Behaviour and Spatial Ecology of the Bornean elephant (*Elephas maximus borneensis*) in Lower Kinabatangan, Sabah, Malaysia Borneo

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DECLARATION

This work has not been submitted in substance for any other degree or award at this or any other university or place of learning, nor is being submitted concurrently in candidature for any degree or other award.

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This thesis is being submitted in partial fulfilment of the requirements for the degree of PhD.

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This thesis is the result of my own independent work/investigation, except where otherwise stated. Other sources are acknowledged by explicit references. The views expressed are my own.

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Pohon sirih pohon selasih
Tumbuh merimbun di hujung laman
Kalungan budi junjungan kasih
Menjadi kenangan sepanjang zaman

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LIST OF PUBLICATIONS

Publications associated with this thesis

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Additional responsibilities arising from this thesis

1. Committee member of Technical Working Group for Malaysia-UNDP Multiple-Use Forest Landscapes Project Area in Sabah.
2. Professional membership: International Union for Conservation of Nature (IUCN) Species Survival Commission (SSC) Asian Elephant Specialist Group (AsESG).
3. Co-supervisor for Master student: Brittany L. Thompson. Registered at University of Amsterdam. Project title: Spatial and temporal trends of Bornean Elephant (*Elephas maximus borneensis*) hotspots in oil palm plantations, Lower Kinabatangan, Sabah.

SUMMARY

The Bornean subspecies of Asian elephant (*Elephas maximus borneensis*) is mainly restricted to Sabah, Malaysia and the survival of these elephants in the wild is being jeopardized primarily through a combination of habitat loss, conflicts with people and low genetic diversity. Lower Kinabatangan Floodplain (LKF) which holds between 200 and 250 elephants is isolated from the other populations in Sabah and highly vulnerable to both anthropogenic and non-anthropogenic pressures such as climate change and further encroachments to their natural habitat. Solutions to these challenges require information on the factors affecting the movement and behaviour of the species.

This thesis examines the behavioural and spatial ecology of the Bornean elephant in the Lower Kinabatangan region of Sabah, in Malaysian Borneo. Elephants were monitored visually, and to facilitate remote-monitoring of movement, six female elephants were fitted with satellite collars during the flooding and non-flooding seasons of 2011-2012 (n=3 individuals) and 2013-2014 (n=3 individuals) respectively. In Chapter 2, the seasonal variations in spatial utilization distribution were quantified using analytical methods such as dynamic Brownian Bridge Movement modelling (dBBMM) and Classification and Regression Tree (CART). This analysis showed that the size of utilization distribution (UD) varied significantly between individuals and seasonally. In both seasons, the elephants were observed to maintain their UD close to the river. In the flooding season elephants were less selective about their space use and were more predictable in their movements than in the non-flooding season and were more mobile in higher elevation and good quality habitats. In the non-flooding season, the utilization distribution of elephants was larger and mostly determined by anthropogenic factors such as roads. The core home range areas of elephants in both seasons mostly reflected the need to satisfy their dietary and water requirements.

In Chapter 3, Brownian motion variance generated from the elephants' movement data was used as a measure of behavioural state relating to motion, to describe the behaviour of the elephants (Chapter 3). Human activities and environmental features were used to explain the changes of motion variance and speed in a fragmented landscape. The data were analysed using generalized additive mixed model (GAMMs). This analysis revealed that elephant movement dynamics and speed show significant temporal (diurnal and seasonal) and spatial (between habitat) variation.

Finally, in Chapter 4, I carried out the first longitudinal analysis of the activity budget of adult female elephants in the oil palm plantations, freshwater swamp and riparian habitats adjoining the Kinabatangan River, in order to understand how elephant behaviours vary in relation to habitat, time of day, season and group size. We used generalised additive mixed models (GAMMs) to examine how the behaviours of 40 individually-identified adult female elephants (primarily feeding, moving, resting, bathing, social interactions, and vigilance) varied in relation to time of the day, season and group size, in the major habitat

types within this landscape. Elephants primarily fed in the morning and evening, and rested in the middle of the day. In oil palm plantations, elephants were observed to associate in smaller groups, and to feed less feed and to socialize less, and to be more restless, vigilant and mobile compared to riparian habitats. A similar comparison between semi swamp and riparian forest showed significantly higher feeding and vigilance behaviour in freshwater swamp forest but no significant difference in resting and moving. Our results show that riparian and seasonal freshwater swamp habitats play an important role as a social arena for the Bornean elephants in LKF, as well as providing food resources and connectivity for movement of elephants across this landscape that is increasingly fragmented by oil palm plantations and other human infrastructure such as roads and bridges.

Chapter 5 summarises the main findings of this thesis and the implications for the conservation of the Bornean elephant at the local, national and global scale. These findings together comprise the most detailed account to date of the behaviour and spatial ecology of wild Bornean elephants, and will be used to inform conservation policy (e.g. maintaining connectivity between patches of natural habitat types) and mitigation of human-elephant conflict (e.g. through an improved understanding of daily and seasonal variation in behaviour, and behavioural differences between habitats).

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CHAPTER 1

GENERAL INTRODUCTION

Asian elephants (*Elephas maximus*) have a remarkable social and cultural value, and are icons for spiritual teaching (Ramanathapillai 2009). They are regarded as the Lord of Beginnings and the Remover of Obstacles to the Hindus and to the Buddhists. In the Holy Quran there is a chapter entitled “Al-Fil” - the Elephant; it describes the events that happened in the year when Prophet Muhammad (peace be upon him) was born, when Allah (He, The Most High) reminded the Quraysh tribe who dominated Mecca, of the favours that Allah had bestowed on them by saving the holy building of the Kaaba from being destroyed by the army of elephants (Figure 1.1). Elephants have participated in human history and as formidable instruments of war (e.g. Hannibal), whereas today it has a more positive role as a flagship species for promoting biodiversity and ecotourism within its range (Sukumar 2003; Barua et al. 2010; Othman et al. 2013).

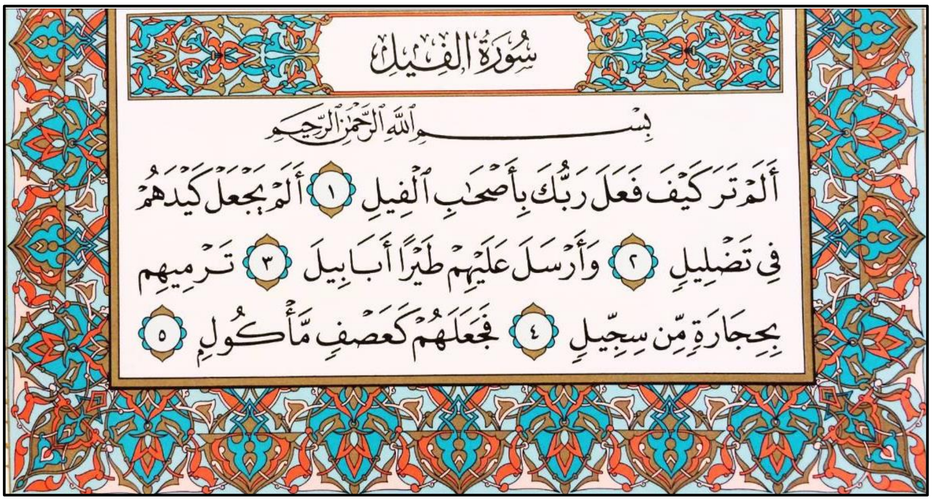


Figure 1.1 “The year of Elephants” as described by the chapter of the Elephant (Al-Fil) reminds the Muslim of the favours of Allah SWT.

