most years (young leaves: 2012,2014,2015; flowers: 2012-2015; and fruit: 2011-2015; p<0.05). Young leaf

availability did not respond to the amount of rainfall (coeff = 0.0006, SE = 0.0005, t = 1.16, p = 0.25), whereas both flower and fruit availability increased with rainfall (flowers: coeff = 0.00018, SE = 8.53e-0.05, t = 2.15, p = 0.032; fruit: coeff = 0.00048, SE = 0.00010, t = 4.82, p<0.001) (Fig. 5.4).

Table 5.1    The 10 most abundant tree species recorded in the botanic plots (1.4 ha) in the Lower Kinabatangan Floodplain; % = percentage of stems of the particular species relative to all stems (N = 1181; vines and trees) recorded. Trees are ranked by descending abundance.

| Latin name (Family) | % |
|---|---|
| *Mallotus muticus* (Euphorbiaceae) | 11.6 |
| *Colona serratifolia* (Malvaceae) | 10.0 |
| *Dillenia excelsa* (Dilleniaceae) | 9.6 |
| *Kleinhovia hospita* (Malvaceae) | 5.9 |
| *Nauclea orientalis* (Rubiaceae) | 4.1 |
| *Antidesma puncticulatum* (Phyllanthaceae) | 2.9 |
| *Pterospermum elongatum* (Malvaceae) | 2.9 |
| *Pterospermum diversifolium* (Malvaceae) | 2.0 |
| *Vitex pinnata* (Lamiaceae) | 1.6 |
| *Dracontomelon dao* (Anacardiaceae) | 1.4 |
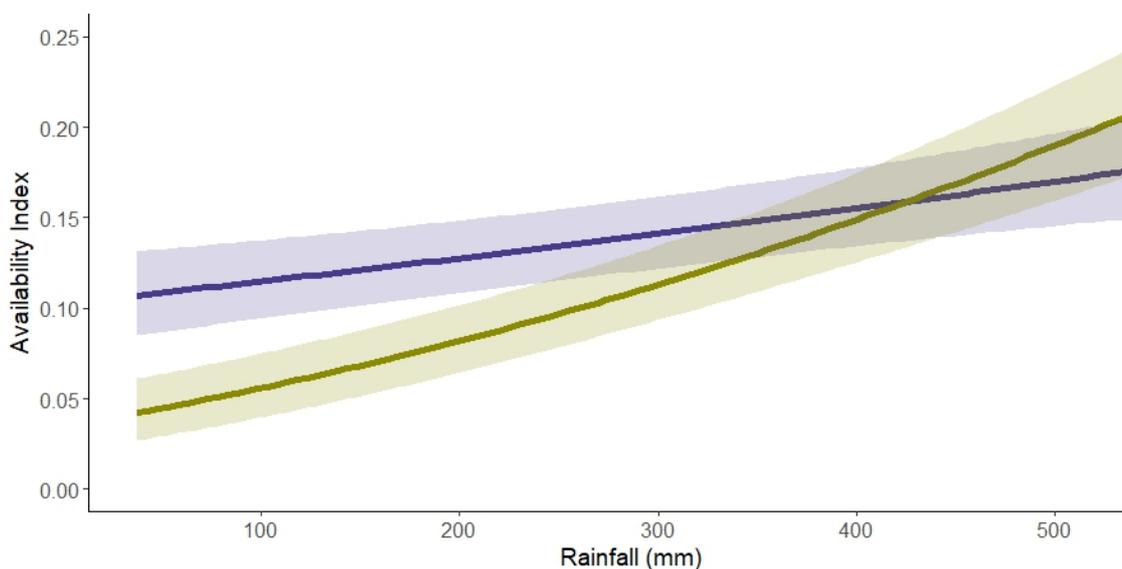


Figure 5.4  The predicted availability of flowers (purple) and fruits (yellow) in response to monthly rainfall. Shaded regions represent the standard error around the predictions.

## 5.3.2 *Movement patterns*

The average straightness index (± SE, N = 10) was 0.38 (± 0.03), i.e. groups moved approximately 2.6 times as far during the day as the Euclidean distance between their start and end point (Table 5.2). The average minimum SI was (SI = 0.003 ± 0.0004), indicating a circular path with the same area used for sleeping on consecutive nights (e.g. Fig. 5.2, panel 3a), whilst the average maximum was 0.89 (± 0.03), indicating a relatively straight path between sleeping sites (e.g. Fig. 5.2, panel 3b). The average minimum and maximum daily path lengths were 285 (± 32) m and 2208 (± 160) m respectively, with a mean distance of 940 (± 38) m (Fig. 5.5). The average speed was 67 (± 3) m/h and the average turning angle was 1.2 (± 0.02) radians (69 degrees).

Table 5.2    Summary of average movement patterns for 10 proboscis monkeys. Overnight data were removed for speed calculations (i.e. removed speeds when there were 10 or more hours between points).

| Group ID | Daily Path Length (m) | | | Speed (m/h) (SE) | SI (SE) | Turning Angle (SE) |
|---|---|---|---|---|---|---|
| | DPL (SE) | Min | Max | | | |
| 1 | 940.6 (19.1) | 174.2 | 2357.9 | 67.0 (0.9) | 0.41 (0.01) | 1.27 (0.01) |
| 2 | 1084.1 (23.5) | 429.9 | 2844.1 | 76.9 (1.3) | 0.28 (0.01) | 1.20 (0.02) |
| 3 | 781.1 (17.6) | 252.2 | 1525.8 | 55.8 (1.1) | 0.36 (0.02) | 1.19 (0.02) |
| 4 | 761.1 (16.4) | 203.8 | 1886.7 | 54.2 (1.0) | 0.36 (0.02) | 1.27 (0.02) |
| 5 | 944.3 (17.0) | 166.7 | 2558.7 | 67.0 (0.9) | 0.40 (0.01) | 1.22 (0.02) |
| 6 | 1028.1 (26.6) | 376.5 | 1771.4 | 74.2 (1.5) | 0.41 (0.03) | 1.09 (0.03) |
| 7 | 885.3 (16.2) | 234.5 | 1836.7 | 63.7 (1.0) | 0.42 (0.02) | 1.24 (0.02) |
| 8 | 954.4 (19.1) | 232.2 | 3037.0 | 68.3 (1.0) | 0.48 (0.01) | 1.27 (0.01) |
| 9 | 891.3 (21.9) | 369.7 | 2404.2 | 65.3 (1.3) | 0.42 (0.02) | 1.22 (0.02) |
| 10 | 1135.1 (20.4) | 409.9 | 1863.7 | 81.4 (1.3) | 0.21 (0.01) | 1.14 (0.02) |
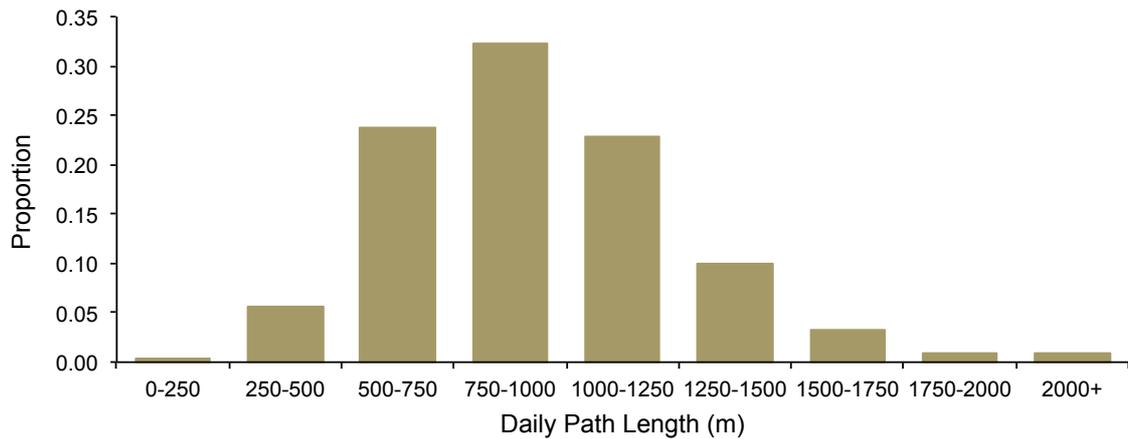
Figure 5.5   The distribution of daily path lengths (N = 2837 days) of proboscis monkeys; only days with more than 10 fix locations were included.

DPL and turning angles responded to phenology patterns or rainfall, whereas path straightness and travel speed did not (Table 5.3, Fig. 5.6). Proboscis monkeys moved shorter distances as rainfall increased and when more young leaves were available. There was evidence that DPL increased as fruit availability increased (p = 0.05), and that turning angle increased with rainfall (p = 0.05), suggesting a change towards more tortuous movements.

Table 5.3   Best-fit generalised additive mixed-effect models for the movement patterns of proboscis monkeys. (N = 55 observations, nine groups).

| Response Variable | Model | Coefficient | SE | t-value | p |
|---|---|---|---|---|---|
| Daily Path Length | *(Intercept)* | 46.16 | 6.74 | 6.85 | p<0.001 |
| | *~ Rainfall*** | -0.17 | 0.08 | -2.20 | 0.03 |
| | *+ Young leaves*** | -15.46 | 7.06 | -2.19 | 0.03 |
| | *+ Fruit** | 55.99 | 28.17 | 1.99 | 0.05 |
| Speed | *(Intercept)* | 29.38 | 4.66 | 6.31 | p<0.001 |
| | *~ Flowers* | -33.56 | 41.83 | -0.80 | 0.43 |
| Straightness Index | *(Intercept)* | 0.12 | 0.04 | 3.38 | 0.001 |
| | *~ Rainfall* | 0.002 | 0.002 | 1.16 | 0.25 |
| Turning Angle | *(Intercept)* | 1.29 | 0.12 | 11.14 | p<0.001 |
| | *~ Rainfall** | 0.01 | 0.01 | 2.01 | 0.05 |

*near significant (p = 0.05); **significant (p<0.05)

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### 5.3.3   Sleeping site selection and edge behaviour

Sleeping trees within 50 m of water accounted for 82% of all sleeping sites (<100 m: 90%, N = 2387 sleeping sites) (Fig. 5.7). Under 5% of sleeping trees were within 50 m of plantations, although more than half of those points came from locations that were also within 50 m of the river (63 nights). The average sleeping site (± SE, N = 10) was 52 (± 16) m from the water, and 841 (± 251) m from plantations. Excluding inland sleeping sites (>200 m from known waterbodies), sleeping sites were 19 (± 3) m from water. More than half the points (55%) that were within 50 m of water were during the first two and last two active hours in a day (i.e. excluding 05:00 and 19:00), and split almost equally between the two time slots (Fig. 5.8).
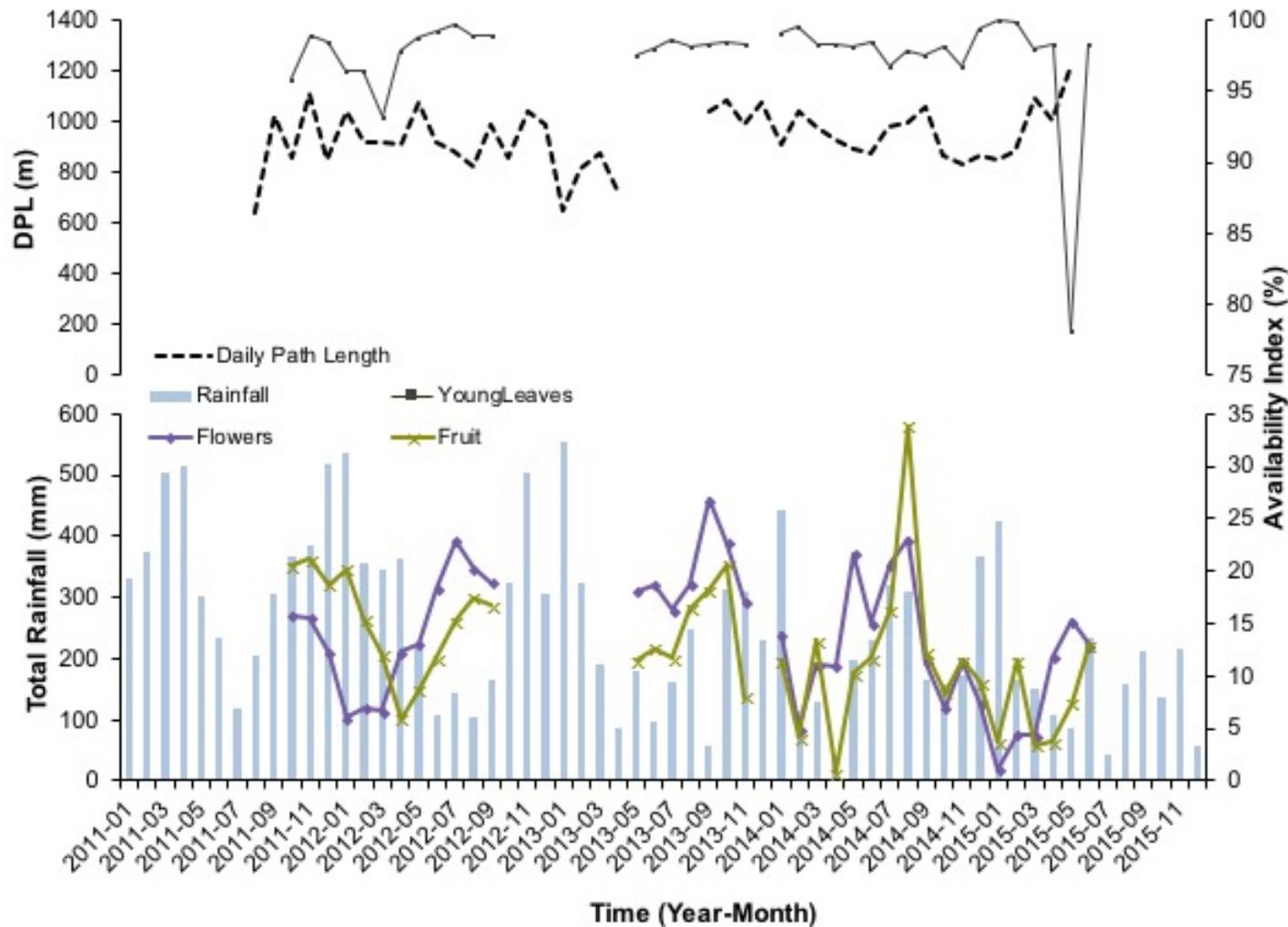
Figure 5.6   Fluctuations in monthly average daily path lengths (DPL; dashed), total rainfall (bars), young leaf (green), flower, (purple) and fruit (black) availability from 2011 to 2015 in the Kinabatangan floodplain.
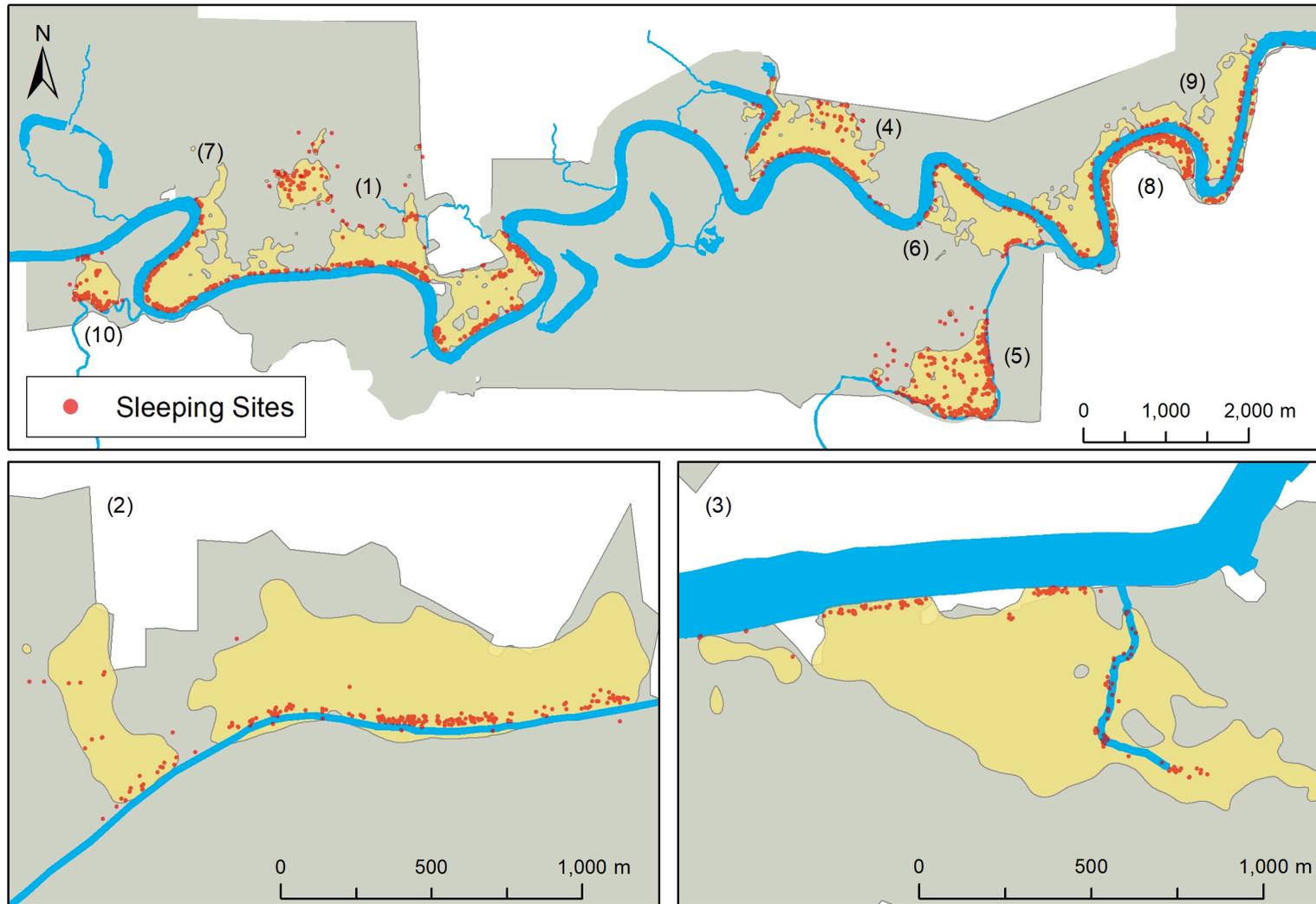
Figure 5.7    Sleeping sites (N = 2387, 10 individuals) of GPS-collared proboscis monkeys along the Kinabatangan River. Numbers represent Group ID.
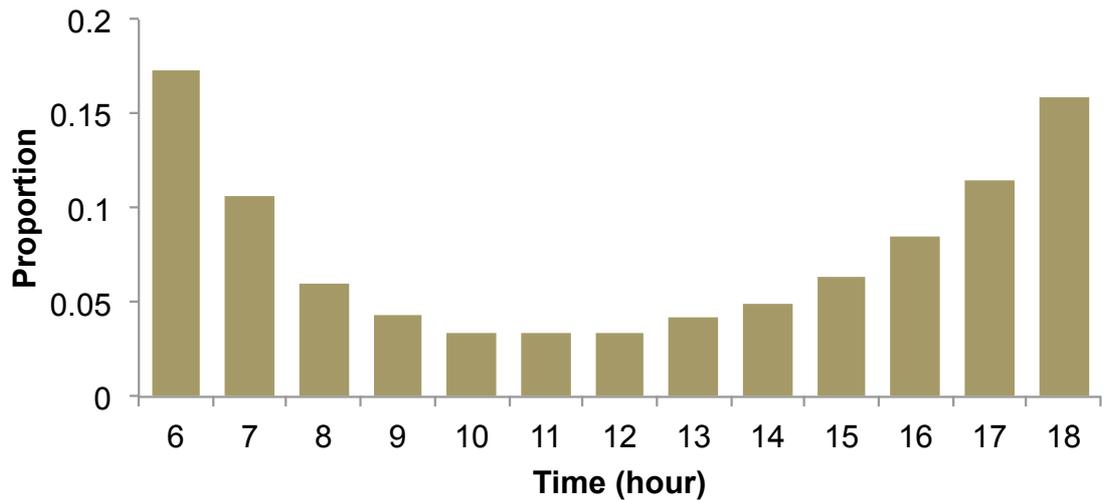
Figure 5.8   The proportion of all GPS fixes that were less than 50 m from water, excluded the sleeping points (05:00 and 19:00; N = 10488).