Unfortunately, nowadays Asian elephants are often despised by local people with whom elephants may come directly into conflict, and regarded as an agricultural pest as a result of the continued conversion of its natural habitat to human uses, and the conflict that arises when elephants continue to use this land (Bandara and Tisdell 2002; Oswin Perera 2009). To make sure that the Asian elephant has a viable long-term future in the wild, we need to understand its ecological needs. Evidence-based conservation of Asian elephants requires the use of robust scientific data to provide the best available evidence to inform wildlife managers (Blake and Hedges 2004; Aarde et al. 2006; Fernando and Pastorini 2011). Currently, in many instances, the decisions made to manage elephants in their natural habitat are based on the experience or opinion (often with little evidence) of the wildlife managers and authorities (Pullin et al. 2004; Sutherland et al. 2004; Young and Van Aarde 2011).

In this chapter, I provide the latest information on the biological and ecological status of the Asian elephants, as discussed by 77 elephant specialists from 15 countries during the 8th Asian Elephant Specialist Group Meeting that was held in November 2016 at Guwahati, India. During this meeting, all the major specialists working on the conservation of Asian elephants gathered to discuss the current status of wild and captive Asian elephants and measures for the long-term conservation of elephants in Asia.

1.1 The Asian Elephant (*Elephas maximus*)

The Asian elephant can be found in 13 countries in Asia (Figure 1.2), and several different sub-species occur in different parts of the overall species range. The nominate subspecies of Indian elephant (*Elephas maximus indicus*) can be found in mainland Asia, in India, China, Vietnam, Myammar, Thailand, Laos, Cambodia and Malaysia. Two sub-species of Asian elephant are found on the islands of Sumatra, Indonesia (*E. m. sumatranus*) and Borneo (*E. m. borneensis*) (Fernando et al. 2006; Azmi and Gunaryadi 2011). Meanwhile, although the status of Sri Lankan elephants is weakly supported by analysis of allozyme loci, but the analysis of mitochondrial DNA (mtDNA) sequences supported the sub-species status for Sri Lankan elephants as *E. m. maximus*. All Asian elephant sub-species are classified as “Endangered” in the IUCN Red List-apart from the Sumatran elephant, for which the status was upgraded in 2011 to “Critically Endangered” (Azmi and Gunaryadi 2011).

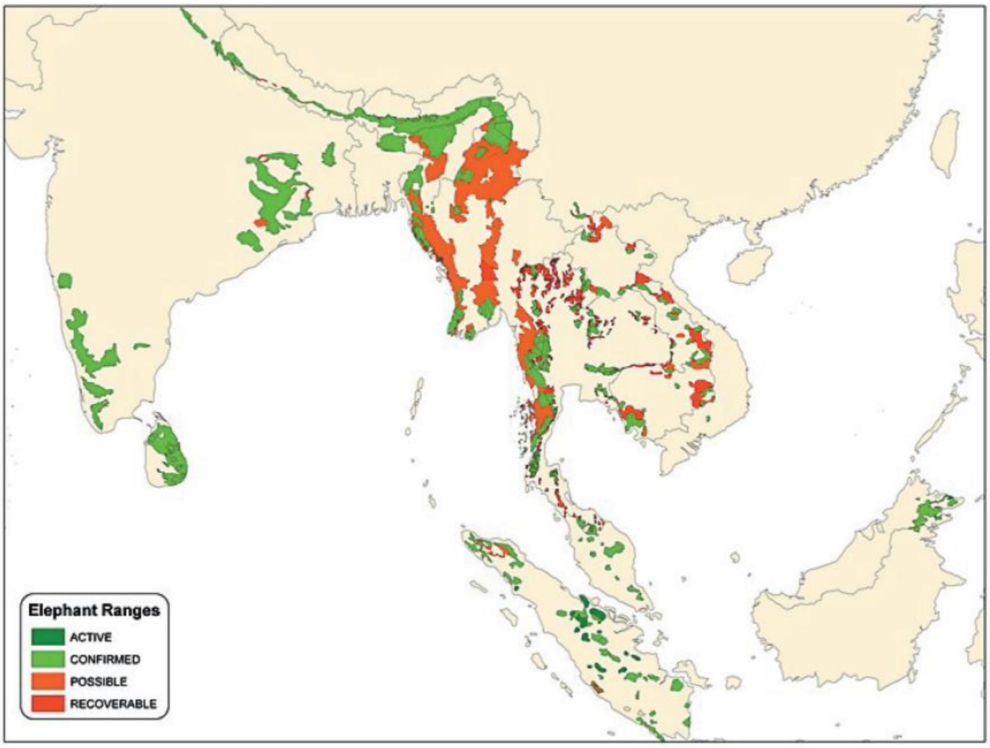


Figure 1.2 Asian elephant distribution across Asia. “Confirmed” are areas in which there is no reasonable doubt that wild Asian elephants occur based on direct field sightings and data from satellite telemetry. “Possible” are areas within the established/well-documented historical range, in which wild Asian Elephants are thought to occur based on confirmed reports which predate January 1998 and where there are no subsequent data to rule out the presence of Asian Elephants. “Recoverable” areas are land where suitable habitat remains over sufficiently large areas that either natural or assisted recovery of the species might be possible within the next 10 years (figure taken from Hedges et al. 2008).

Very little is currently known about the population size and trend of the different Asian elephant sub-species, mostly due to a lack of long-term population monitoring programs, and inconsistency in systematic collection of data due to lack of funding and personnel (Blake and Hedges 2004; Hedges 2012). Population estimation is important for management of elephants, to know the current status of the species and how these are changing over time. In addition, by knowing the population size, we will be able to learn whether conservation objectives are being met, to understand and predict response to future management and to react adaptively to new conservation challenges as they arise (Nichols and Ullas 2012).