The selected locations varied with weather and phases of the moon. Increased rain led to sleeping closer to water (coeff = -6.29e-07, SE = 2.98e-07, t = -2.11, p = 0.04), whilst proboscis monkeys slept further inland when the moon was closer to full (coeff = 0.06, SE = 0.01, t = 5.96, p<0.001). Sleeping sites were also further inland as maximum daily temperature increased (df = 5.23, F = 10.55, p<0.001).

For the days that proboscis monkeys returned to the water to sleep, the average MDD ranged from 112 (± 2) m to 320 (± 8) m across the 10 groups with an overall average of 227 (± 18) m (Fig. 5.9). The average time that the proboscis monkeys reached their MDD from the river was 12:00 (range 10:00-13:00). MDD was never more than 762 m (max MDDs range: 230-762 m) from water, and the minimum MDD ranged from 9 – 135 m. Home range area did not correspond with MDD (LM, $R^2$ = 0.008, p = 0.81), but MDD was larger when more forest was available (LM, $R^2$ = 0.42, p = 0.04).
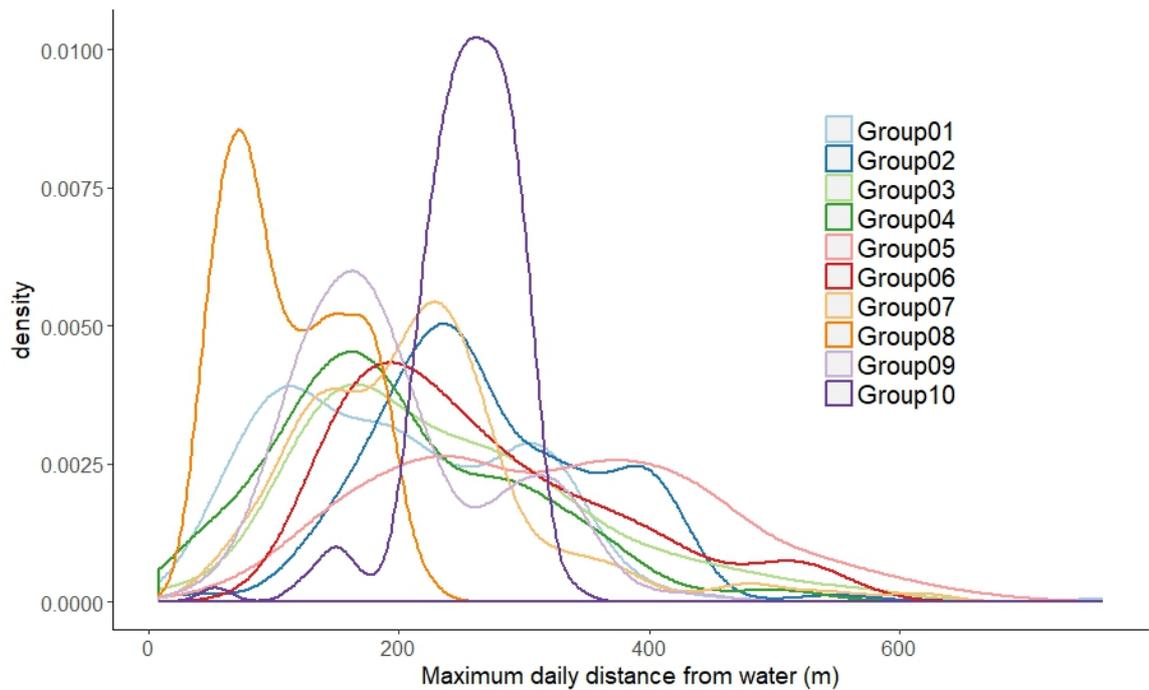
Figure 5.9   Maximum daily distance travelled inland by proboscis monkeys before returning to the river to sleep.

Movement patterns changed as individuals moved further from edges (Fig. 5.10). Turning angles were widest closest to the river (~1.8 radians or 100 degrees) then abruptly dropped to ~1.0 (57 degrees) around 200 m from the river (edf = 4.85, F = 447.30, p<0.001): this indicated a change from tortuous to straighter movement. Simultaneously, speed increased up to 70 m/h (edf = 4.97, F = 1188.00, p<0.001). Once more than 300 m from the water, turning angles steadily became more tortuous, increasing to ~1.3 (74 degrees) and speed decreased to 25 m/h. Turning angle (edf = 3.29, F = 6.39, p<0.001), and speed (edf = 4.62, F = 21.10, p<0.001) both followed similar patterns when moving away from plantations as from water. However, turning angles were narrower when close to plantations (up to 1.4 radians or 80 degrees), whereas close to rivers they were almost 2 (115 degrees), indicating less tortuous movements closer to plantations. Speed was also generally faster when close to plantations than it was when close to water – when <100 m from plantations, speed varied between 45 and 55 m/h (cf. 20-50 m/h near water).
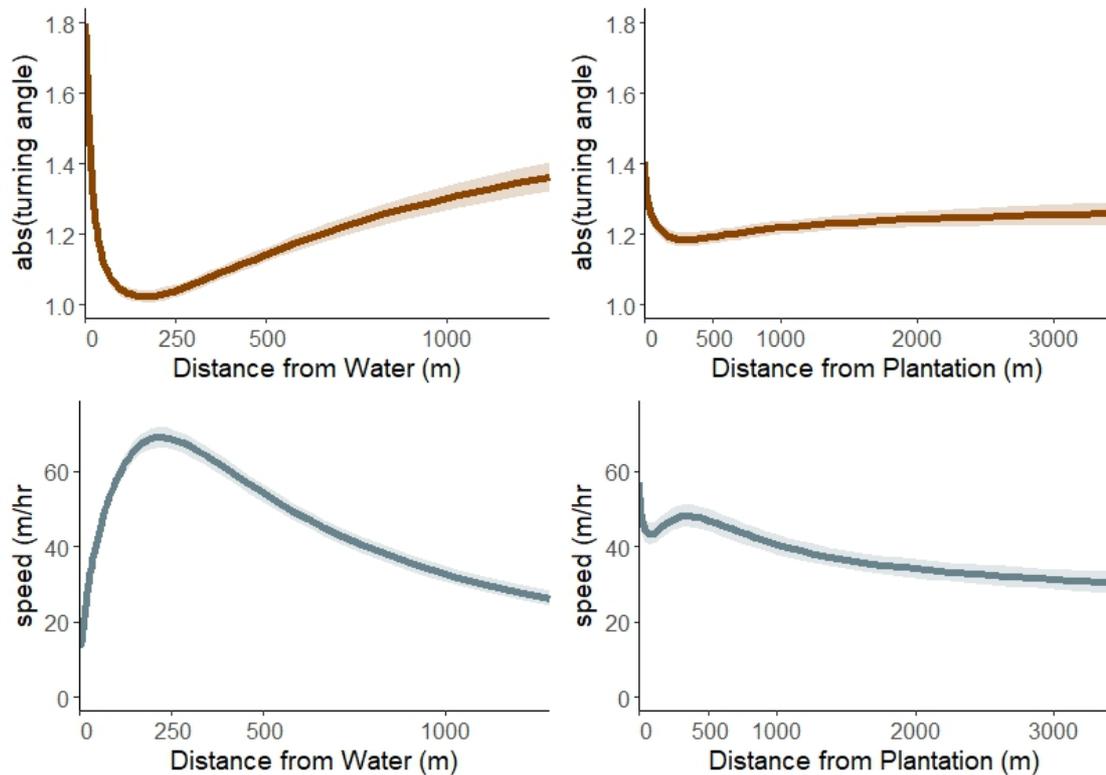
Figure 5.10 Response of turning angle (top) and speed (bottom) as proboscis monkeys' proximity to edges change. Shaded regions represent the 95% confidence interval around the predictions.

### 5.3.4 Movement in high intensity and recursion areas

The average residence time (± SE, N = 10) in the high intensity patches (ID patches) was 3.0 (± 0.2) h, and average recursion time was 14.9 ± 2.2 and 8.6 ± 2.0 days for ID and RD patches respectively (Fig. 5.11, see Table A4.1 for individual differences). Average movement speeds (± SE, N = 10) inside ID patches were much slower than outside the patches (45 (± 3) and 72 (± 3) m/h, respectively), but more similar for RD (68 (± 4) and 61 (± 2) m/h, respectively). The points that were in both ID and RD patches had slower speeds inside than outside (45 (± 4) and 72 (± 2) m/h, respectively). Turning angles followed the inverse pattern. Turning angles were wider inside ID patches (in: 1.34 (± 0.02), out: 1.15 (± 0.02)) and inside the IDRD patches (in: 1.28 (± 0.06), out: 1.20 (± 0.02)), indicating more tortuous movement inside ID & IDRD patches than outside. Finally, turning angles are tighter inside the RD patches than outside (1.09 (± 0.04) and 1.26 (± 0.02), respectively), indicating more directed movement within RD patches. Time spent inside ID patches decreased during times

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with more flowers (best-fit: ~flowers; coeff = -40.83, SE = 14.48, t = 2.82, p = 0.01), but the time between visits to ID or RD patches did not significantly change in response to environmental variables (ID best-fit: ~flowers, coeff = -55.73, SE = 38.65, t = -1.444 p = 0.16; RD best fit: ~young leaves, coeff = 0.27,SE = 0.25, t = 1.06, p = 0.30).
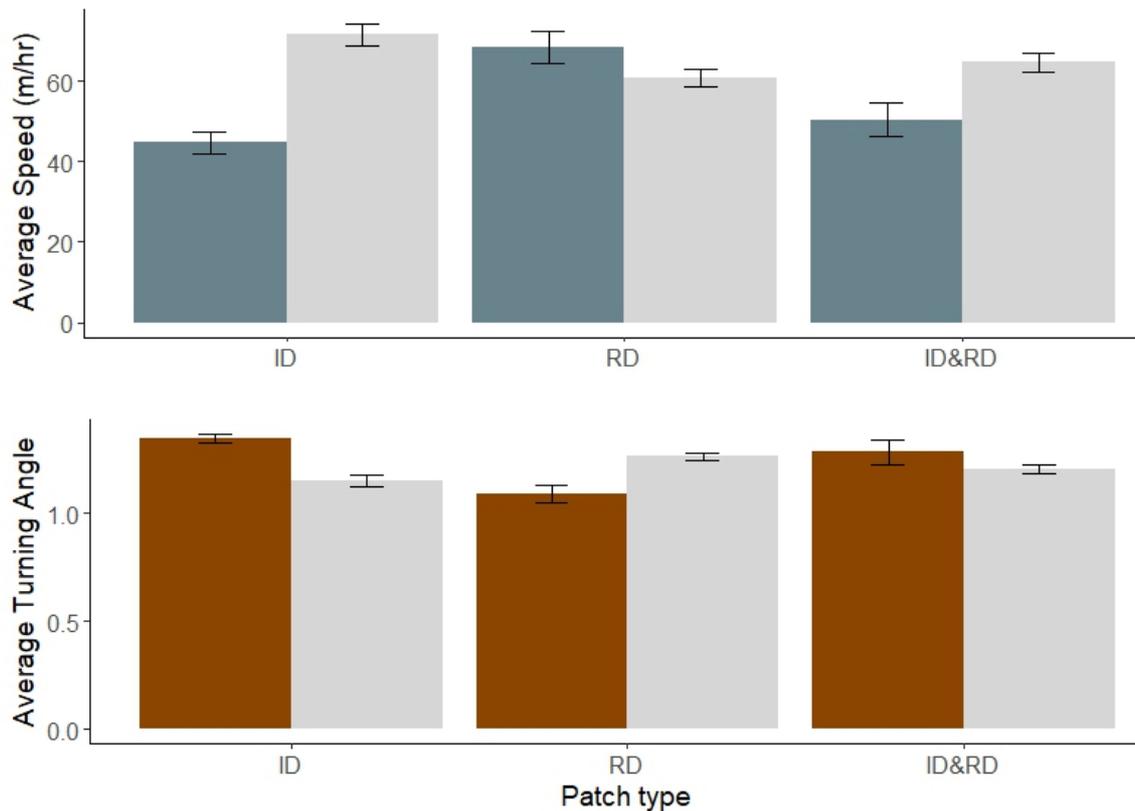


Figure 5.11 The average travel speed (top) and turning angle (bottom) of proboscis monkeys inside (dark) and outside (light) high use patches. Error bars represent the standard error of averages (N = 10 individuals).