The methods used to estimate population size in Asian elephants include; block counts, drive counts, water hole counts, distance sampling, dung counts, DNA census methods, physical and photographic capture–recapture methods (Goswami et al. 2007; Vidya et al. 2007; Hedges et al. 2008; Pastorini et al. 2010; Goswami et al. 2012; Hedges et al. 2013). However, all methods have their advantages and disadvantages. Elephant surveys along transects are difficult to implement in areas with steep mountainous terrains, swamps and other inaccessible areas (Nichols and Ullas 2012). Visual methods are limited in sites where elephants show systematic evasive movement due to their wariness of people. Elephant dung surveys along transects have a scientific basis and have an advantage of higher sample size compared to more direct counting methods involving visual detection of elephants along transects (Pastorini et al. 2010). However, dung counting is an indirect method where defecation rate and decay rates are very hard to estimate (Hedges et al. 2013). Photographic capture-recapture gives survival, recruitment and movement rates over time. However, no extrapolation can be made to non-sampled areas and it is difficult in sites where elephant detections are low because of poor visibility or low densities (Goswami et al. 2007; Goswami et al. 2012). DNA-based capture-recapture has higher accuracy and precision than dung-based distance sampling (Vidya et al. 2007). It also provides additional information on population structure, inbreeding and relatedness within the population (Gray and Phan 2011). However, it requires high technical expertise, it is expensive for large populations and it has potential for misidentification of individuals. Non-invasively collected sources of DNA (i.e. hair, feces and saliva) could potentially cause genotyping error as it yields little target DNA and may contain polymerase chain reaction (PCR) inhibitors (Taberlet et al. 1996; Wagner et al. 2006). So that microsatellite genotypes from these samples for example could be affected by misprinting (false alleles) and allelic dropout (failure of alleles to amplify) (Creel et al. 2003). Therefore, distance sampling or capture-recapture based methods are often the most accurate. For high density populations, direct distance sampling or photographic capture-recapture should be preferred and at low density or in regions with difficult terrain, DNA-based capture-recapture should be for selected regions.

Based on official estimates during the AsESG meeting 2016, the global Asian elephant population (all sub-species combined) is currently reported to be between 45,826 and 53,306 elephants, spread across 13 range states (Table 1.1). However only about 6% of these numbers have been estimated with a method that stands up to scientific scrutiny and can be termed as reliable. Most of the reported numbers are ambiguous given that the methods used are either not accepted as reliable or are not reliable at the scale they were conducted. There is therefore an urgent need to use more reliable and well-established methods to estimate elephant population size, where necessary, and more importantly to agree on methods to map the distribution of elephants in SE Asia. Between 10–13% of the reported numbers seem to be doubtful given that no actual field surveys have taken place and are based solely on informed guesses made on the basis of a few signs encountered, or best-guess estimates based on interviews and conversations with local communities. In certain populations, the application of molecular genetic studies to estimate the population size is hindered due to a lack of genetic diversity in the elephant population inhibiting individual identification, or the species can be elusive and occurs at low densities, making genetic sampling problematic (Fernando et al. 2003; Gray and Phan 2011).

Table 1.1 Estimates of wild Asian elephants across the range and tabulation of the reported numbers according to data quality.

Country	Reported Population Size	Estimation methods		
		Reliable estimates (Dung transects, fecal DNA, capture-recapture etc.)	Possible estimates (Actual counts, block counts, camera trap video captures of herds, etc.)	Doubtful estimates (based on signs, and interviews with local people etc./informed guesses etc)
India	29,391–30,711		29,391–30,711	
China	219–242 (Zhang et al. 2015)	219–242		
Malaysia (Peninsular)	1,223 – 1,463 (Saaban et al. 2011)	744		479–719
Malaysia (Sabah)	2,040 (Alfred et al. 2010)		1,184–3,652	
Thailand	2,490–3,300	800–1,100	800–900	990–1,300
Cambodia	281–319	201–314	48	
Myanmar	2,000–4,000			2,000–4,000
Vietnam	84–105	24–25		60–80
Bangladesh	270–327		270–327	
Nepal	107–145	80	27–65	
Laos	600 – 800 (Khounboline 2011)			600–800
Indonesia	1,700	852	868	
Kalimantan (Indonesia, Borneo)	60–100			60–100
Sri Lanka	5,879		5, 879	
Bhutan	250–500		250–500	
Total (Min–Max)	**45,826–53,306**	**2,920–3,357**	**38,717–42,950**	**4,189–6,999**

Asian elephants face many threats in the wild, primarily related to habitat loss and fragmentation (Dawson and Blackburn 1991; Leimgruber et al. 2003; Songer et al. 2012). Human populations are growing throughout all of the countries in the Asian elephant's range. This has resulted in the destruction of the forest for agriculture, livestock grazing, and infrastructure development such as settlements, and through heavy logging practices (Sukumar 2003; Fernando and Pastorini 2011). Only half of natural vegetation types (including grassland, shrubland/savanna and forest) are now left to support a viable elephant population in Asia (Leimgruber et al. 2003).

As the natural habitat of Asian elephants shrinks, elephants are forced to locate food sources outside of the forest (Fernando, Wikramanayake, et al. 2008; Kumar et al. 2010). Often, these food sources are local villagers' subsistence crops such as banana, paddy (*Oryza sativa*) and oil palm (*Elaeis guineensis*). As a result, human-elephant conflict (HEC) is on the rise and is becoming a major challenge for elephant conservation across the range states. Several traditional methods, like the strategic positioning of bee hives (which elephants avoid) and fencing with chilies, have been tried to mitigate HEC, as well as modern methods such as electric fencing (Oswin Perera 2009; Desai and Riddle 2015). However, in many instances attempts to mitigate HEC fail due to several factors such as electric fences not being maintained, elephants being blamed for loss caused by other species, superstitions and political reasons (Linkie et al. 2007; Sillero-Zubiri et al. 2007). Managing HEC requires a very good understanding of the human and political dimensions of the situation (Zimmermann et al. 2009). The causes of such conflicts can be complex, but there is currently a poor understanding of what drives HEC and how we can influence it. Human fatalities also regularly result from the clash of humans and elephants, so every unsuccessful attempt to mitigate HEC adds to making the conflict worse. In addition to habitat loss and HEC, Asian elephants are also poached regularly for their ivory tusks and other body parts (Sukumar 2003; Desai and Riddle 2015).

Among other issues that were discussed during the AsESG meeting 2016 were revolving the number and welfare of captive elephants in the 13 range countries. Captive elephants are traditionally used for labor, forest patrolling, ceremonial processions, display, toruism and entertainment (Harris et al. 2002; Lorimer 2017). Welfare of captive elephants is a concern as there is (i) inconsistent management of captive elephants, (ii) intense criticism of elephant management in tourism in particular and (iii) a need for practical guidelines and standards to effectively manage elephants under different captive conditions. Currently, these captive elephants are estimated to number around 15,106 and thus represent a substantial proportion of the global population. Future conservation management of the species and its subspecies could draw on this captive group of elephants for management of genetic diversity in the wild, captive breeding and reintroduction programs.

1.2 The Bornean Elephant (*Elephas maximus borneensis*)

The Bornean elephants have the smallest distribution range of the four sub-species (Othman et al. 2013). It differs in its morphology and behavior from other sub-species, some claim that Bornean elephant are milder tempered (Shim 2000; Othman et al. 2013; Payne and Davies 2013). The heights of male Bornean elephants, which were measured during translocation due to conflict, range between 1.57 m – 3.64 m with an average of 2.17 m. While females are between 1.45 m – 2.26 m, with an average of 1.96 m. The Bornean elephant is distributed only in the northeast of Borneo island, mostly in the east of Sabah in Malaysia and across to the north Kalimantan of Indonesia. Since 2013, the Bornean elephant is protected under the Schedule I "Totally Protected Species" which is the highest level of protection under the Sabah Wildlife Conservation Enactment 1997. Consequently, any person caught killing or hunting an elephant will receive a mandatory six months to five years jail sentence (Elephant Action Plan, 2012-2016).

It is estimated that there are currently about 2,040 elephants in Sabah, roaming in five managed elephant ranges (Alfred *et al.*, 2010). The managed elephant ranges are Lower Kinabatangan, North Kinabatangan, Central

Sabah, Tabin and Ulu Kalumpang with estimates of 298, 258, 1,132, 342 and 10 elephants respectively (Figure 1.3) (Elephant Action Plan, 2012-2016). There have been several attempts to estimate the size of Bornean elephant population (Table 1.2). The most up-to-date estimation was done between 2007-2008 using the dung count method (Alfred et al. 2010), however many elephant experts in Sabah believe that these numbers are overestimated and there is an urgency to re-survey the elephant population following robust methodology.

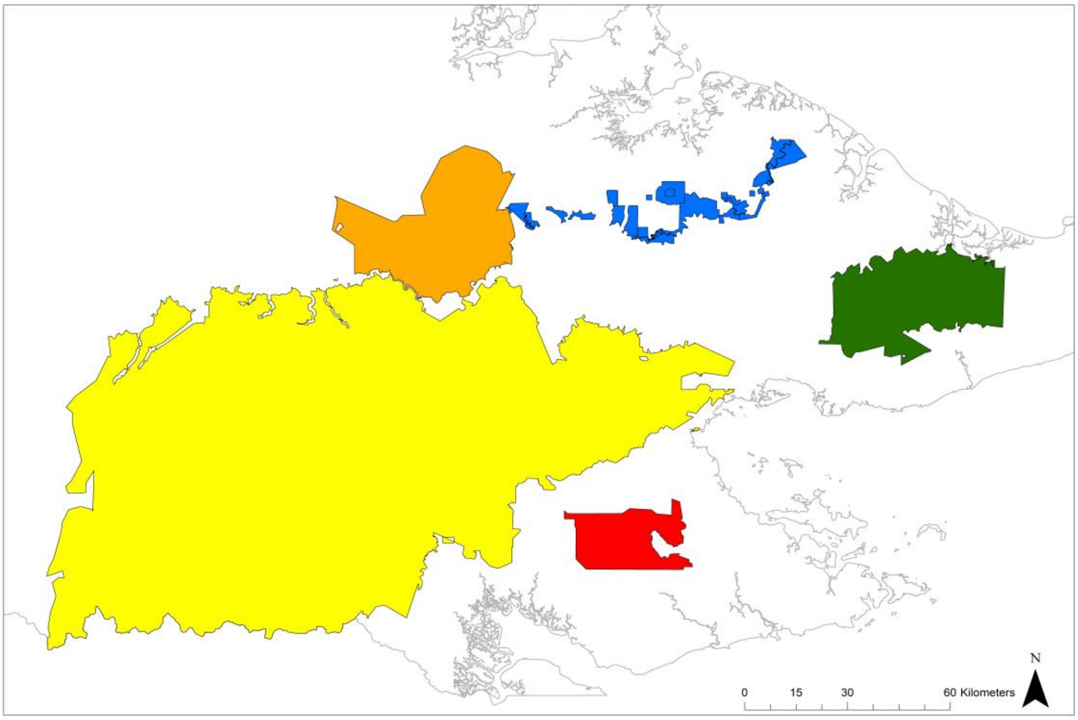


Figure 1.3 The Bornean elephant distribution in Sabah. Each of the colours represent a Managed Elephant Range (MER); Green = Tabin, Yellow = Central Sabah, Blue = Lower Kinabatangan, Orange = North Kinabatangan and Red = Ulu Kalumpang. MER is a concept which provides a landscape-level approach which sets the elephant's ecological requirement as the priority while allowing for compatible human activities such as reduced-impact forestry, slow rotation shifting cultivation, and controlled livestock grazing in the area (Santiapillai and Jackson 1992; Hedges et al. 2008).

Table 1.2 Population size estimation for the Bornean elephant.

Number of elephants		Method(s)	Sources
Min.	Max.		
NA	2,000	Unknown	(de Silva 1968)
500	2,000	Direct observation of animals	(Davies and Payne 1982; Payne and Davies 2013)
1,127	1,632	Direct count, dung count, questionnaire survey	(Ambu et al. 2002)
1,184	3,652	Dung-count	(Alfred et al. 2010)

Similar to the other elephant populations across Asia, the major threats to the survival of the Bornean elephant are 1) habitat loss and fragmentation; 2) low genetic diversity; 3) poaching, illegal killing, snare trapping and illegal trade and 4) poor public awareness about the conservation needs for the species (Elephant Action Plan, 2012-2016).

1.3 Major Threats to Bornean Elephants

1.3.1 Habitat loss and fragmentation

Sabah started to expand its agricultural sector in the early 1980s, and is currently the largest producer of oil palm in Malaysia (Abram et al. 2014). The rapid and uncontrolled pace of agricultural expansion has resulted in a declining forest area and quality (McMorrow and Mustapa 2001; Reynolds et al. 2011), affecting many animal and plant species and reducing biological diversity and the size of species populations (Fitzherbert et al. 2008; Fayle et al. 2010). Habitat loss and fragmentation force elephants to travel widely to find resources such as food, minerals and safety (Sitati et al. 2003; Joshi and Singh 2007; Alfred et al. 2012). Currently, the Bornean elephant is found in five Managed Elephant Ranges (MERs), with two of these, Lower Kinabatangan and Tabin, being isolated from the other populations by human settlements, roads, logging activities and land transformation to oil palm plantations (Elephant Action Plan, 2012-2016).

Habitat loss and fragmentation has not only reduced the gene flow between sub-populations, but has also created conflicts with people (Goossens et al. 2016). Only a few conservation planning projects have taken into account the land use of elephants, such as shown in Othman *et al.* (2013). Human-elephant conflict have increased costs on both sides: 1) economic losses from crop raiding and infrastructural damage by elephants and 2) protective actions and retaliation measures by people that cause injury or death of elephants (Sitati et al. 2003).