## 5.4 Discussion

This study focused on how environmental factors or proximity to forest edges influence the food availability, movement patterns and location of sleeping sites of proboscis monkeys. Increased rainfall was associated with decreased distance travelled, more tortuous turning angles and increased availability of fruit and flowers. There was little or no association of environmental factors with travel speed or straightness. Increased young leaf availability was not associated with changes in rainfall, but was with shorter

daily distances travelled. The animals moved faster with less tortuous paths when they were closer to plantations than to water, and slower and more tortuous when they were inside high intensity patches. Sleeping site selection was associated with environmental factors, whereby proboscis monkeys slept inland during drier periods, brighter moon phases and warmer temperatures. It is suggested that proboscis monkeys live in habitats that are suitable for their dietary needs throughout the year, but that human behaviour and changes to their forest have the greatest impact on their movements.

### 5.4.1 General movement patterns of proboscis monkeys

Most colobine species have daily path lengths <1000 m (Kirkpatrick et al. 1998). The daily distance travelled by proboscis monkeys fits into the higher end of this spectrum, with an average DPL of 937 m. The DPL estimates were slightly higher than previous proboscis monkey records (799 m Matsuda et al. 2009a and 910 m Boonratana 2000), and included some of the highest daily path lengths recorded for colobines (Kirkpatrick et al. 1998). Unlike Matsuda et al. (2009a), the current study had fewer short DPL days and a more similar distribution between short DPLs (6%: 0-500 m) and long DPL days (5%: >1500 m). Daily path lengths greater than 1800 m have not previously been reported for proboscis monkeys (Boonratana 2000; Matsuda et al. 2009a). However, 1.7% of DPLs in this study exceeded 1800 m (40 events total from 8 of the 10 groups), with a maximum of 3037 m, which may indicate a poorer quality habitat (Di Fiore 2003).

Boyle et al. (2009) found that Northern bearded saki monkeys (*Chiropotes satanas chiropotes*) travelled in more 'circular' patterns when in smaller fragments, returning to areas close to the daily starting point (low straightness index, SI). No relationship was found for proboscis monkeys (Fig. A5.1). Proboscis monkey routes were slightly more circular than saki monkeys living in continuous forest (0.39 and 0.43 respectively).

Although the majority of the proboscis monkeys in the current study had similar SI values (0.36-0.42), there were three exceptions. First, the group with smallest available forest area (Table 4.2, Group 8) had the most straight daily paths (SI = 0.48), which may be because the majority of the forest was too narrow (50 – 100 m) to allow for more circular movements. In addition, this group also had the longest maximum DPL (>3000 m) of all groups, and one of the highest recorded amongst colobines (Kirkpatrick et al. 1998). The other exceptions were the two groups with the most circular daily paths (Group 10: SI = 0.21, Group 2: SI = 0.28) were also the fastest moving groups with the longest average DPLs. The proboscis monkey group with the smallest SI (Group 10) was in the second smallest forest block, which followed the expectation as per Boyle et al. (2009). However, Group 2, with the second smallest SI, was living in the largest available forest block, which seemingly contradicted expectations. The range of this group was along a tributary heavily utilised for tourism (Fig. 5.7, panel 2), and because of the high levels of boat traffic along this tributary, a small SI may suggest that the group was limited to use one bank with <350 m forest width rather than additionally utilising the larger forested area on the other side, as was observed with a group along a different tributary of similar width (Fig. 5.7, panel 3). Proboscis monkey groups had been observed crossing this tributary regularly in the past (Matsuda et al. 2008), but as boat traffic has been steadily increasing over the years (Leasor and Macgregor 2014), researchers and tour guides have commented that they observe groups crossing less often than in the recent past (Awareness, Education and Tourism Small Group Discussion: International Workshop for Proboscis Monkey Conservation, Kota Kinabalu, Sabah, 20-25 February 2017). Boat traffic has been shown to discourage river crossing and reduce population density of proboscis monkeys (Yeager 1992), and may be essentially dividing the habitat and disrupting proboscis monkey ranging activities, resulting in ranging behaviour that would be indicative of living in smaller forest fragments. Regulations of boat traffic for tourism

should be a priority when developing a management strategy to avoid effectively isolating populations or groups within their habitat.

### 5.4.2 Seasonal movement patterns

The spatial and temporal distributions of food resources influence the ranging patterns of primates (Di Fiore 2003; Matsuda et al. 2009a; Santhosh et al. 2015). Colobine monkeys tend to travel further and feed more during times when high energy foods are available, and travel less during periods of high leaf consumption to maximise digestion and reduce energy expenditure (banded leaf-monkeys *Presbytis melaphos,* see Bennett 1986; king colobus *Colobus polykomos*, see Dasilva 1992; northern plains gray langurs *Semnopithecus entellus,* see Newton 1992; golden snub-nosed *Rhinopitecus roxellana,* see Li et al. 2000, Angolan black-and-white colobus *C. angolensis ruwenzorri*, see Fashing et al. 2007). This pattern was thought not to hold true for proboscis monkeys (Boonratana 2000; Matsuda et al. 2009b). It was put forward that DPL may increase during times of high young leaf consumption because more travelling increases the diversity of leaves consumed, preventing the accumulation of secondary compounds (Agetsuma and Noma 1995; Matsuda et al. 2009b). However, the current study found that proboscis monkeys did seem to follow the typical pattern of leaf-eating colobines, supporting the idea that proboscis monkeys decrease travel during periods of high young leaf consumption as they need to allocate more time to digesting fibre-rich foliage to obtain the required nutrients (Zhou et al. 2007), and increase daily distance travelled during periods of high fruit availability, which are more efficiently digested plant parts and less evenly distributed (Zhou et al. 2007; Santhosh et al. 2015; Thiry et al. *unpublished manuscript*). Inconsistent results within a species could reflect how primates cope with resource scarcity, including changes in ranging behaviour, adjusting diet or time spent in feeding patches, or may be correlated to changes in habitat quality between studies correlated or different climatic conditions (Di Fiore 2003).

In the current study, DPL showed a negative relationship with the availability of young leaves and a positive relationship with the availability of fruit. Perhaps due to the difference in the amount of rainfall between the studies, rainfall was more important here than for Matsuda et al. (2009b). During the study period for Matsuda and colleagues (2005-2006), there was lower annual rainfall (2509 mm) than four of the five years of the current study, with two thirds of months recording <200 mm of rain (cf. only 35% of the months <200 mm in the current study). The main effect of food availability on ranging behaviour seen by Matsuda et al. (2009b) could be a reflection of variation in rainfall between the seasons during that study period. The observed differences in seasonal variation of rainfall between studies may therefore make comparisons more difficult.

Rainfall was also associated with changes in daily movement, but the relationship was complex. Proboscis monkeys tended to sleep closer to the river during wetter periods, moved less (shorter DPL) and had more tortuous daily paths. Concomitantly, there was evidence that fruit availability increased with rainfall, but was also associated with increased movement, in an apparently contradictory result. Unpacking this relationship will require further work. It may be that rainfall has contrasting effects at different temporal scales, with proboscis monkeys being less mobile on wet days, but the general changes of food availability during the wetter months of the years may on average see increased mobility. Distinguishing climate and food availability, and helping to resolve the causal relationships, would be a valuable next step.

### 5.4.3   Environmental factors influencing location of sleeping sites
Proboscis monkeys are known to sleep near rivers, lakes, and in mangroves, and the characteristics of the sleeping trees selected along rivers have been widely documented (e.g., Bernard et al. 2010; Thiry et al. 2016; Feilen and Marshall 2017). Proboscis monkeys slept an average of 52 m from the water (including inland

sleeping), which is consistent with previous studies stating that they sleep within 50 m from the river (Bernard et al. 2010). Evidence from previous studies suggests that proboscis monkeys sleep further inland following extreme weather conditions viz. heavy rains or flooding (Boonratana 2000; Matsuda et al. 2009a). Although river level was not measured during the current study, there did not seem to be a noticeable association between periods of flooding and inland sleeping (*pers. obs.*). River levels in the study area tend to be affected mainly by rainfall upstream in the catchment, rather than locally, and it was notable that proboscis monkeys actually tended to sleep closer to water on wetter days.

The effect of moonlight on primates has mainly been studied in nocturnal or cathemeral primates (e.g., Nash 2007; Starr et al. 2012). In a review on sleep-related behavioural adaptions in anthropoid primates, Anderson (2000) discussed general behavioural changes of diurnal primates due to moonlight, such as an increased night-time activity during bright moonlight that could reflect predator activity or other environmental disturbances. Increased nocturnal travel and feeding behaviours were observed for West African chimpanzees (*Pan troglodytes verus*) during fuller moon phases in the dry season (Pruetz 2018), whereas low-level nocturnal activities appeared unaffected by moon phase for vervet monkeys (*Chlorocebus pygerythrus*) and olive baboons (*Papio anubia*) (Isbell et al. 2017). However, the influence of moon phase on sleeping site selection by diurnal primates has not been explored to date, and so the result here that individuals sleep further inland as the moon waxes is an important finding. Sleeping inland may make proboscis monkeys less conspicuous at night, as being along the riverbank during a bright moon would leave them more visible and exposed, such as to their main terrestrial predator, the Sunda clouded leopard (Matsuda et al. 2009c). Indirect observations of predation events (e.g. finding freshly injured or killed individuals in early morning) are consistent with clouded leopards hunting overnight or at dawn (Otani et al. 2012; *pers. obs*.). Although two directly observed clouded leopard

predation events on proboscis monkey were recorded during day-time hours (Matsuda et al. 2009c), this should be considered quite rare due to the relatively few observations of clouded leopards being active during those hours (Hearn 2013; M. Evans, *unpublished data*). Therefore, it would still be considered more efficient for proboscis monkeys to reduce predation risk during clouded leopard's usual active hours.

Bright moonlight may also disrupt primate sleeping rhythms due to increased human activity (Anderson 2000). There appears to be more boat traffic on the Kinabatangan River during times when the moon is bright, either for fishing or hunting (*pers. obs.*), and sleeping inland may counteract this disturbance to sleeping wildlife. Anecdotal observations support the idea of a disturbance effect. For example, a temporary fishing camp set up along the riverbank in Lot 7 was associated with proboscis monkeys sleeping 1-1.2 km inland for more than one week. Sleeping site selection may also be affected by other types of disturbance, such as the visit of a large herd of elephants (*Elephas maximus borneensis*) on the river bank of Lot 7, which was associated with a proboscis monkey group sleeping ~1 km inland for five days.

Inland sleeping may also be a response to climate. The thermoregulatory response to heat stress in primates is less studied than in other animals (Pruetz 2018). There is some evidence for diurnal behavioural adaptations, such as increased resting and grooming in chacma baboons (*P. hamadryas ursinus*) during times of increased heat stress (Hill 2006). Increased nocturnal behaviour during fuller moon phases was only observed during the dry season for West African chimpanzees, and was thought to be an adaptation to avoid the high temperatures in savannah environments (Pruetz 2018). Forest edges tend to have higher ambient temperature than inside (Broadbent et al. 2008), and therefore proboscis monkeys may be adapting their sleeping patterns to escape the heat by going further inland when maximum temperatures are highest.

### 5.4.4 Edge effects on daily movement

Due to the tendency to return to the river to sleep, it was expected that the daily distance that the proboscis monkey groups would travel before they need to turn around and return to the river would be similar between groups. This was enhanced by the observation that they tended to move at similar speeds among groups (Table 5.2) and throughout the day (data not shown). Apart from one group, all others travelled on average ~200-350 m away from the river each day, and the average time the maximum distance was reached was around 12:00. In accordance with Matsuda et al. (2009a), groups did not range more than 780 m from the water if they were returning to the water to sleep. For the group that lived in the thin forest strip with maximum width of ~300 m (Group 8), the average MDD was 110 m, but there was still a high frequency of points that reached ~200 m.

Many studies have investigated the relationship primates have with forest edges by focussing on topics such as density and distribution (Lehman et al. 2006; Grow et al. 2013), gastrointestinal parasite infection (Chapman et al. 2006a), home range size and daily path lengths (Huang et al. 2017), or changes in diet or activity patterns (Boyle et al. 2009; Kulp and Heymann 2015; reviewed in Chapter 2). These studies generally compared fragmented and continuous forests, but studies that examine how primate movement changes with their proximity to forest edges are lacking. Proboscis monkeys moved more quickly near forest-plantation edges, as expected due to their observed low preference for such areas (Fig. 4.5). Increased movement has also been observed in areas that are used less often by black crested gibbons (*Nomascus concolor*) (Ni et al. 2018), and olive baboons were observed moving faster and straighter in more disturbed areas (i.e. on roads or in less dense vegetation) (Strandburg-Peshkin et al. 2017). The wider turning angles and slower speeds closer to water relative to plantation may be because proboscis monkeys are sleeping near the water. Once proboscis monkeys get close to the river (ca. 50 m), they only have to move slowly before finding and settling into their sleeping tree. This was observed by a slightly

higher frequency of points within 50 m of the river the few hours before sunset (16:00-17:00) than the rest of the day (apart from early morning). The sharp drop in turning angle and corresponding increase in speed with increasing distance from water, peaking at ~200 m distance, suggests more active and directed movements to and from the riparian strip. After 200 m, the movement became less directed, reflecting perhaps a slower foraging pattern (higher turning angles and slower speeds).

### 5.4.5 *Movement patterns of high use areas*

On average, proboscis monkeys used high intensity patches for three hours at a time and visited about every two weeks, whereas highly frequented areas were visited approximately weekly. An increase in DPL during times of high fruit availability could indicate patch depletion (Snaith and Chapman 2005), but because recursion rates to high intensity patches were not influenced by month, these areas were not likely being used more heavily during different times of the year. This could mean that food resources were spatially spread out so that even during times of high fruit availability, proboscis monkeys did not need to remain in small areas for longer, which had been seen in previous studies (Boonratana 2000; Matsuda et al. 2009a). The spatial spread of food resources is also supported by the increased DPL observed during times of high fruit availability, whereby groups travel more to find food and do not stay in one small area. It could also indicate that there was less risk of resources being over-exploited. If proboscis monkeys had used high intensity areas more often or for longer periods during times of low food availability, then over-exploitation of resources might be expected.

It has been clearly demonstrated that primates are capable of remembering food locations (Garber and Jelinek 2005; Janson and Byrne 2007). How they retain this information has been much discussed (Bonnell et al. 2013). Along with their ability to remember areas within their habitat, primates employ movement strategies depending

on the availability and distribution of food resources (Reyna-Hurtado et al. 2017). When food resources are abundant and evenly distributed (e.g. leaves), primate movement strategies may be characterised as randomly derived (i.e. Brownian movement: step lengths show an exponential distribution with random turning angles) (Reyna-Hurtado et al. 2017). When food resources are patchily distributed or rare (e.g. fruits), a non-Brownian movement strategy (e.g. Levy walk: series of short-similar lengths interspersed with occasional very long steps) may be demonstrated (Ramos-Fernández et al. 2004). Although it is generally understood that movement strategies can be predicted from a primate's diet (i.e. folivores follow a more Brownian strategy and frugivores follow a more non-Brownian strategy), these strategies are now understood to adjust to changes in food availability (Schreier and Grove 2010; Reyna-Hurtado et al. 2017). It was not possible to estimate movement strategies using the data collected in the current study as hourly GPS fixes were too coarse a scale (Plank and Codling 2009). However, it is still be possible to identify some basic movement patterns of proboscis monkeys based on the difference of movement when inside or outside of high use areas. As expected, proboscis monkeys had slower and more tortuous movements inside high intensity patches, as these were areas more likely to be used for feeding and resting. Movement outside high intensity areas were less tortuous and faster, suggesting they were directing their movements towards food/rest sites. Recursion areas tended to have slightly faster and less tortuous paths than outside, although the difference in speed was not as great. These results suggest a functional difference between high intensity and recursion areas. As recursion areas are not necessarily being used for extended periods of time, the less tortuous paths could indicate these areas were important as routes to other areas. For the areas that were used both frequently and intensively, speeds were also slower and more tortuous turning angles than those outside.