1.3.2 Low genetic diversity

Previous uncertainty over the evolutionary origin of the Bornean elephant has been greatly clarified by a series of population genetic analyses using recent techniques such as the full-likelihood Bayesian approach. In a comparison of model's estimation based on relevant demographic and historical parameters, such as the effective population sizes of founding populations, and putative introduction times, using both microsatellite and mitochondrial data, Sharma et al. (2018) concluded that new analyses supported a natural colonisation of Bornean elephants via the Sunda shelf at the end of the Pleistocene bottleneck, 11,400-18,300 years ago. This conclusion strongly reinforces the conservation value of this species and its future.

However, the Bornean elephant is still susceptible to stochastic events such as disease outbreaks or climate change due to the low levels of genetic variation in both the mitochondrial control region and in nuclear genetic markers such as microsatellites and single nucleotide polymorphisms (SNPs) (Sharma et al. 2012; Goossens et al. 2016). The progressive loss of elephant habitat to agricultural expansion, logging activities and human developments mean that exchange of individuals and genes between the fragmented elephant sub-populations is now highly restricted. This with reduction in gene flow between populations, will in turn cause inbreeding in the populations (Fickel et al. 2007).

1.3.3 Illegal killing and Poaching

Illegal killing of elephants as an act of retaliation is becoming a popular option to some people who are directly affected by HEC. In 2013, 14 elephants were found dead over a period of 4-5 weeks in the Forest Management Unit (FMU) 23, a Yayasan Sabah concession area in the Gunung Rara Forest Reserve (Othman et al. 2013). The Sabah Wildlife Department (SWD) determined that the elephants died of poisoning. Until now no arrests have been made although a large financial reward was offered for information leading to the arrest of the parties responsible for the death of the endangered elephants.

In 2016, a few Bornean elephants, including one of our collared male elephants, Sabre, have been slaughtered for their tusks. Soon after the event, a woman carrying five pieces of elephant tusks was arrested in Nunukan, North Kalimantan and these tusks were believed to have come from Sabah. Although all necessary information was provided to the investigators and to the police, no arrest has been made (Figure 1.4). This has brought into question the reliability of the relevant authorities who are responsible for the prevention of illegal wildlife poaching and other illegal activities in Sabah.

Figure 1.4 The remains of Sabre found without his tusks with the satellite collar next to the skull.

1.3.4 Public Awareness

Elephants are sometimes depicted as vengeful animals both by local and international media (Barua 2010; Fernando 2010; Anonymous 2015), but in many cases of HEC, the real culprit was not always the elephants (Linkie et al. 2007). This erroneous description of elephants' behaviour has led to negative perceptions among local people and influences their attitude and tolerance towards elephants (Ebua et al. 2011; Kansky and Knight 2014). In addition, some stakeholders who have converted lands for new initiatives that have failed to take responsibility for preventing, mitigating and managing HEC that has consequently arisen (Fernando 2010; Othman et al. 2013). At the same time, there is no or little coordination among stakeholders to create effective awareness among the public regarding the conservation of the Bornean elephants (Hai et al. 2001).

Despite these negative cultural perceptions of elephants, there are growing numbers of private companies in Malaysia that have recognized the importance of promoting sustainable financing through suitable private–public partnerships and payment for ecosystem services (Hai et al. 2001; Clements et al. 2010; Goossens and Ambu 2012; Payne and Davies 2013). This is important as industry is one of the main players in conservation, both locally and internationally. Industry is not only able to provide support in terms of funding, but can also improve forest connectivity and protection so that animals of formerly fragmented sub-populations can meet and breed naturally (Goossens and Ambu 2012).

1.4 Movement Ecology

Living organisms move in order to survive; including finding mates to reproduce, feeding or escaping threats (Holyoak et al. 2008). Movement ecology research emphasizes "the need to understand the movement of living organisms of all kinds, in the context of their internal states, traits, constraints, and interactions among themselves and with the environment" (Nathan and Giuggioli 2013). For example, moving from one area to another may increase the fitness of a species, potentially enabling avoidance of inbreeding and extinction (Goossens et al. 2016). Movement ecologists are interested in understanding why an organism moves (internal state), or what are the movement strategies (motion capacities), or when and where it moves (navigation capacities) as well as what are the external factors affecting movement (Figure 1.5).

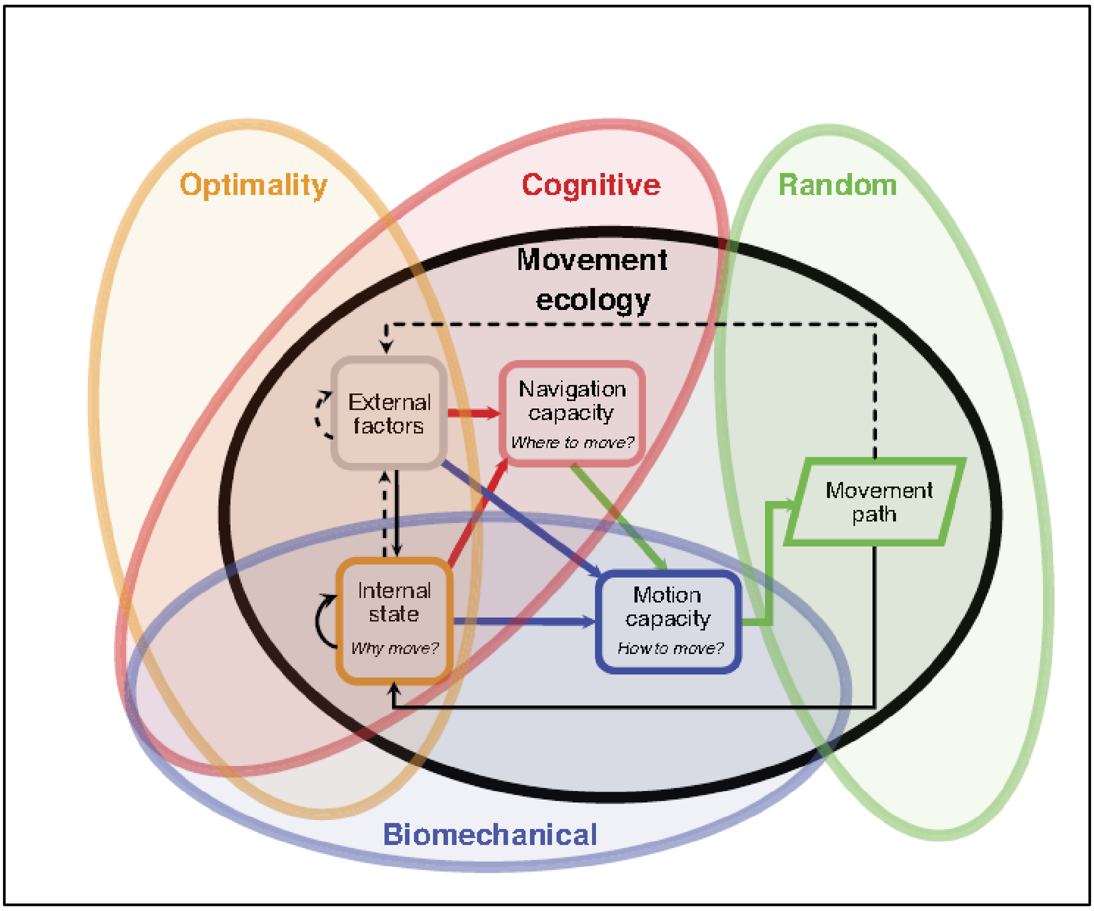


Figure 1.5 A movement ecology framework that integrates four existing paradigms for studying the movements of organisms (adapted from Nathan et al. 2008).