*5.4.6 Future considerations*

On the basis of GPS movement data, proboscis monkeys do not seem to be over-exploiting high use areas in this study, and therefore are likely to have sufficient food resources throughout the year and across seasons. However, human activity is expected to have a major impact on proboscis monkey ranging behaviour and food availability through climate change (Struebig et al. 2015). Although the pronounced and unpredictable seasonality of fruiting in Borneo is already largely affected by El Niño-Southern Oscillation (ENSO) events, the predicted influence of climate change on rainfall patterns, exacerbated by deforestation, could further accentuate the effects of ENSO (Wich and van Schaik 2000; Struebig et al. 2015; Hanya and Bernard 2016; Korstjens and Hillyer 2016). By the end of this study, the total annual rainfall was half of that in the first year, and was leading into an ENSO year (Chen et al. 2016). The reduction of rain and strengthening of ENSO events due to climate change would result in longer time between fruiting events, but also an increase in the frequency of forest fires (Wooster et al. 2012); previously burned forests have been shown to be unsuitable habitat for proboscis monkeys (Sha et al. 2008) and other Bornean primates (maroon langur *Presbytis rubicunda* and Bornean white-bearded gibbon *Hylobates albibarbis*, Singh et al. 2018). During particularly dry years (e.g. 2015), proboscis monkeys had been seen coming down to the riverbank to drink (*pers. obs.*) and could be at increased risk of predation by crocodiles. As seasonality becomes more pronounced in Borneo, establishing and maintaining wide riparian buffers will be crucial in reducing risk and severity of fire, and improve post-fire recovery (Jain et al. 1996; Agee 1998).

Proboscis monkeys move differently near forest-plantation edges than forest-river edges, and this needs to be considered when developing conservation plans to ensure forests are of sufficient size to contain enough food resources, and that does not push them into stressful environments to access (i.e. faster movements near plantations). Along with improving the structural integrity of the riverbanks (Horton et al. 2017) and

protecting existing habitats (Abram et al. 2014), reducing disturbances along riverbanks and plantation boundaries could also be considered. Proboscis monkeys would then be able to take advantage of the high-quality food sources associated with forests exposed to increased sunlight without having to adjust their ranging behaviour. The adaptable and resilient nature has allowed proboscis monkeys to survive thus far in a habitat with unpredictable seasons and that has experienced major forest loss. But for proboscis monkeys to continue being a focal species for tourism in Borneo, habitat protection and restorative actions must be taken alongside monitoring human behaviour to limit the additional disturbances proboscis monkeys may face due to their tendency to spend time along forest edges. How proximity to non-riparian edges confounds proboscis monkey movement can be used to strengthen the data provided to government agencies responsible for putting in place and enforcing conservation management plans.

# Chapter 6 Combining drones and satellite tracking as an effective tool for informing policy change in riparian habitats: a proboscis monkey case study

## 6.0 Abstract

Rapid reaction times to undesirable events are becoming increasingly important for the protection and conservation of habitats and species. This study demonstrates how Unmanned Aerial Vehicles, or drones, and satellite tracking of individual animals can be combined to identify important conservation issues (e.g. deforestation). When quickly disseminated, the information can lead to a rapid change in conservation policy. An adult male proboscis monkey, belonging to a one-male social group, was GPS tracked for six months in Sabah, Malaysian Borneo during 2012. Riparian habitats featured heavily (25.4% of total time, 88.6% of all sleeping sites) in its group's home range. A fixed-wing drone was used in 2015 to map the habitat in high-resolution. These data revealed that 47.5 ha of forest had been cleared shortly before the drone flights. GPS tagging data revealed the importance of this area for a one-male proboscis monkey group. A total of 30.1% of the proboscis monkey's home range area had been cleared, as well as 11.4% of sleeping sites. Furthermore, drone images revealed that the felling extended to the river's edge, disregarding water resources laws requiring riparian reserves of a minimum of 20 m. Following this discovery, a press release including drone imagery combined with GPS data was published linking habitat destruction to a species that is economically important for the tourism industry in Sabah. The day following dissemination of the data, the Sabah State Government ordered an immediate cessation on further land clearing at sensitive riparian reserves along the river. The current study proposes that this combination of satellite and aerial data provides the potential for an effective conservation tool for endangered, iconic and economically important species. This visually compelling data, feasible over large spatial scales, can directly inform policy change in a quick and timely manner.

## 6.1 Introduction

Human activities can result in the removal of wildlife from their natural habitats, as well as the degradation of habitats due to legal, accidental and illegal human activities (e.g., logging, fire, hunting, pollutant spills) (Butchart et al. 2010). The ability to monitor habitats in near real-time has become increasingly important for the protection and conservation of broad ecosystems, specific habitats, or even individual species. Once an infraction or undesirable event has been detected, the reaction times of the administration, enforcement or policymakers can be crucial for continued protection or management of an area (Navarro et al. 2012). By being able to prevent or curtail detrimental events, future impacts are minimised and are, therefore, easier to manage (Manyangadze 2009).

Environmental monitoring networks have been established for a variety of purposes, such as monitoring water quality, detecting harmful algal blooms, or detecting forest fires. These networks provide a source of data for policymakers and governmental agencies, as well as facilitate in rapid and effective management responses (Glasgow et al. 2004; Manyangadze 2009; Navarro et al. 2012). Real-time remote monitoring, in particular, has advanced the field of animal movement research (Wall et al. 2014). Satellite tracking is a powerful tool that can highlight the home range nuances of a species without observer bias (Chapters 4 and 5). It can also provide evidence of resource utilisation (e.g. for feeding or sleeping) that may otherwise be difficult to obtain on shy or cryptic species, or in logistically remote locations or challenging terrain (Chabot and Bird 2015; Schweiger et al. 2015; Chapter 5). Satellite tracking can provide real-time locations of multiple animals, which can be used to detect changes in movement patterns, or send alerts due to a cessation of movement, allowing the researcher to respond accordingly (Wall et al. 2014).

Autonomous unmanned aerial vehicles (referred to as "drones" hereafter) are a remote-sensing platform commonly used for near real-time imagery of an area. Applications for drones are continuously diversifying, and they are being used increasingly as a tool to supplement more traditional methods in wildlife studies (see reviews by Chabot and Bird 2015; Linchant et al. 2015). Drones are also practical for wildlife habitat research and monitoring due to their ease of use, low cost, low environmental impact, versatility and their ability to cover areas which may otherwise be inaccessible (Dufour et al. 2013; Evans et al. 2015; Ivošević et al. 2015). Many of the vegetation-related studies using drones have focussed on wetlands, coastal areas and riparian habitats, detecting finer-scale habitat details undetectable by ground surveys, leading to improved habitat classifications and vegetation biomass calculations (Husson et al. 2014; Chabot and Bird 2015). Through frequent and repeatable flights, drones have also been used in the detection of illegal activities. These range from logging, mining, poaching and habitat encroachment (Coulter et al. 2012; Paneque-Gálvez et al. 2014; Chabot and Bird 2015), to detecting camps or campfire smoke in areas where human presence is prohibited (Koh and Wich 2012).

Illegal activities are of particular concern for riparian zones, which are amongst the most severely altered and degraded habitats across the world (Nilsson and Berggren 2000). Human settlements tend to develop along waterways because of the importance of rivers for transportation and movement (Yeager and Blondal 1990; Meijaard and Nijman 2000a). However, riparian zones have a fundamental function in the ecosystem, and its removal or alteration can have negative effects on existing ecosystems (Fernandes et al. 2011; Kuglerová et al. 2014). Furthermore, riparian zones often have higher levels of animal and plant diversity than non-riparian forests and can act as important corridors during migration and dispersal (Naiman et al. 1993; Spackman and Hughes 1995). Although there is no standard optimal design for the ideal width of a riparian zone, there is often national or regional legislation in place to

maintain some level of riparian protection (Blinn and Kilgore 2001; Lee et al. 2004; Kuglerová et al. 2014).

Proboscis monkeys (*Nasalis larvatus*) are large-bodied folivorous primates endemic to the island of Borneo and are heavily associated with riverine, lake, swamp and mangrove forests. Proboscis monkeys tend to use forests near rivers as predator protection (Thiry et al. 2016) or for feeding on higher-quality food (Thiry et al. *in review*). They generally do not travel more than a half day's journey away from water before returning back (Fig. 5.9). Due to their habitat preferences, the majority of studies on proboscis monkeys have been restricted to riverbank observations (e.g. Bennett and Sebastian 1988; Bernard et al. 2010; Feilen and Marshall 2017). Proboscis monkeys can live in disturbed or secondary forest, but generally avoid severely disturbed areas, agricultural areas, extensive grasslands and human settlements (Salter et al. 1985; Bernard and Zulhazman 2006). Proboscis monkeys are one of the focal species for tourism in Borneo (Leasor and Macgregor 2014), but only 15% of proboscis monkeys in the Malaysian State of Sabah are found in fully protected areas (Sha et al. 2008).

The largest known population of proboscis monkeys in Sabah is in Lower Kinabatangan Floodplain, more than one-third of which is found in unprotected areas (Sha et al. 2008). The forests have varying degrees of protection, with about 27,000 ha in the Lower Kinabatangan Wildlife Sanctuary (LKWS) and 15,000 ha as Virgin Jungle Reserves (VJR), interspersed with about 10,000 ha of unprotected (private) or state forest (Ancrenaz et al. 2004). The forested areas are surrounded by large and small-scale agriculture, mainly for oil palm (*Elaeis guineensis*), as well as human settlements. A 20 m riparian zone along both banks of every river greater than 3 m in width is designated as a riparian reserve under Sabah's Water Enactment 1998 Section 40(1), which includes the Kinabatangan River and its estuaries or tributaries (State of Sabah

1998). Furthermore, the Land Ordinance (Sabah Cap 68) specifies that riparian reserves in Sabah are the property of the State (State of Sabah 2013).

Combining proboscis monkey GPS tracking data with high-resolution remote sensing datasets, such as those obtained using drones, can potentially provide opportunities for detailed analysis of interactions between animals and their habitat (Schweiger et al. 2015). The aims of this study are to (1) demonstrate the increased effectiveness of drone datasets when paired with the satellite tracking data of an endemic, endangered species to rapidly raise awareness and facilitate policy changes regarding riparian habitat destruction; (2) compare the extent of forest clearing in the area after the tracking period was complete to investigate the potential impact deforestation could have on the ranging of a one-male group of proboscis monkeys; and (3) show how these visually compelling data can engage the general public and initiate discussions on policy reform and conservation action.

## 6.2   Forest imagery

In July 2015, 273.5 ha of unprotected forest were mapped using a fixed-wing drone. This forest connects the protected forest blocks under the LKWS jurisdiction (Lot 3) and Pangi VJR, and provides important habitat for many of Borneo's symbolic species, including proboscis monkeys and orangutans (*Pongo pygmaeus*) (Ancrenaz et al. 2004), and serves as an important corridor for elephants (*Elephas maximus borneensis*) (Estes et al. 2012). The forest extends along the south bank of the main river and is bisected by a tributary (Fig. 6.1).
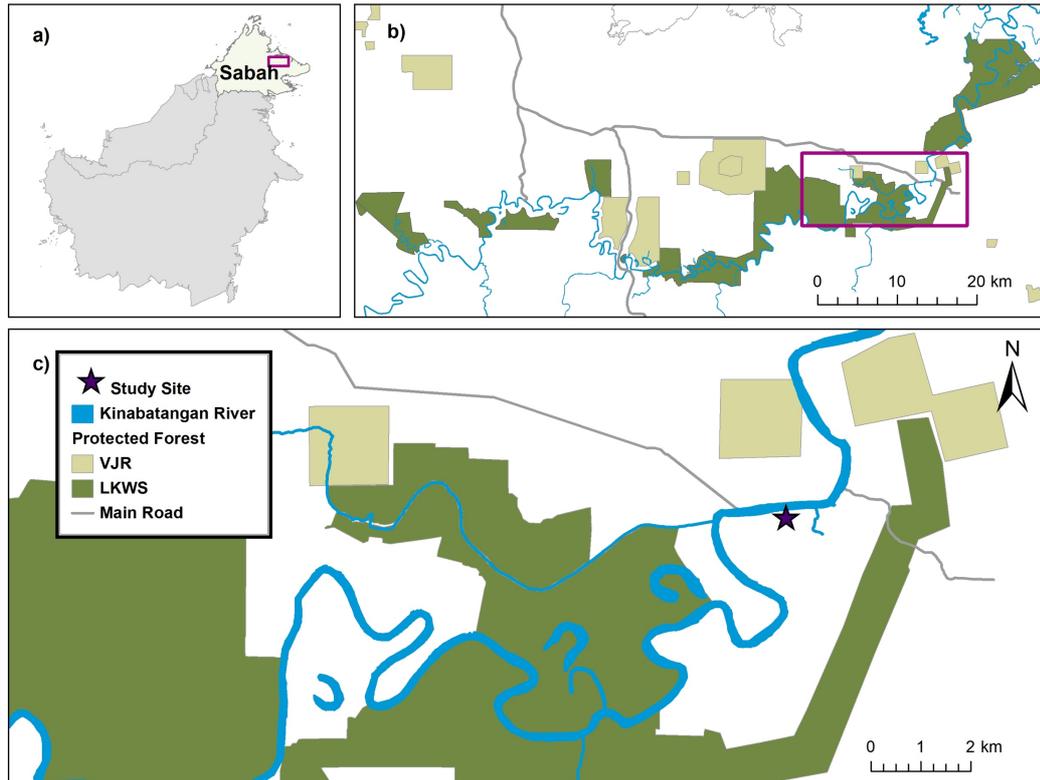
Figure 6.1 Study site (c) within the Lower Kinabatangan Floodplain in Sabah, Malaysian Borneo (a). Dark areas indicate protected forest within the Lower Kinabatangan Wildlife Sanctuary (LKWS) and light areas indicate protected Virgin Jungle Reserve (VJR) (b). The white area represents a mixture of private and state forest, human settlements and large- and small-scale agriculture.

Images from Google Earth Pro (Google Earth 7.1 2014) were digitised and processed in ArcGIS 10 (ESRI 2011) to estimate the extent of forest prior to the most recent logging. Areas that were already non-forested prior to the clearing event were determined based on ground-truthing from surveys in 2012 and by the size of oil palm trees or the condition of the non-forested areas in the 2014 Google Earth image (e.g., worn houses, well-established gardens). As the annual dynamism (mean tree mortality and recruitment) in Southeast Asian tropical forests is 1.59 ± 0.39% (Phillips et al. 1994), the 2014 image was assumed to be representative of the forest cover during 2012. The non-forested areas were digitised in ArcGIS 10, and the area calculated and subtracted from the total forested area based on the Google Earth image.

A drone (Bormatec-MAJA: Bormatec, Mooswiesen, Ravensburg, Germany) was fitted with a Canon S100 digital camera (Ota, Tokyo, Japan) that was customised with firmware enhancement created using a Canon Hack Development Kit (CHDK). To obtain >60% sequential picture overlap, the flights were flown at an altitude of 315 m, with transects 170 m apart, and an inter-image gap of 3 sec.

Of the area covered by the drone, 13.1 ha were already non-forested during the satellite tracking period in 2012, consisting of houses, gardens, and small-scale oil palm plantations. From the drone images, a further 47.5 ha had been cleared in late May 2015, accounting for 18.3% of the forested area (Fig. 6.2).



Figure 6.2   The 273.5 ha area surveyed by the drone with corresponding pre-logged images in 2012 (top) and the logged areas detected by the drone images in 2015 (light brown, bottom); dark brown indicates the areas that were not forested during the tracking period of the proboscis monkey (2012).

## 6.3   Home range & habitat loss

Within the unprotected forest study site, an adult male proboscis monkey had been fitted with a GPS collar in May 2012 and tracked for 169 days. The utilisation distribution was estimated using biased random bridges, with the total home range defined by the 90th percentiles of the utilisation distribution, and core range as the 50th percentiles (see Section 3.2 for detailed methodology). Sleeping sites were defined as the GPS fixes at 19:00.

The home range of the proboscis monkey group was estimated to be 49.8 ha (core range 14.6 ha), which fell entirely within the area surveyed by the drone. The riparian reserve was heavily utilised, with 25.4% of all GPS points found within the legally defined 20 m riparian reserves, as were 88.6% of all sleeping sites (Fig. A6.1). A total of 9.4% (6.1 ha) of the core and home ranges fell within the legally protected riparian reserve (1.5 ha and 4.6 ha respectively).

A total of 0.98 ha of forest was cleared within 20 m of the main river and tributary. Of the riparian reserve cleared, 0.63 ha was within the proboscis monkey's home range. Approximately 11% of the sleeping sites were located in areas that were subsequently logged, of which all but one had been within the legally protected, government-mandated riparian reserve. Moreover, 30.1% of the total home range area (14.1 ha), and 24.9% of the core range area were cleared (3.6 ha) (Fig. 6.3). The proboscis monkeys entered the area that was later cleared in 2015 on 123 of the 169 tracking days, with an average of 4.6 (± 2.7) fixes (30.7%) a day within those areas (Fig. 6.3).
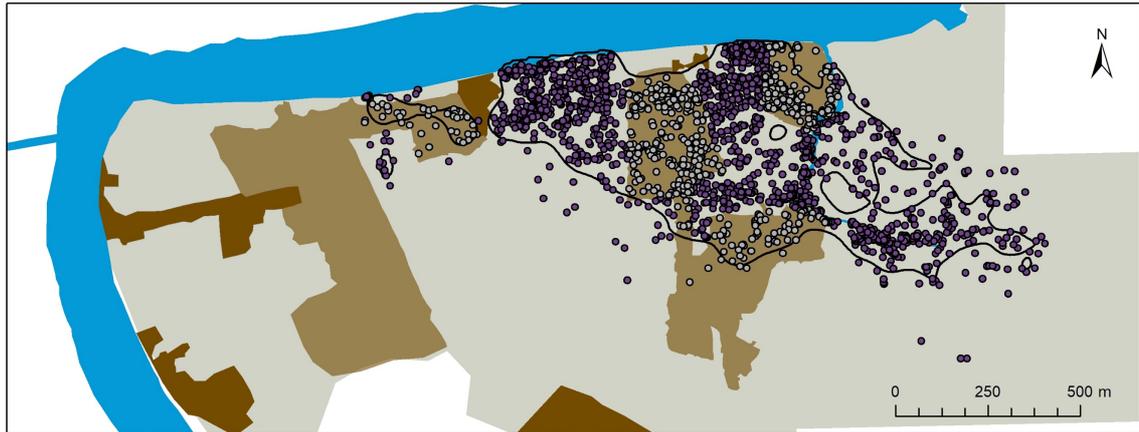
Figure 6.3   The forested area surveyed by the fixed-wing drone (grey) with corresponding pre-logged images in 2012 (dark brown) and the logged areas detected by the drone images in 2015 (light brown) along the Kinabatangan River (blue). Points indicate all GPS fixes from an adult male proboscis monkey throughout the tracking period (2012); white points indicate those affected by the deforestation event. Home range is delineated by the dark outline, as calculated using biased random bridge.

## 6.4   Dissemination of findings

A local landowner had cleared the riparian reserve under the Federal Government's Rubber Industry Smallholders Development Authority (RISDA) (Daily Express 2015). This Federal Government agency did not consult with the State Government's Wildlife Department, which manages the conservation areas adjacent and close to the private lands that were targeted by the RISDA scheme (H. Kler, *pers.com.*). Money was given as an incentive to clear the privately-owned property, and then the landowners were provided with rubber trees to plant on their land. A press release was prepared by DJS and BG, using the drone and satellite tracking datasets, to highlight the association of the habitat destruction to a species that is economically important for the tourism industry in Sabah (Borneo Post 2015) (Fig. 6.4). The press release was published in local and national newspapers, as well as on the main social media outlet (Facebook) for Danau Girang Field Centre. This Facebook page is regularly used for publishing press releases and other urgent conservation issues, and therefore any heightened interest in this particular press release would not simply be because it was the only urgent conservation issue posted. The impact the press release had through social

media was assessed by (1) the number of reaches per post (the total number of unique people the post had been served to) and (2) post engagements (the number of unique people who engaged in certain ways with the post; e.g., commenting, liking, sharing or clicking on particular elements of the post) (Wijedasa et al. 2013). The number of reaches and engagements of the press release posts were compared to those of all the other posts on the Danau Girang Facebook page, spanning from a month before and after the press release date.



Figure 6.4    Examples of the drone images used in the press release, showing the extent of clearing and removal of the riparian reserve in relation to proboscis monkey GPS fixes (white points).

There were 69 postings on the Danau Girang Facebook page from July 1 to August 31, 2015, four of which were based on the press release that included the drone and satellite imagery. The four posts based on the new imagery had more than three times as many reaches per post as the remaining 65 posts (mean number of users (± SE) = 6274 (± 4781) and 2039 (± 160), respectively). The average number (± SE) of post

engagements for the drone and satellite tracking posts increased to 573.5 (± 492.9) users from 165.7 (± 14.7) users. The following day, the Sabah State Government announced that there would be an immediate cessation of land clearing along sensitive riparian reserves in the Kinabatangan River (The Star 2015). A formal investigation was conducted which confirmed a number of infractions had taken place (Sabah Forestry Department 2016).

## 6.5   Discussion & conclusions

This study is the first known case of the effective combination of drone and satellite tracking data and its application in prompting immediate conservation action. The study showed the importance that riparian reserves have in the daily ranging and sleeping selection of proboscis monkeys, with a quarter of all points falling within the reserve. Furthermore, 89% of all sleeping sites were within this riparian reserve. The drone dataset was used to show that 30% (14.8 ha) of the group's total home range area was cleared in 2015, including 11% of their sleeping sites.

In addition to the quantitative data extracted, the visually compelling images captured by combining drones and satellite tracking can be utilised as a powerful awareness tool for the general public. Social media has the power to influence policymakers, increase accountability, and encourage shifts in behaviour. This can result in unprecedented government responses (Nghiem et al. 2012). Due to the long-established culture of wildlife consumption and insufficient knowledge in environmental issues in Asian-Pacific countries (Lo et al. 2012; Kwan et al. 2016), there is a disconnect between more tangible conservation issues, such as animal abuse, and more conceptual issues, such as deforestation or wildlife trade (Wijedasa et al. 2013). There is also a belief that pro-environmental behaviour is motivated by scientific background (Lo et al. 2012), and therefore does not have a widespread emotional impact on lay people. Public engagement on emotive issues, such as with animal abuse, is heightened when

compared to intangible long-term conservation issues (Wijedasa et al. 2013). For example, when an organisation highlighting conservation issues in Malaysia reported an incident showing a picture of tourists harassing a green sea turtle (*Chelonia mydas*), it generated a 405-fold increase in social media reaches, and caused an investigation and ultimately forced public apologies (Wijedasa et al. 2013). A week later, when the same organisation reported on the illegal wildlife trade of tiger claws, it generated only a 6-fold increase in social media reaches, as it did not spark the same emotional outrage as animal abuse (Wijedasa et al. 2013). Linking the culturally intangible issue of the destruction of a riparian reserve to the moral outrage involving a family unit of proboscis monkeys, one of Sabah's iconic species, invoked a strong emotional response. There was a threefold increase in the number of social media reaches, and an immediate cessation of land clearing ordered along sensitive riparian reserves along the Kinabatangan River. Furthermore, as the study site is one of the key destinations for local and international tourists to see proboscis monkeys (Fletcher 2009; Leasor and Macgregor 2014), public engagement may have been stronger than if the habitat loss had happened in a less popular area.

An issue highlighted in this case study is the importance of aligning conservation with economic incentives and regulation when multiple agencies are involved. The RISDA initiative promised participants economic incentives and rubber trees to plant once the area was cleared, but there was no responsibility or accountability taken by the initiative for any laws broken (H. Kler, *pers.com.*). The participants were not provided with information on land use or watershed laws prior to clearing (e.g. no cutting of riparian reserves, no open burning). Once an offence was committed, there was no legal or financial support to the local landowner, despite the role of the RISDA scheme in the situation, nor was the RISDA scheme required or requested to finance the reforestation of the riparian reserve (H. Kler, *pers.com.*). Furthermore, past experience has shown that planting rubber trees in this region has failed due to elephant conflict

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with young rubber trees (H. Kler, *pers. com.*), and therefore the clearing should have been avoided altogether, not just of the riparian reserve. It is important that when initiatives like this are proposed, all relevant parties (including wildlife and forestry departments) are involved in finding the most suitable areas and giving the participants the full information on the laws. This cooperation can maximise success as well as minimise negative effects on the environment. There must also be an agreement of who will be held responsible if a land-clearing related offence is committed. There needs to be an update in the legislation clarifying when a violation has been committed, as well as specifying the responsible party for restoring the damaged land. Furthermore, there needs to be consistency in enforcement and convictions, so large corporations are held to the same standards as the local landowners.

Chapters 4 and 5 showed that riparian and floodplain forests are important habitats for proboscis monkeys. To reduce the risk of predation, proboscis monkeys may select sleeping sites close to rivers as protection, reducing the area they need to guard against predators (Matsuda et al. 2011b; Thiry et al. 2016). This is particularly the case for groups with vulnerable or small individuals, i.e. reproductively active groups (such as the focal group of this study), as opposed to all-male groups (Thiry et al. 2016). The removal of trees changes the composition and structure of both edge and interior forest, as well as exposes the newly created edge to different environmental conditions (Broadbent et al. 2008). Furthermore, while some mammal species avoid edge habitats, others such as proboscis monkeys' main terrestrial predator, the Sunda clouded leopard (*Neofelis diardi*), increase their relative habitat use near edge habitats (Brodie et al. 2015), and therefore edges could also increase the risk of predation events.

The loss of the riparian zone is not only detrimental to the particular proboscis monkey troop whose home range was partially destroyed in this study but has overarching

deleterious effects on the ecosystem as a whole. Despite widespread concerns about the negative effects of riparian zone destruction, forestry practices are still increasing in intensity to meet global demand (Laudon et al. 2011; Kuglerová et al. 2014). The heightened rate of habitat loss means that traditional research studies are often too slow to react to habitat alteration. By providing compelling research and visual aids, using a combination of satellite tracking and drone imagery, rapid responses by authorities and policymakers can be more effective when dealing with time-sensitive issues. Furthermore, the awareness raised using these means can also identify the need to update policies to identify responsible parties, and hold them accountable, should encroachment occur in the future.

# Chapter 7  General Discussion

Due to the widespread prevalence of forest loss across the tropics (Hansen et al. 2013), most studies on wild primates must consider a conservation aspect due to the potential influence of habitat loss or degradation (Cowlishaw 1999; Estrada et al. 2017). Primates respond to fragmentation or other human disturbances (e.g., wildfires, logging, hunting) according to differences in their ecological traits (Michalski and Peres 2005). The logistical challenges of following primates in many of these habitats, either due to the remoteness of the area or the skittish nature of primates in disturbed habitats, make it difficult to understand these responses. However, with advances in GPS-collar technology, it has become possible to obtain these ranging data, which can then be used to infer behaviours or predict responses of primates in a degraded or changing habitat to improve conservation initiatives.

## 7.1  Summary of findings

This thesis focused on the spatial and temporal ranging patterns of proboscis monkeys in a degraded habitat. It showed that certain home range estimators were more suitable based on the research aims and the characteristics of the habitat or movement dataset than others; biased random bridge method being the most suitable for this particular study (Chapter 3). Proboscis monkeys did not show strong patterns in resource use or home ranging based on structural forest characteristics (Chapter 4), but were associated with greater tree height and proximity to forest edges. However, differences in landscape and environmental factors did seem to lead to variation in short-term movements and sleeping site selection (Chapter 5). Changes in movement patterns corresponded with seasonal changes in potential food sources, but also changed within the home range based on proximity to forest edges or in intensively used areas. Finally, this study presented an example of the direct conservation action that can be prompted by the combination of visually compelling GPS-collar and aerial

remote sensing data (Chapter 6).

Together, these findings suggest that proboscis monkeys in the Kinabatangan are more generalist in their habitat requirements than expected and can cope in areas of different sizes of forests with varying disturbance levels, although fully understanding the true impacts on the population's viability or reproductive success over time requires longer term studies. There were few overarching trends of resource utilisation or movement patterns based on the amount of habitat available or disturbance level. Although movement patterns within intensively used areas suggest that proboscis monkey activity was different within those areas (i.e. foraging and resting) (Chapter 5), the areas were not structurally different from the rest of the habitat (Chapter 4). These findings have provided an increased understanding of the potential consequences of human-mediated disturbances to proboscis monkey habitat use and can be used to inform the management of degraded landscapes, such as by identifying areas that require protection, corridor connection, habitat reclamation or habitats to be left for regeneration.

A general trend observed was the difference in habitat use and movement patterns close to oil palm plantation edges as compared to water edges. Proboscis monkeys tended to move faster and in directed steps when close to plantations as compared to close to rivers, suggesting a stressful movement environment (Chapter 5), as further supported by the low preference of proboscis monkeys using areas near oil palm boundaries as seen in Chapter 4. The plantation boundaries were expected to be a source of high quality food due to the increased sunlight (Ganzhorn 1995), but the faster and straighter movements up to 500 m from plantations (Chapter 5) and less use of areas within 2 km (Chapter 4) suggest unfavourable conditions near plantations, such as predation, or noise pollution from humans, vehicles, heavy machinery or dogs. Although proboscis monkeys do move near plantation edges, likely due to food

availability, their movement patterns suggest that they may not be able to take full advantage of the higher food quality near these edges, and therefore are not exploiting the potentially increased resources available. Additionally, the sleeping site selection suggested that plantation edges are avoided (Chapter 5). The preference to sleep away from plantation edges, as well as shifts of sleeping site locations during times of brighter moon phases, also suggests that proboscis monkeys are trying to avoid disturbance (Chapter 5). Although proboscis monkeys can survive in small forest blocks, there is still a general trend suggesting preference for using inland forest for daily activities. These results indicate the importance of ensuring the amount of forest available for proboscis monkeys is sufficient to provide suitable areas for feeding or refuge, or so they do not need to travel into stressful environments to access food resources.

Home ranging research plays an important role in conservation to determine strategies for managing wild areas (Boyle et al. 2009; Sawyer 2012; Garabedian et al. 2017). An important component of such research is the choice of method to estimate the range (Chapter 3). The biased random bridge method was the most suitable for this study, as the aim was to estimate general home range use in an area with pre-identified barriers (i.e. rivers), and to identify core ranging areas within that range. Grid-cell method may be useful to identify areas of importance within the home range, but not for calculating home range size. If the aim of a landscape management strategy is to identify areas that are avoided by an animal, then a local convex hull method could be more suitable. This study showed the value that degraded habitats can still have and stressed the importance in selecting the most suitable estimator based on management aims in order to develop the most appropriate strategy for populations living in these degraded habitats.

As a whole, this thesis expands our understanding of proboscis monkeys. Previous studies had suggested that their foraging behaviour seemed to contradict the general patterns observed in colobine monkeys (Boonratana 2000; Matsuda et al. 2009b). However, by increasing the number of groups studied and extending the study period to incorporate numerous seasons, this study suggests that the foraging behaviour of proboscis monkeys is more similar to other colobines than previously thought (Chapter 5). Proboscis monkeys were seen travelling further during times of high fruit availability and decreased their travelling distances when young leaves were highly abundant. The seasonal changes in food availability may become more pronounced in light of the changing climate, the effects of which are being exacerbated by deforestation (Struebig et al. 2015). Furthermore, climate change is expected to accentuate the effects of El Niño-Southern Oscillation (ENSO) events, causing a decrease in rainfall and an increase in the frequency and severity of forest fires (Wich and van Schaik 2000; Hanya and Bernard 2016). The decrease in rain would reduce the frequency and duration of fruiting seasons (van Schaik et al. 1993), and consequently would condense the periods in which proboscis monkeys are able to feed on higher quality food sources. Therefore, it is important that there is enough forest available to provide the nutrients proboscis monkeys require to sustain their large body size.

## 7.2   Limitations and recommendations for future work

This thesis contributes to our understanding of how primates behave in a degraded habitat. Previous knowledge on proboscis monkeys had been limited to a single group or to riverside behaviour (e.g., Boonratana 2000; Matsuda et al. 2009a; Bernard et al. 2010; Feilen and Marshall 2017). This study provides confirmation of this riverside preference, but also expands upon this to show the intensity with which proboscis monkeys use forest throughout their range and how their movement changes depending on where they are in the forest. As one of the first studies to track multiple primates using GPS collars in a relatively short time period, this thesis provides a

standard for the possibilities of examining habitat use in primatology with advanced technology.

There were, however, components of proboscis monkey movement and behaviour that this study was not able to investigate and would be useful to consider for future studies. Firstly, diet was not examined, and the indirect link between food availability and movement patterns meant it was not possible to make causal links between environmental factors and movement behaviour. By following the groups, some valuable ranging data might have been lost during the habituation process and the animals fleeing. However, the phenology data were considered representative of proboscis monkey food availability because all of the top 10 tree and top 2 vine species (Table 5.1) were known food sources for proboscis monkeys (Thiry et al. *in review*) and because proboscis monkeys have been observed feeding on abundant food types (Matsuda et al. 2009b). Genetic analysis of proboscis monkey faecal samples in the Lower Kinabatangan is currently being conducted to further examine the link between food availability and food consumption (V. Thiry, *pers. com.*). Distinguishing the relationship between climate and food availability also requires further work to help resolve the causal relationships associated with movement patterns.