Most previous movement studies of Asian elephants have investigated the navigation capacity of the species (Baskaran and Desai 1996; Williams et al. 2008; Alfred et al. 2012; Sitompul, Griffin and Fuller 2013). However, an urgent priority is to use the insights provided by movement ecology to tackle the impact of habitat loss and expanding human populations on elephant populations throughout their ranges, and to reduce HEC (Sukumar 1989; Leimgruber et al. 2003; Songer et al. 2012).

1.5 Justification of the PhD Study

Elephants and humans are competing for the same scarce and limited resource, namely land. Humans have become more intolerant of HEC, and elephants turn a blind eye to many of the current mitigation efforts (Fernando 2010). To prevent the escalation of HEC cases, we must develop and implement an evidence-based plan for elephant management. This way, we can conserve the Bornean elephant, prevent economic losses to anthropogenic activities from elephant depredation, prevent HEC becoming a major socio-economic and political issue, and allow development of sustainable eco-tourism around viewing elephants.

In this PhD study, I have investigated the movement strategies and behaviour of adult female elephants in a highly fragmented and human-dominated landscape in the Lower Kinabatangan Floodplain (LKF), Sabah, Malaysia. By using both conventional and new technologies such as geographic information system (GIS), I aimed to facilitate the evidence-based management and conservation of one of the most important sub-populations of Bornean elephants, territories based on robust scientific data.

1.6 Study Area

This study was conducted in the Lower Kinabatangan Floodplain (LKF), focusing on the area between the villages of Abai and Batu Puteh (approximately 5°18'N to 5°42'N and 117°54'E to 118°33'E) (Figure 1.6). These are the only ecologically suitable areas that remain available for the elephants in this floodplain (Alfred et al. 2012; Estes et al. 2012). Within the LKF, there are approximately 27,000 ha that were gazetted as a Wildlife Sanctuary in 2005, known as the Lower Kinabatangan Wildlife Sanctuary (LKWS), in addition to the existing forest reserves and virgin jungle forest reserves. The LKWS is divided into 10 forest patches (known as Lot 1-Lot 10) from Abai to Lokan, in order to connect the coastal mangrove swamps with dry land forest upriver (Azmi 1998). These forest patches are surrounded with oil palm plantations, but the patches themselves still hold a variety of endemic species to Borneo, such as the iconic orang utan (*Pongo pygmeus*), proboscis monkey (*Nasalis larvatus*), Sunda clouded leopard (*Neofelis diardi*) and various insect and bird species (Azmi 1998; Ancrenaz et al. 2004; Abram et al. 2014).

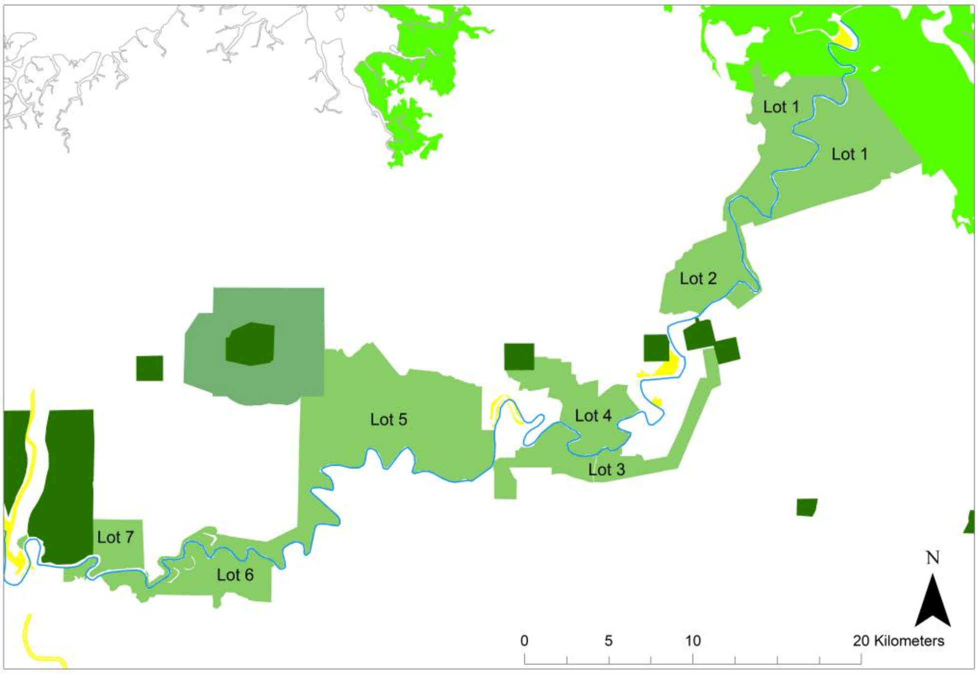


Figure 1.6 Map of the ecologically suitable habitat that is available for the Bornean elephants in the Lower Kinabatangan Floodplain. White = Oil palm plantation, fir green = Class VI-Virgin Jungle Reserve, green = Class I - Protection Forest Reserve, fern green = wildlife sanctuary, yellow = villages, medium apple = Class V – Mangrove Forest Reserve.

1.7 Weather Conditions

Data on rainfall were available from 2010 to 2013, compiled by the Meteorological Department of Malaysia. Annual rainfall averaged about 3400 mm, and the major season as of high and low rainfall were categorized as flooding and non-flooding respectively. However, we did not encounter any major flooding that during the three years of fieldwork (2010-2013). Due to the absence of data on the Kinabatangan River water level, I assumed that the flooding season is likely to happen during the months that received the highest rainfall, which was between December and March (Figure 1.7). To define for the non-flooding season, I selected the months with the lowest rainfall which was from May to August. In certain parts of the river (*i.e.* small tributaries like Menanggol River), the water level could rise up to four meters during flooding season (Matsuda, Tuuga and Higashi 2010). The mean minimum and maximum temperatures were approximately 24˚C and 32˚C, respectively (Ancrenaz et al. 2004).

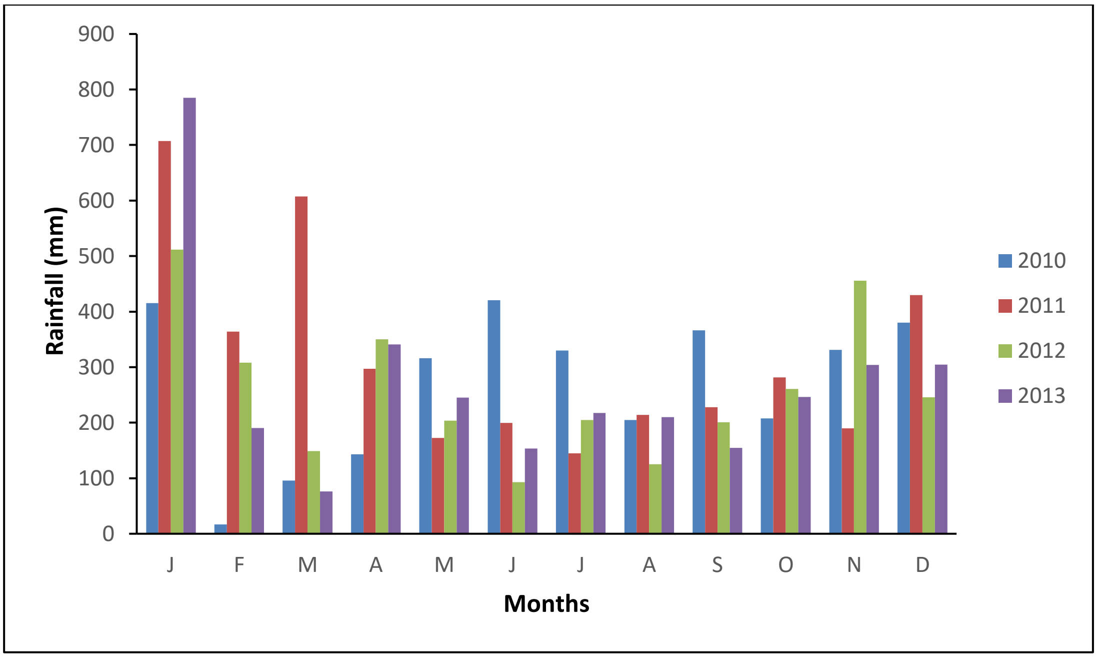


Figure 1.7 Monthly rainfall for Lower Kinabatangan from 2010-2013. The flooding season was defined as December until March, while the non-flooding season was defined as May until August.

1.8 The Bornean Elephants of the LKF

The elephant population in LKF is isolated from the other elephant populations in Sabah and its movement is restricted to certain parts of LKWS (from Abai to Batu Puteh only) by human settlements, oil palm plantations and a highway (Figure 1.6). In 2002, it was estimated that there were between 95-115 elephants in the LKF (Ambu et al. 2002). However, this estimation was an approximation as the extent of suitable habitat was not determined (Alfred et al. 2010). The recent survey using dung counts showed that there are approximately 298 elephants, though the sex ratio and age class profile remains unknown. A recent attempt to use genetics (microsatellite, mitochondria and SNPs) to estimate the population, to examine relatedness and parentage analysis and to determine the sex ratio was hindered due to the very low genetic diversity in the Bornean elephant population. Usually, the elephants were seen to move in a large group, of between 70-150 animals including both female and male elephants (Figure 1.8, *pers. obs.*). The best time to allocate individuals to their family group is when the elephants are crossing the main river. During these crossings, the large herds separate into family groupings which can be clearly be seen due to the greater visibility of individuals at this time (*pers. obs.*). The elephant sub-population in LKF has the highest population density among all elephant sub-populations in Sabah, with 2.15 individuals per km^2 (Alfred et al. 2010). It is likely that the current d ensity of elephants in LKF is due to the recent reduction and fragmentation of the available area of ecologically suitable habitat, rather than being the result of an increasing population size.

This sub-population also contains higher levels of genetic variation compared to the other sub-populations and can therefore be regarded as a "genetic bank" for the Bornean elephant in Sabah (Goossens et al. 2016). It will provide a good genetic resource for elephant introduction and translocation programmes if needed in the future. However, this population is vulnerable to both anthropogenic and non-anthropogenic pressures such as climate change and further encroachments to its natural habitats (Estes et al. 2012; Abram et al. 2014).

All observations and data collected in this study were made only on the adult females. Studies have shown that adult females influence and guide the movement patterns and habitat utilization by the family group as a whole (Sukumar 2003; Gobush et al. 2009; de Silva 2010; de Silva et al. 2011). The female groups behave differently from bulls or male groups. Adult females generally avoid areas with risks, they are more selective in the resources they use and they need to be closer to water and shade because of their smaller size and the presence of young (Shannon et al. 2006; McComb et al. 2011;

Evans and Harris 2012; Srinivasaiah et al. 2012; von Gerhardt et al. 2014). Studies in South India show that adult males and only some female family units raid crops (Balasubramanian et al. 1995). The likelihood that females also actively do crop raiding or venture into risky habitats is highest when the density of the population is high or when there is a significant level of habitat fragmentation which compresses the elephants into small habitat fragments (Desai and Riddle 2015). The frequent use of non-natural habitats represents the challenge of conserving the Bornean elephants in these human dominated landscapes (de Silva et al. 2011; Lee and Moss 2012; Srinivasaiah et al. 2012).

Figure 1.8 A mixed herd which is formed by both females and males in all age classes spending time feeding along the Kinabatangan River.

1.9 Aims and Objectives

The main aim of this study is to provide information on the movement and behavioural ecology of Bornean elephants, in order to facilitate their conservation, and to improve decision making by the relevant authorities in Sabah, to protect the remaining forested area in LKF.

The specific objectives that I will be addressing in order to achieve the overall aim are:

I. Analyses of the utilization distribution of elephants in LKF (Chapter 2)
   - Identify the utilization distribution (ud), core area (50% of UD) and wider home range (95% of UD) of adult females in and around LKF.
   - Identify environmental and human variables that influence utilization distribution of the Bornean elephants.

II. Movement behaviour (Chapter 3)
   - Calculate the motion variance and ground speed of adult females.
   - Elucidate the relationship between elephant behaviour, motion variance and ground speed.
   - Identify environmental and human variables that influence motion variance and speed.

III. Spatial and temporal variation in behaviour of elephants in LKF (Chapter 4)
   - Quantify the activity budget of elephants in different habitat types.
   - Quantify the daily and seasonal routines of elephant behaviour.

Coupling movement and behavioural should provide new insights into the proximal mechanisms and causes of elephants' space use and this approach is novel to LKF. By achieving the main and objectives as stated above, we will be able to identify the constraints to elephants’ movement and understand their perception and adaptation to their surroundings.