A second component that requires further investigation is the sampling rate at which the GPS fixes were taken. GPS fixes were taken at hourly intervals and therefore the resolution may have been too coarse to determine the foraging strategy of proboscis monkeys (e.g. Brownian vs. Levy movements); a fix interval of at least every 15 min or whenever movement occurs >15 m is recommended for a study of that nature (Reyna-Hurtado et al. 2017). It is possible that proboscis monkeys are moving at more irregular speeds than suggested by this study, i.e. faster speeds covering longer distances in a shorter time frame than what is captured by the hourly fix intervals. As the LiDAR-based structural measures had relatively little relationship to proboscis monkey

resource use, linking high frequency (15 min intervals or whenever movement >15 m occurs) movement data with LiDAR data to identify individual trees, or travel routes, may help to strengthen causal inference between food availability and movement. Although it seems as though proboscis monkeys are not over-exploiting their habitat (Chapter 5), a finer-scale study may also provide a more direct conclusion on whether the available forest is sufficient for their needs. However, as proboscis monkeys had been shown to travel only 3.5% of the day (Matsuda et al. 2009b), it was determined that the benefits of longer fix intervals (e.g. extends battery life while still capturing resource use) would outweigh those of shorter intervals (e.g. more detailed movements of how they get to their resources).

The third component that was not investigated in this thesis was group size and composition. This would have been beneficial to try to account for differences in ranging behaviour between groups. All 10 groups appeared to be of similar size (~10-20 individuals), but accurate counts of the size and composition (number of different age groups) could have provided some interesting insight and indicators of group success. Fourthly, it could be useful to track neighbouring proboscis monkey groups to investigate group overlap. There is up to 100% spatial overlap in riverine proboscis monkey home ranges (Boonratana 2000), but there is still no information on the temporal overlap or resource use between neighbouring groups. Having this information could better inform topics such as the carrying capacity of the forest. Finally, proboscis monkey behaviour (diet, social interactions, ranging) varies among populations in mangrove, peat swamp and riverine forests (Yeager 1989; Boonratana 2000; Bismark 2009; Matsuda et al. 2009b). Tracking individuals in a number of different habitat types would improve our knowledge on the resource and habitat use of proboscis monkeys and could provide information on any flexibility observed across the species. The development of a conservation strategy for the management of the

species is necessary, and should incorporate aspects of population monitoring, habitat protection and restoration, tourism and translocation.

This thesis identified the difference in usage between plantation and river edges, suggesting a stressful environment or unfavourable conditions near plantations. Conducting direct observations of human-related activities and proboscis monkey behaviour along plantation boundaries could untangle this further. By understanding the disturbances along plantation boundaries, recommendations to reduce the impact of plantations could be provided that allow proboscis monkeys to take greater advantage of the potentially increased food available near plantation edges. Direct observations of human activity along rivers at night could help further explain the relationship of proboscis monkeys sleeping further inland during times when the moon is bright or during drier periods.

A number of technologies were incorporated in this thesis for a greater understanding in the habitat use and movement patterns of proboscis monkeys: GPS collars, Light Detection and Ranging (LiDAR) and Unmanned Aerial Vehicles (UAV). It is important for researchers to be aware of the positive and negative aspects of using new technologies when developing future research projects, as it is normally associated with a large financial cost. The central piece of technology used in this thesis, GPS collars, is still not heavily utilised in primatological studies, largely due to the potential risk involved in capturing arboreal and social animals (Juarez et al. 2011). Without an experienced team, incorrect capturing techniques can result in animals falling or disappearing from the capture team's view before becoming fully sedated, putting the animal at risk of hurting itself or being predated upon. Additionally, separating an individual from their social unit is a potential risk that needs to be considered before

deciding to capture. The proboscis monkeys in this study were captured at night and released before dawn so their social unit did not leave during the capture or sampling process. The weight of the primate can also limit collar size, and therefore the collar battery longevity and frequency of GPS points taken, which can then limit the research questions available for investigating, such as taking GPS points at short intervals for identifying foraging strategies or longer intervals for migration patterns. Critical evaluations of the technology, use, and performance of GPS telemetry in ecology has been widely explored (e.g., Cagnacci et al. 2010; Friar et al. 2010; Hebblewhite and Haydon 2010; Forin-Wilart et al. 2015; Vance et al. 2017; Chapter 3). The GPS collaring for this project was performed in conjunction with a team led by qualified veterinarians who were sampling proboscis monkeys for another purpose, and therefore were able to maximise the amount of information collected once the animals were anaesthetised by attaching GPS units. Once a project has identified and minimised the risks, the benefits of using GPS include obtaining detailed location (Chapter 3) and habitat use (Chapters 4 to 6) data without the logistical constraints involved when habituating and following groups in the field (Section 2.3.6). GPS collars can also provide important information such as activity (Markham and Altmann 2008), group coordination (Markham et al. 2013) and between group interactions (Strandburg-Peshkin et al. 2017).

Combining high-resolution habitat data together with GPS collar data further improves the benefit of using collars. The two different methods used in this thesis to understand the habitat use were through LiDAR (Chapter 4) and UAVs (Chapter 6). LiDAR data provides the user with a wide range of information; along with data such as

tree height and internal canopy structure (Chapter 4), the data can be used to calculate carbon stocks (Asner et al. 2018) or identify trees based on their spectral or chemical properties (Asner and Martin 2008). However, the cost of collecting LiDAR data can be quite high. For example, a typical commercial aerial LiDAR flights cost at minimum $20,000USD per flight (Erdody & Moskal 2010), which makes it inaccessible for many researchers. Highly specialised equipment and expertise in collecting and processing LiDAR data, and are normally only flown once to provide a snapshot of the landscape at a single point in time. Therefore, depending when the flights are flown within the study period, or how dynamic the landscape is, the data collected may be not correspond to the same conditions that the animals were experiencing while they were being tracked.

UAVs on the other hand, can be used to collect high spatial resolution datasets at a lower cost with less logistical barriers than LiDAR (Dandois & Ellis 2013). Because of their almost negligible operational costs, once the UAV equipment is initially purchased (plane and software: $2,000 - $4,000USD (Koh & Wich 2012, Dandois & Ellis 2013), UAVs can be used as a low-cost monitoring tool that is flown as frequently as needed. However, despite the cost-effectiveness of the UAVs, the type of data that are available from those flights are not yet as accessible as they are from LiDAR. UAVs generally are only able to provide images of the landscape and some canopy height data, but the quality of these data can be unreliable and highly inaccurate. In order to obtain useful height data, calibration is required, by using ground-truthing stations at the time of flying or existing LiDAR data (Messinger et al. 2016). It is important for researchers to fly at the optimal height and interval that will give them the overlap and

coverage that they need, with still a suitable resolution, which may require some testing in the field, as each site may have different requirements (LiDAR: see Lovell et al. 2005; Heinzel and Koch 2011; UAV: see Koh and Wich 2012).

## 7.3 Implications for proboscis monkey conservation in Sabah

### 7.3.1 Population monitoring
The last Sabah-wide proboscis monkey survey was conducted in 2005 and estimated just under 6,000 individuals (Sha et al. 2008). This is the most complete survey to date, but missed some known isolated populations (e.g. Sebatik and Pitas). The survey was carried out during the mornings and afternoons, but due to low detection rates during morning surveys, this is expected to be an underestimate (Matsuda et al. *in press*). A decrease in group size in the Kinabatangan between 2004-2014 indicates a response to habitat loss since the initial survey (Matsuda et al. *in press*), and It will be vital to replicate this study to obtain this information for the remaining proboscis monkey populations across Sabah. Moreover, reports of populations along rivers further inland Sabah need to be verified and monitored.

This study confirms the importance of riparian forests to proboscis monkeys (Chapters 4, 5 and 6) and validates the use of boat surveys for large-scale method of surveying populations. However, lakes and tributaries must be included in these surveys, as some groups may never travel near the main rivers (Chapter 4). The results also show that although proboscis monkeys do not have particularly large home ranges relative to their body size, their ranges can consist of a large proportion of river edge, especially along river bends. Because the Kinabatangan River can be ~120 m wide in some places (Horton et al. 2017), and observers are ~50 m from either riverbank, it can be difficult to detect proboscis monkey groups that are not directly on the river edge or in emergent trees. More accurate population estimates may be obtained by observing a

single riverbank in a day by travelling closer along one side of the river to improve detection rate and group counts. It would also increase the distance travelled per survey and decrease the chance of recounting groups. Barriers such as roads, villages or wide tributaries should be used as natural end points in the survey where possible. The surveys can identify shifts in group size or population density that may reflect long-term reactions to changing environments.

### 7.3.2 Habitat

Proboscis monkeys live in a landscape that has been heavily disturbed. Borneo lost 62% of its old-growth forest from 1973 to 2015 (Gaveau et al. 2016). Sabah lost forest at even a faster rate during this period, losing half its intact forest in just half the amount of time (Osman et al. 2012). Only 15% of proboscis monkeys in Sabah are living in totally protected forest (Sha et al. 2008) and in the Kinabatangan, a quarter of potential proboscis monkey habitat is unprotected (Matsuda et al. *in press*). However, this thesis suggests that proboscis monkeys seem resilient and adaptable to the forest that they have available. Besides a preference for taller trees, the most important characteristic is proximity to forest edges (Chapter 4). The preference towards river edge and not for plantation edge was also supported by the differences in how proboscis monkeys move in relation to those edge types (Chapter 5). The conservation priority should ensure that the remaining habitat is protected and that riparian forests are no longer targeted. Once the existing habitat is secured, other areas worth exploring include:

- Riparian reserve restoration: Besides the benefit of restoring riparian forests to increase proboscis monkey habitat (either though natural regeneration or reforestation efforts), it would also increase the stability of the riverbanks. Around 1 – 1.3 m of forest is lost annually along the Kinabatangan River due to erosion (Horton et al. 2017).

- Reclaim underproductive oil palm plantations: Large areas of land near the river have been classified as underproductive oil palm, making them not economically worthwhile (Abram et al. 2014). Some areas have already been abandoned, but still belong to the plantation. Plantations should be encouraged to offer up the land where they are not able to grow oil palm.

- Riparian reserve width: Riparian reserves are defined as the land within 20 m from rivers that are greater than 3 m wide (State of Sabah 1998). However, on the basis of this thesis, 20 m are insufficient for proboscis monkeys. Proboscis monkeys sleep on average more than 50 m from rivers, but also travel on average 230 m inland daily (Chapter 5). Furthermore, proboscis monkeys do not always return to the river, as they have been observed travelling up to 1.2 km inland and staying inland for more than a week at a time (Chapter 5). Finally, the preference for staying away from plantation edges (Chapter 4) and the change in movement patterns near plantations (Chapter 5) reinforces that proboscis monkeys should have enough habitat to allow them to range without obstruction and provide sufficient food resources without the disturbances caused by being obstructed or being near plantations.

- Enforcement: Riparian reserve laws are inconsistently enforced, and large corporations may not be held to the same degree of responsibility for violations as smallholders (Chapter 6). The laws should be made clear as to who is responsible for any land issues – e.g. RISDA case (Chapter 6). Establishing a monitoring network that includes remote sensing activities (habitat monitoring), and involves local communities in volunteer programmes, such as Sabah's Honorary Wildlife Warden Programme, could be used to monitor and regularly report on actions and threats. After the initial LiDAR flight of the study site (Chapter 4), fixed-wing drones can be used as a more cost-effective monitoring tool (e.g., annual or biannual flights) to ensure that protected areas are not encroached (Chapter 6).

- Education: Local landowners are often unfamiliar with land laws. Community forums should be held to inform the local communities what the laws and punishments are for land violations, but also to explain the potential benefits of co-existence with local wildlife and to discuss options for developing their land in a way to promote this, such as live fences.

### 7.3.3    Tourism

Proboscis monkeys are a focal species for tourism in Sabah. Although often referred to as eco-tourism, the lack of guidelines for tour operators, guides, boat drivers prevents it from being true eco-tourism and has been referred to instead as nature tourism (Leasor and Macgregor 2014). Although tourism is a major source of income for Sabah, overtaking the logging industry and providing MYR7.25 billion to the local economy in 2016 (The Malaysian Insight 2018), there are many foreign tour operators bringing their own guides, and with little financial gain realised by local communities (Awareness, Education and Tourism Small Group Discussion: International Workshop for proboscis monkey conservation, Kota Kinabalu, Sabah, 20-25 February 2017). Without the local communities seeing the long-term financial benefits that tourism can bring, there is little incentive to maintain the forest rather than the immediate financial gain they can obtain by converting it for agriculture or selling it to a corporation for conversion. In order for local communities to have ownership over their environment, tourism regulations should demand authorised local tour guides and boat drivers rather than foreign guides. This thesis can provide tangible support to the importance of maintaining riparian forests for the survival of proboscis monkeys and hence the long-term financial success that can be possible through tourism.

As the most popular viewing times of proboscis monkeys are early morning and late afternoon, boats may be disruptive to ranging, river crossing behaviour (Yeager 1992; Chapter 5), and sleeping site selection, but also to feeding behaviour (Pople et al.

*unpublished manuscript*). Proboscis monkeys tend to eat more leaves in the afternoon in order to digest more fibrous material overnight (Matsuda et al. 2014; Thiry et al. *in review*), but when boats approach, feeding behaviours are reduced and stress-related behaviours increase (Pople et al. *unpublished manuscript*). Limiting the number of boats that can enter small tributaries can reduce the stress that animals may be experiencing. There are often boats that go out at night for wildlife spotting, and therefore, guidelines also need to include nocturnal observations of proboscis monkeys to avoid increasing disturbance when they are trying to sleep.

Regular monitoring of tourists and proboscis monkey groups in major tourist destinations should be conducted. Proboscis monkey observations should include recording number of groups, group composition, activity patterns, and river-crossing behaviour. Tourist observations should include: number of people on boat, number of boats, and behaviour of tourists/guides/boat man. These data can be used to monitor the effectiveness of the guidelines and suggest improvements where necessary. Regular monitoring by enforcement agencies should increase and can be supported through voluntary initiatives as Sabah's Honorary Wildlife Warden Programme).

Guidelines to be considered for proboscis monkey tourism include:

- Approved tour guides and local boat drivers who have undertaken official training (Continuing Tourism Related Education, CTRE), which should include guidelines for proboscis monkey tourism.

- Tourist/Guide/Driver behaviour: no vocal playbacks, spotlights, laser pointers, feeding, smoking, or littering. Speaking should be kept to a minimum and at hushed levels.

- Boat behaviour: slow boat speed when approaching group, recommended distance of 20 m on main rivers; in tributaries on the opposite bank, never

perpendicular or directly under the group (can allow for crossing behaviour). The engine should not be revved.

- Number of boats: limit the number of boats that can enter a tributary at once. Research is needed to identify the current number in order to make an informed suggestion as to how many it should be.

### 7.3.4 Translocation

Proboscis monkey translocation is not recommended. According to the IUCN guidelines, primates should not be released in a habitat where that species is already present (IUCN 1998). However, due to the rate at which forest is being lost in Sabah, it has become a critical issue and has occurred a number of times without any strict protocols. Therefore, if translocation is deemed necessary, then a protocol must be developed and adhered to. This study showed the effectiveness of GPS tracking to monitor short-term movement patterns (Chapters 5), and this should be essential in the post-release monitoring protocol. Collars can be programmed so that fix rates change throughout the post-release monitoring if necessary, going from frequent (detect small-scale movements; <1 h) to less frequent (hourly - daily). Having data from wild individuals from a similar habitat type will be essential in determining whether the ranging data observed in the translocated individual appeared normal. Regular visual observations need to be made to ensure the health of the animal and to monitor any change in social status. GPS collaring neighbouring wild groups would improve the success of releasing proboscis monkeys in areas with a pre-existing population, as it would provide a greater understanding in how neighbouring groups interact and therefore how wild groups may respond to released individuals.

## 7.4 Conclusion

Understanding the behavioural and movement patterns of primates in disturbed habitats is important to understand the ecological requirements of the species.

However, at a time where habitat loss is a critical issue, the focus needs to be turned towards the survival of the species rather than the ecological comparisons to other primate species. Due to the complex interaction of a species to its environment (e.g., local climate, forest availability, local pressures), effective conservation strategies must examine populations or ecosystems on a case-by-case situation. The findings from this study provide a positive outlook for the survival of proboscis monkeys in the Kinabatangan Floodplain, and will be incorporated in a 10-year State Action Plan for proboscis monkeys in Sabah. This thesis highlights the conservation value that degraded forests still have, and that the protection of these areas is important for the survival of this endemic primate and coexisting species.

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# Appendix 1   Parameters for home range estimations

Table A1.1 Collaring period and number of points used for home range estimates for the complete model (hourly fixes, using 4 or more satellites, no 05:00 point), Simulation 1 which reflects low fix rate (every 4 h), and Simulation 2 reflects fix failures.

| Group ID | Collaring Date (# days collared) | Complete | Simulation 1 | Simulation 2 |
|---|---|---|---|---|
| 1 | 2011-08-11 (364) | 5039 | 1439 | 3461 |
| 2 | 2012-05-16 (230) | 3175 | 903 | 2163 |
| 3 | 2012-05-18 (169) | 2311 | 665 | 1547 |
| 4 | 2012-09-24 (222) | 3081 | 881 | 2128 |
| 5 | 2013-09-03 (368) | 5037 | 1446 | 3440 |
| 6 | 2014-04-24 (109) | 1498 | 428 | 1049 |
| 7 | 2014-04-26 (240) | 3309 | 948 | 2234 |
| 8 | 2014-04-28 (401) | 5569 | 1591 | 3699 |
| 9 | 2014-05-19 (135) | 1805 | 512 | 1279 |
| 10 | 2014-05-20 (150) | 2045 | 585 | 1379 |

Table A1.2a  Model parameters used for the complete models of adaptive local convex hull and adaptive time local convex hull; max. distance is the maximum distance between fixes, and is used as the starting point for determining the *a*-value.

| Group ID | Max. Distance (m) | *a*-value (*a*-LoCoH) | *a*-value (T-LoCoH) | *s*-value (T-LoCoH) |
|---|---|---|---|---|
| 1 | 3442 | 1620 | 690 | 0.020 |
| 2 | 2383 | 1250 | 730 | 0.028 |
| 3 | 1898 | 1480 | 580 | 0.015 |
| 4 | 2509 | 2500 | 560 | 0.025 |
| 5 | 1598 | 1640 | 760 | 0.028 |
| 6 | 1577 | 1470 | 750 | 0.048 |
| 7 | 2380 | 1150 | 740 | 0.023 |
| 8 | 3497 | 1000 | 640 | 0.019 |
| 9 | 3760 | 1060 | 1170 | 0.029 |
| 10 | 998 | 790 | 630 | 0.070 |

Table A1.2b  Model parameters used for the simulated models of adaptive local convex hull (a-LoCoH) and adaptive time local convex hull (T-LoCoH). S1 = Simulation 1, S2 = Simulation 2.

| Group ID | a-value (a-LoCoH) | | a-value (T-LoCoH) | | s-value (T-LoCoH) | |
|---|---|---|---|---|---|---|
| | S1 | S2 | S1 | S2 | S1 | S2 |
| 1 | 3640 | 3170 | 1200 | 830 | 0.041 | 0.020 |
| 2 | 1300 | 1340 | 1270 | 870 | 0.043 | 0.024 |
| 3 | 1990 | 2840 | 1050 | 760 | 0.035 | 0.038 |
| 4 | 1260 | 2200 | 940 | 860 | 0.053 | 0.025 |
| 5 | 1940 | 1770 | 1130 | 1190 | 0.054 | 0.033 |
| 6 | 1100 | 1230 | 1230 | 1140 | 0.075 | 0.045 |
| 7 | 1420 | 1100 | 1260 | 1110 | 0.048 | 0.024 |
| 8 | 770 | 1020 | 1320 | 870 | 0.028 | 0.019 |
| 9 | 1270 | 1390 | 1300 | 1240 | 0.050 | 0.028 |
| 10 | 1390 | 920 | 1000 | 930 | 0.078 | 0.066 |

# Appendix 2   Additional home range estimation results

Table A2.1 Home ranges (90%) for each proboscis monkey group using four estimates (ha): grid-cell method (GCM), adaptive local convex hull (*a*-LoCoH), adaptive time local convex hull (T-LoCoH, 90%) and biased random bridges (BRB); N = number of GPS fixes used.

| Group ID | N | GCM | *a*-LoCoH | T-LoCoH | BRB | Average (SE) |
|---|---|---|---|---|---|---|
| 1 | 5039 | 167.3 | 124.7 | 144.2 | 164.9 | 150.4 (10.1) |
| 2 | 3175 | 76.5 | 48.1 | 56.7 | 62.6 | 61.0 (6.0) |
| 3 | 2311 | 55.5 | 37.9 | 42.2 | 49.8 | 46.2 (3.9) |
| 4 | 3081 | 92.3 | 76.9 | 79.5 | 91.7 | 85.0 (3.9) |
| 5 | 5037 | 112.3 | 76.2 | 82.6 | 83.4 | 88.6 (8.0) |
| 6* | 1498 | 62.0 | 55.8 | 60.4 | 67.1 | 61.3 (2.3) |
| 7* | 3309 | 87.3 | 61.3 | 74.4 | 92.9 | 79.0 (7.0) |
| 8 | 5569 | 53.3 | 21.5 | 31.3 | 44.4 | 37.7 (7.1) |
| 9* | 1805 | 89.3 | 92.1 | 110.0 | 127.2 | 104.8 (9.0) |
| 10* | 2045 | 35.0 | 19.6 | 23.9 | 24.1 | 25.7 (3.3) |

*females

Table A2.2 Summary of complete models for overall (90%) and core (50%) home range comparison variables: home range area; boundary complexity (edge density); patchiness, barrier detection and area-under-the-curve (AUC) for: grid-cell method (GCM), adaptive local convex hull (*a*-LoCoH), adaptive time local convex hull (T-LoCoH), and biased random bridge (BRB).

| Method | Area (ha) | Edge Density (m/ha) | Patch Count | Area in river (%) | AUC |
|---|---|---|---|---|---|
| 90%:  GCM | 83.1$^a$ | 202.8$^a$ | 18.9$^a$ | 5.0$^a$ | 0.998$^a$ |
| *a*-LoCoH | 61.4$^b$ | 134.8$^b$ | 2.3$^b$ | 0.3$^b$ | 0.841$^b$ |
| T-LoCoH | 70.5$^c$ | 122.5$^b$ | 1.5$^b$ | 0.7$^b$ | 0.807$^c$ |
| BRB | 80.8$^a$ | 109.0$^b$ | 5.1$^c$ | 3.0$^c$ | 0.969$^d$ |
| Chi-sq value* | 31.2 | 31.8 | 54.1 | 46.2 | 112.92 |
| 50%:  GCM | 50.5$^A$ | 272.3$^A$ | 21.8$^A$ | 4.6$^A$ | - |
| *a*-LoCoH | 15.7$^B$ | 333.3$^A$ | 5.8$^B$ | 0.6$^B$ | - |
| T-LoCoH | 24.7$^C$ | 192.3$^B$ | 2.4$^C$ | 1.0$^B$ | - |
| BRB | 23.3$^C$ | 204.5$^B$ | 5.9$^B$ | 0.90$^B$ | - |
| Chi-sq value* | 74.7 | 27.3 | 49.6 | 36.9 | - |

a,b,c Pair-wise results from Tukey test; results significantly different from another (p<0.05) are indicated by a different letter, those with the same letter showed no significant difference. *Chi-square values for GLMM likelihood ratio test: for all tests, df = 3 and p <0.001.

Table A2.3 Home range sizes (ha) for each collared proboscis monkey using four methods for each simulation: (1) grid-cell method (GCM), (2) adaptive local convex hull (a-LoCoH), (3) adaptive time local convex hull (T-LoCoH), and (4) biased random bridge (BRB). Simulation 1 (S1) simulated low fix rate (every 4 h) and Simulation 2 (S2) simulated fix failures.

| (1) Group ID | GCM Complete | S1 | S2 | (2) Group ID | a-LoCoH Complete | S1 | S2 |
|---|---|---|---|---|---|---|---|
| 1 | 167.3 | 70.0 | 138.8 | 1 | 124.7 | 128.6 | 133.2 |
| 2 | 76.5 | 38.3 | 69.3 | 2 | 48.1 | 44.7 | 47.5 |
| 3 | 55.5 | 28.3 | 49.3 | 3 | 37.9 | 34.5 | 41.2 |
| 4 | 92.3 | 42.5 | 79.8 | 4 | 76.9 | 74.9 | 74.7 |
| 5 | 112.3 | 74.5 | 103.5 | 5 | 76.2 | 75.9 | 78.0 |
| 6 | 62.0 | 24.3 | 51.5 | 6 | 55.8 | 47.7 | 50.8 |
| 7 | 87.3 | 41.0 | 71.3 | 7 | 61.3 | 59.4 | 61.5 |
| 8 | 53.3 | 37.8 | 48.3 | 8 | 21.5 | 20.0 | 21.0 |
| 9 | 89.3 | 27.5 | 67.8 | 9 | 92.1 | 85.9 | 95.2 |
| 10 | 35.0 | 23.3 | 32.3 | 10 | 19.6 | 18.6 | 20.0 |

| (3) Group ID | T-LoCoH Complete | S1 | S2 | (4) Group ID | BRB Complete | S1 | S2 |
|---|---|---|---|---|---|---|---|
| 1 | 144.2 | 156.7 | 146.7 | 1 | 164.9 | 227.6 | 164.0 |
| 2 | 56.7 | 56.6 | 58.9 | 2 | 62.6 | 89.1 | 63.0 |
| 3 | 42.2 | 42.9 | 44.2 | 3 | 49.8 | 67.8 | 49.5 |
| 4 | 79.5 | 83.3 | 87.2 | 4 | 91.7 | 119.6 | 90.2 |
| 5 | 82.6 | 84.9 | 86.6 | 5 | 83.4 | 100.5 | 84.0 |
| 6 | 60.4 | 64.0 | 62.8 | 6 | 67.1 | 80.1 | 66.2 |
| 7 | 74.4 | 78.6 | 80.7 | 7 | 92.9 | 190.6 | 95.7 |
| 8 | 31.3 | 42.5 | 32.7 | 8 | 44.4 | 127.4 | 52.4 |
| 9 | 110.0 | 105.5 | 104.3 | 9 | 127.2 | 188.4 | 123.5 |
| 10 | 23.9 | 22.8 | 25.3 | 10 | 24.1 | 34.2 | 24.0 |

Table A2.4 Summary of simulation core range models (50%) for grid-cell method (GCM), adaptive local convex hull (*a*-LoCoH), adaptive time local convex hull (T-LoCoH) and biased random bridges (BRB). Simulation 1 simulated low fix rate (every 4 h) and Simulation 2 simulated fix failures.

| Simulation | Ave. Area (ha) | Ave. Edge Density (m/ha) | Ave. Patch Count | % Area in river | % Point Inclusion |
|---|---|---|---|---|---|
| *GCM: Complete* | *50.5[a]* | *272.3[a]* | *21.8* | *4.6* | *84.3[a]* |
| Simulation 1 | 27.0[b] | 468.1[b] | 26.6 | 6.5 | 74.1[b] |
| Simulation 2 | 40.0[c] | 320.9[a] | 25.3 | 4.4 | 78.9[a,b] |
| *a-LoCoH: Complete* | *15.7* | *333.3* | *5.8* | *0.5* | *49.5* |
| Simulation 1 | 13.7 | 294.2 | 3.9 | 0.9 | 47.8 |
| Simulation 2 | 16.1 | 301.0 | 5.3 | 0.5 | 49.1 |
| *T-LoCoH: Complete* | *24.7* | *192.3* | *2.4* | *1.0* | *51.4* |
| Simulation 1 | 27.1 | 144.0 | 1.6 | 1.2 | 51.7 |
| Simulation 2 | 26.8 | 153.2 | 1.8 | 0.8 | 51.0 |
| *BRB: Complete* | *23.3[a]* | *204.5[a]* | *5.9[a]* | *0.9* | *56.6* |
| Simulation 1 | 31.0[b] | 115.0[b] | 2.3[b] | 2.3 | 58.7 |
| Simulation 2 | 23.0[a] | 208.7[a] | 6.7[a] | 0.8 | 56.4 |
| Chi-sq value* | 219.5 | 169.4 | 188.7 | 105.2 | 270.1 |

a,b,c Pair-wise results from Tukey test; results significantly different from another (p<0.05) are indicated by a different letter, those with the same letter showed no significant difference; *Chi-square values for GLMM likelihood ratio test: for all tests, df = 11 and p <0.001.

Group 1:

Group 2:

Group 3:

Group 4:

Group 05:
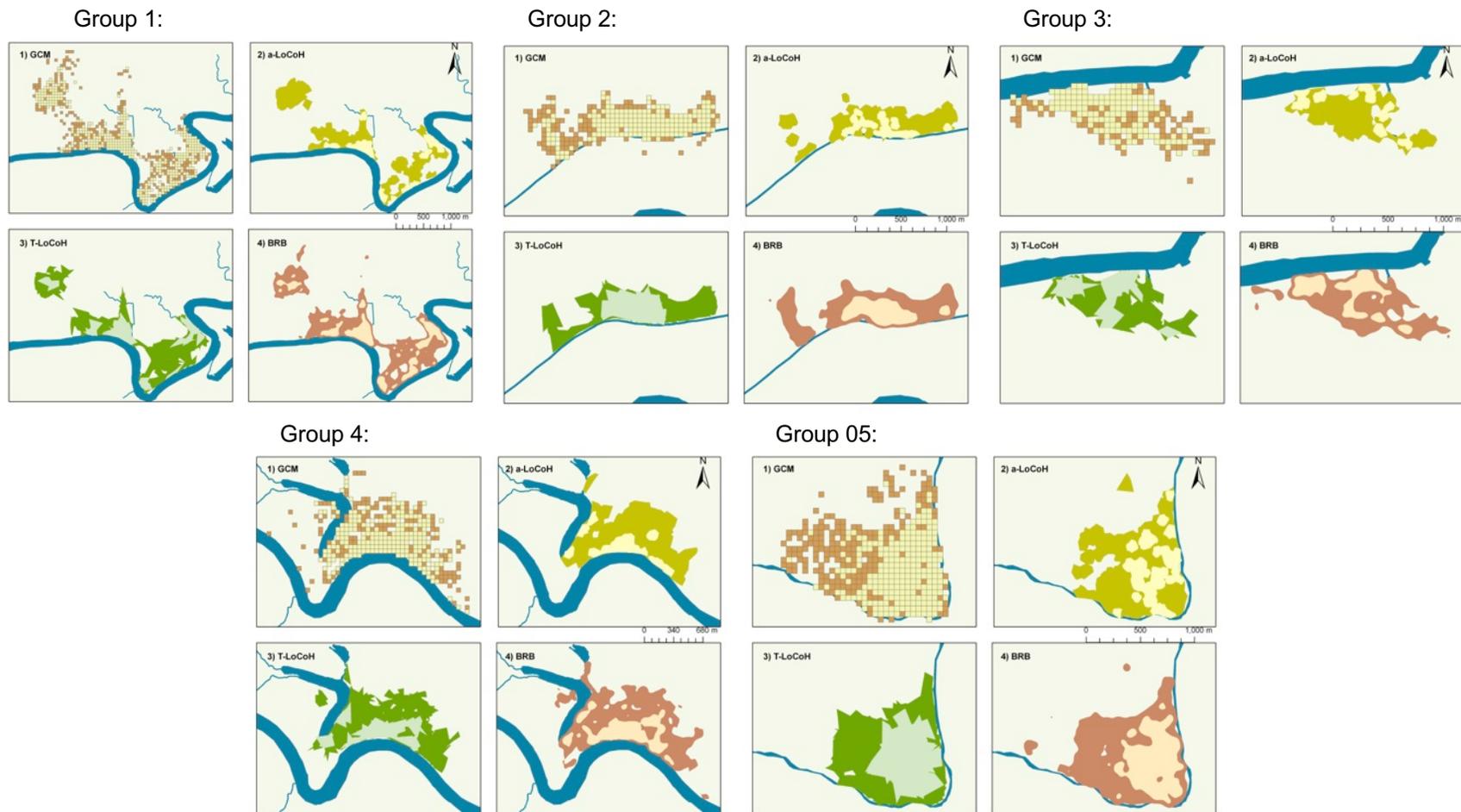
Figure A2.1a    Home range estimates for five proboscis monkeys groups in the Lower Kinabatangan Floodplain (Groups 1 to 5): 1) Grid-cell method (GCM), 2) adaptive local convex hull (*a*-LoCoH), 3) adaptive time local convex hull (T-LoCoH), and 4) biased random bridges (BRB); light colour = 50% core range, and dark colour = 90% overall home range.
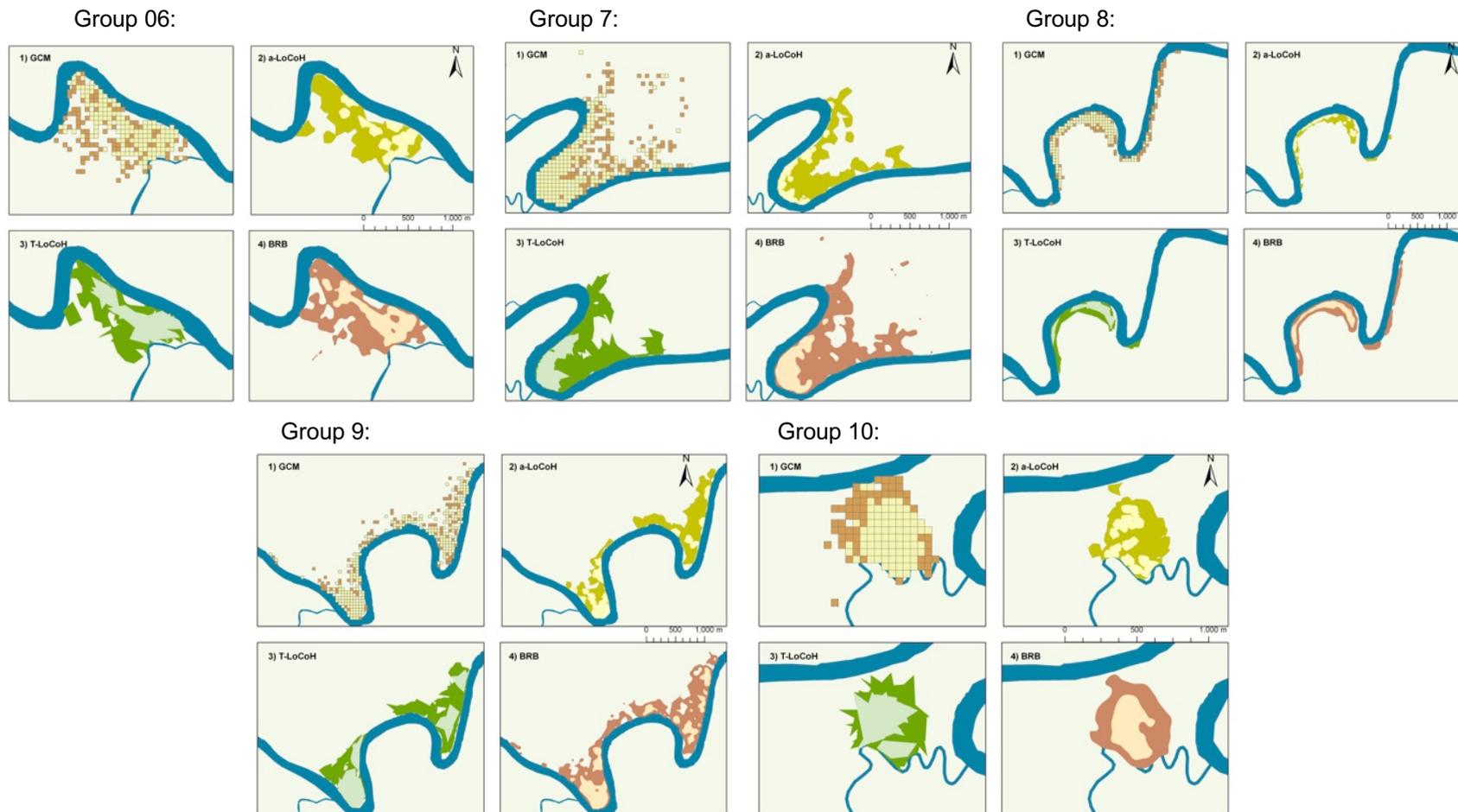
Figure A2.1b    Home range estimates for five proboscis monkey groups in the Lower Kinabatangan Floodplain (Groups 6 to 10): 1) Grid-cell method (GCM), 2) adaptive local convex hull (*a*-LoCoH), 3) adaptive time local convex hull (T-LoCoH), and 4) biased random bridges (BRB); light colour = 50% core range, and dark colour = 90% overall home range.

# Appendix 3 Calculating and selecting LiDAR-derived structural parameters

## A3.1 LiDAR-derived structural parameters calculations

### A3.1.1 Canopy and crown features

Focal statistics were calculated for top-of-canopy parameters using the *pktool* plugin (http://pktools.nongnu.org) in QGIS 2.18 (QGIS Development Team 2009): mean canopy height, maximum canopy height, standard deviation in canopy height, and modal and median canopy height. Additional top-of-canopy height distributions parameters were calculated in R 3.1 (R Core Team 2015) using the focal tool in the *raster* package (Hijmans 2016): skewness, kurtosis, coefficient of variation in height, quadratic mean of canopy height, and interquartile range. Canopy crown features were extracted using the grid calculator in SAGA 4.0 (Conrad et al. 2015) Canopy cover (CC10) was defined as the proportion of area occupied by vegetation above 10 m: the number of pixels with vegetation ≥10 m were divided by the total number of pixels over a 10 x 10-m area (Davies et al. 2017). The Crown Island Area Index (CIA) was the final measurement to describe the general outer-canopy topography, which identified trees above the main canopy level (e.g. emergent trees). A pixel was classified as a CIA when a canopy height pixel was greater than two-thirds the global 0.99-quantile (Nieschulze et al. 2012). Canopy gaps were identified using two different methods. The first definition of a gap was using the classical definition of Brokaw's law (GBRO), which defined gaps as canopy openings that reach down to an average height of 2 m or less (Brokaw 1982). However, as a 2 m threshold may not account for the differences in canopy heights within and between habitats types, a modified adaptive median threshold was also calculated (GADP), which identified gaps based on changes in canopy height relative to the surrounding canopy height (Nieschulze et al. 2012). Using this method, a pixel was classified as a gap when its height was less than the median height within a local neighbourhood minus the corresponding interquartile distance, or when the height is less than 1 m (Nieschulze et al. 2012). Areas 12 $m^2$ or

greater were classified as gaps for GBRO and GADP (Davies et al. 2017). The gap index for GBRO and GADP was calculated as the proportion of cells in a 3 x 3 m window that were gaps.

*A3.1.2 Vertical canopy*
To examine the internal structure in the forest, the LiDAR point cloud was binned into volumetric pixels (voxels) at 1-m height intervals using the raster calculator in ArcGIS 10 (ESRI 2011). The percentage of returns above 3 m was calculated for the canopy density (VCD), and the percentage of returns from 1-3 m was calculated for the understory density (VUD) (Vogeler et al. 2014). The vertical distribution ratio (VDR) was calculated by subtracting the median canopy height from the top-of-canopy height and dividing it by the canopy height (Goetz et al. 2007). An alternative measure of canopy vertical complexity was canopy layering (VCL), derived by counting the number of 1-m canopy layers where vegetation was present within each height column (Davies et al. 2017). A structural diversity index (LiDAR-derived Height Diversity Index, referred to hereafter as vertical diversity index, VDI) and corresponding evenness (LiDAR-derived Height Evenness Index, VEI) were calculated as structural complexity surrogates, as per Listopad et al. (2015), with the modification of using the 1 m height intervals rather than 0.5 m. The VDI is a variation of the Shannon-Diversity index whereby species is replaced by height, and VEI is a variation of Pielou's Evenness Index, where the VDI is divided by the maximum height classes represented in a plot (Listopad et al. 2015).

Table A3.1 Standard deviation, proportion of total variance and loading coefficients between the original 20 LiDAR-derived structural parameters for the first four principal components. The highlighted cells indicate the highest or second highest loading coefficients that were selected to represent their corresponding PC, based on the potential ecological relevance to proboscis monkeys.

| | PC1 | PC2 | PC3 | PC4 |
|---|---|---|---|---|
| Standard deviation | 3.107 | 1.803 | 1.324 | 1.020 |
| Proportion | 0.483 | 0.163 | 0.088 | 0.052 |
| Cumulative | 0.483 | 0.645 | 0.733 | 0.785 |
| **HMEAN** | **-0.312** | 0.000 | -0.156 | 0.042 |
| HMAX | -0.272 | 0.226 | -0.131 | 0.127 |
| **HSD** | -0.078 | **0.503** | -0.060 | -0.063 |
| HMODE | -0.291 | -0.053 | -0.154 | -0.028 |
| HMED | -0.310 | -0.019 | -0.160 | -0.002 |
| HSKEW | 0.168 | 0.171 | 0.069 | 0.300 |
| HKURT | -0.029 | -0.221 | -0.192 | 0.315 |
| HCOV | 0.187 | 0.399 | -0.093 | -0.008 |
| HQM | -0.310 | 0.043 | -0.164 | 0.038 |
| HIQR | -0.054 | 0.496 | -0.016 | -0.163 |
| CC10 | -0.288 | -0.035 | 0.023 | 0.020 |
| CIA | -0.240 | 0.017 | -0.369 | 0.066 |
| GBRO | 0.142 | -0.037 | -0.463 | 0.026 |
| GADP | -0.043 | -0.048 | -0.092 | **-0.856** |
| VCD | -0.248 | -0.067 | 0.391 | 0.001 |
| VUD | 0.242 | 0.085 | -0.339 | 0.028 |
| VDR | 0.163 | 0.372 | 0.044 | 0.096 |
| VCL | -0.284 | 0.135 | -0.023 | 0.075 |
| VDI | -0.281 | 0.144 | 0.172 | 0.076 |
| **VEI** | -0.100 | 0.118 | **0.411** | 0.019 |

# Appendix 4 Patch visitation durations and rates for each individual

Table A4.1 Average individual residence times (hours), recursion rates (days) and the number of patches for each home range (N = 10 proboscis monkeys); SE is the standard error in patch visitation or recursion rates per individual.

| Group ID | Residence time (SE) | Average days between visits | | | | Number of patches | |
|---|---|---|---|---|---|---|---|
| | | ID | SE | RD | SE | ID | RD |
| 1 | 3.1 (0.8) | 27.7 | 10.2 | 20.0 | 8.4 | 36 | 12 |
| 2 | 3.0 (0.5) | 11.1 | 4.8 | 1.5 | 0.1 | 18 | 1 |
| 3 | 3.4 (0.5) | 6.6 | 1.6 | 15.8 | 2.6 | 11 | 5 |
| 4 | 3.1 (0.6) | 12.5 | 5.4 | 10.3 | 3.3 | 38 | 8 |
| 5 | 3.9 (0.8) | 23.3 | 15.6 | 10.9 | 2.3 | 16 | 3 |
| 6 | 2.3 (0.5) | 14.5 | 7.4 | 1.3 | 0.1 | 23 | 1 |
| 7 | 2.7 (0.6) | 18.8 | 8.6 | 7.5 | 2.1 | 33 | 3 |
| 8 | 3.5 (0.8) | 12.5 | 6.1 | 9.2 | 2.1 | 13 | 2 |
| 9 | 3.0 (0.7) | 5.7 | 3.9 | 8.6 | 2.3 | 30 | 11 |
| 10 | 2.4 (0.2) | 16.0 | 8.7 | 1.1 | 0.0 | 13 | 1 |

# Appendix 5 Relationship between proboscis monkey movement patterns and available forest
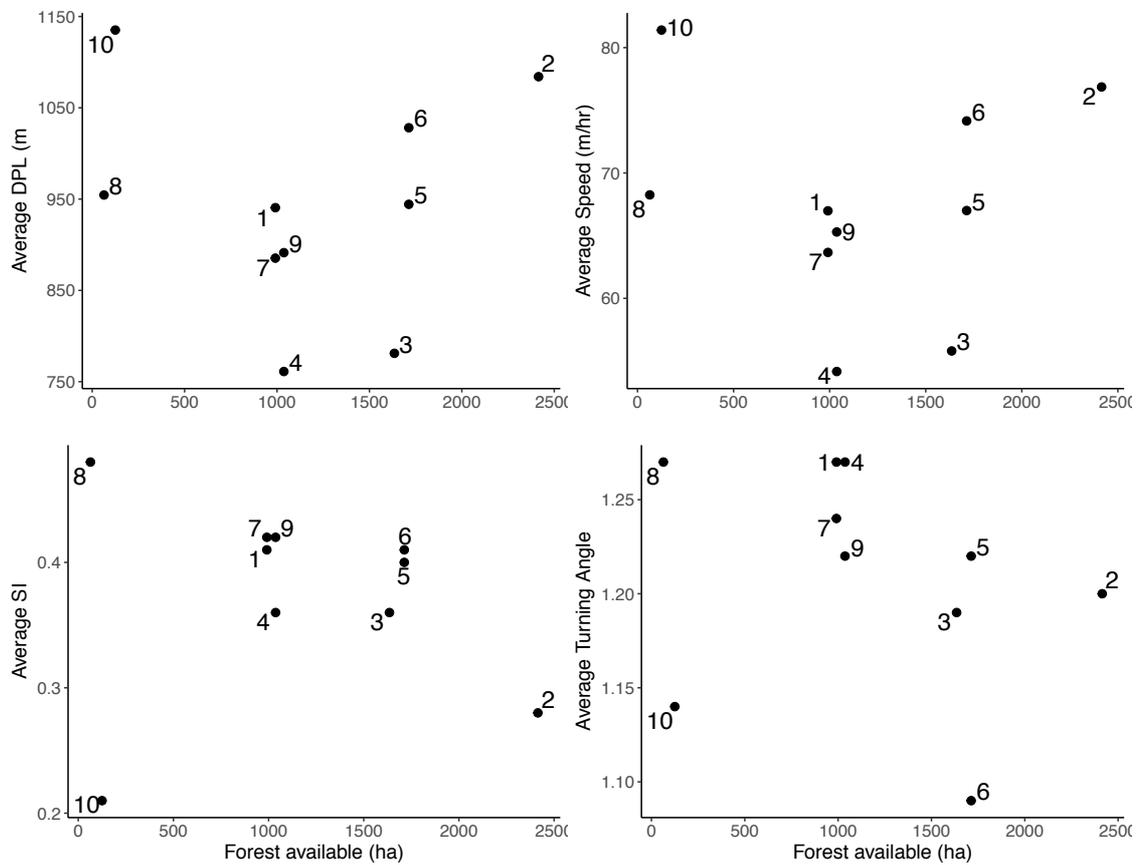


Figure A5.1 Kendall's tau correlation test was used to test for relationship between forest availability and movement patterns (daily path length (DPL), speed, straightness index (SI) and turning angle. Numbers represent Group ID. No correlations were found for any of the variables (all p>0.1).

# Appendix 6   Detailed map of proboscis monkey (Group 3) sleeping sites in relation to forest clearing
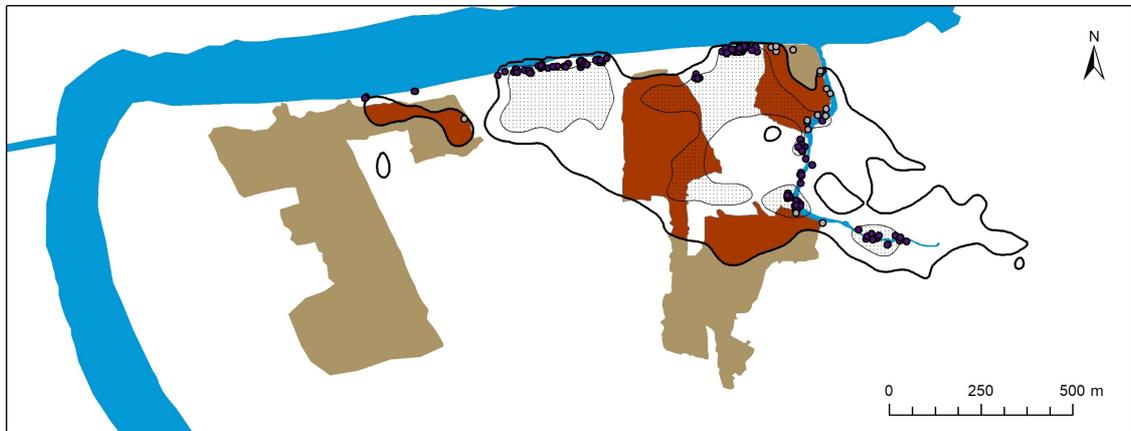


Figure A6.1 The logged areas detected by the drone images in 2015 (light brown), along the Kinabatangan River (blue). Dark points indicate GPS fixes of the sleeping sites from an adult male proboscis monkey throughout the tracking period (2012); white points indicate those sleeping sites affected by the deforestation event. Home range is delineated by the dark outline, as calculated using biased random bridges and the patterned areas delineate the core range.