CHAPTER TWO

MOVEMENT ECOLOGY OF BORNEAN ELEPHANTS IN A LANDSCAPE DOMINATED BY OIL PALM PLANTATIONS

2.1 Introduction

An animal moves to meet its nutritional and physiological requirements, and therefore its movements can be used as a behavioural assay of the state of its environment (Borger et al. 2008; Giuggioli and Kenkre 2014). Currently, only about half of the historic availability of suitable habitat for Asian elephants remains across their geographical range (Leimgruber et al. 2003; Songer et al. 2012). Human-modified landscapes usually contain few suitable resources for elephants, and where resources are patchily distributed in human-modified landscapes they cannot readily sustain the needs of the elephant population (Fischer and Lindenmayer 2007). As a result, elephants may start to venture outside their favoured forested habitats in order to fulfil their needs. This can potentially lead to human-elephant conflicts, when elephants intrude on areas that are used by- and valued by- humans (Sillero-Zubiri et al. 2007; Fernando et al. 2012; Othman et al. 2013).

Human-elephant conflict (HEC) is identified as the major threat to Asian elephants in the species' range countries. HEC usually arises due to a clash of interests between elephants and people over land and resources (Santiapillai 1997; Leimgruber et al. 2003; Riddle et al. 2009; Fernando et al. 2010; Songer et al. 2012). Elephants are highly mobile and have a strong spatial memory that helps them efficiently to access critical resources and to avoid risk (Sukumar 2003; Polansky et al. 2015). HEC mostly occurs when the traditional routes used by elephants along "habitat corridors" that connect these critical areas or disjunct home ranges become converted to human-altered habitats, and thus elephant access to these core areas is denied (Joshi and Singh 2007; Gubbi 2012; von Gerhardt et al. 2014). Elephants may also be attracted to crops that are highly palatable, resulting in elephants repeatedly returning to agricultural areas (Surendra Varma, *pers. comm.*). Abandoning the traditional routes could be detrimental to the welfare of the elephants as these areas provide them with valuable resources and keep them from danger (Fernando et al. 2009; Fernando et al. 2012; Fagan et al. 2013; Jachowski et al. 2013). Therefore, in order to minimize the impact of HEC; rigorous research into the movement ecology of the animal species is crucial, especially in heterogeneous landscapes (Fagan et al. 2013; Nathan and Giuggioli 2013).

2.2 Home Range (HR) and Utilization Distribution (UD) of Asian Elephants

Many Asian elephant populations occupy remote and inaccessible areas (Blake and Hedges 2004; Riddle et al. 2009; Kumar et al. 2010). Our understanding of the movement behaviour and habitat utilization of Asian elephants in their natural habitat has increased with the aid of Global Positioning System (GPS) telemetry technology (Sitati et al. 2003; Fernando, Wikramanayake, et al. 2008; Graham et al. 2009; Kumar et al. 2010; Alfred et al. 2012; Sitompul, Griffin, Rayl, et al. 2013). This technology has previously been used as an early detection system to mitigate HEC (Venkataraman et al. 2005; Fernando, Kumar, et al. 2008).

Space use by animals is commonly reported as either “home range”, or as “utilization distribution” (UD); the former referring to the total area used by an animal and the latter is referring to the variation in the amount of time spent in geographical space (Getz et al. 2007; Fieberg and Borger 2012; Powell and Mitchell 2012). The advantage of calculating the UD over home range is that UD provides a useful summary of how intensively animals use different areas, rather than a simple two-dimensional representation of the spatial limits of the home range of a given individual (Fieberg and Kochanny 2005; Horne et al. 2007; Kranstauber et al. 2012; Allen 2013). UD is an important metric for other types of analyses of telemetry data; for example, the UD may provide the most informative measure of use in habitat selection studies (Millspaugh et al. 2006). A core area is the part of a home range or utilization distribution that is used with greater intensity and that usually contains high densities of critical resources for the species (Wilson et al. 2010; Powell and Mitchell 2012). By identifying these core areas, we are able to understand the movement strategies of that species and its interaction with the environment.

In general, both African and Asian elephants are known to alter their behaviour in response to habitat features, including water, slope, vegetative cover and human presence (Sukumar 2003; Grainger et al. 2005; Loarie et al. 2009). African elephants were observed to have larger home range sizes compared to those of Asian elephants, mostly due to limited and patchy essential resources such as water and food (Sukumar 2003). Analysis of movement data has revealed that the spatial memory and social rank of the African elephant facilitates resource acquisition when resources are patchy (Wittemyer et al. 2007; Polansky et al. 2015). African elephants avoid human activities, and therefore human-derived landscape features such as roads and infrastructures can hinder the movements of elephants across the landscape (Buij et al. 2007; Blake et al. 2008). Other important environmental factors that trigger long distance movements of African elephants are seasonal change in rainfall, water surface, vegetation productivity and possibly vegetation nutrient content (Wall et al. 2013; Garstang et al. 2014).

Previous studies of Asian elephants have quantified the home range size and examined how elephants use the landscape, in order to facilitate movements and reduce the incidence of human-elephant conflict (Baskaran and Desai 1996; Stuwe et al. 1998; Fernando, Wikramanayake, et al. 2008; Williams et al. 2008; Kumar et al. 2010; Alfred et al. 2012; Sitompul, Griffin and Fuller 2013). Asian elephants are typically highly faithful to their home range, which varied in size - depending on environmental features such as rainfall, habitat types, water and food availability (Baskaran & Desai, 1996; Fernando *et al.*, 2008b; Williams *et al.*, 2008; Kumar *et al.*, 2010; Alfred *et al.*, 2012; Sitompul *et al.*, 2013). The existence of both natural barriers such as limestone outcropping, and non-natural barriers such as electric fencing, could also influence the size of the elephants' home ranges (Williams et al. 2008; Fernando et al. 2010; Estes et al. 2012). Most of these studies were conducted in medium-rainfall seasonal deciduous forest in India, or in dry zone habitats in Sri Lanka, but very few studies have investigated the movement patterns and utilization distribution of elephants in high-rainfall zones (such as tropical forest).

The first elephant movement study in rainforest habitat was carried out in Peninsular Malaysia (Stuwe et al. 1998). This early study used satellite telemetry on one female and one male elephant, to identify the best translocation practices based on the movement strategies of these elephants after being translocated. They found out that the movements of elephant female were erratic at the beginning and covered a large area, and shifted its home range twice in a novel environment. The authors assumed that the female might have searched for its family group because she was separated with them during the translocation. The authors also recommended that current translocation practices for females may need to be reviewed.

The first movement study of Bornean elephants compared space use of elephants in fragmented and non-fragmented habitats (Alfred et al. 2012). This study showed that that the home range sizes of an adult female elephant inhabiting fragmented habitats such as in the Lower Kinabatangan Floodplain (LKF) was larger than in non-fragmented habitats (n = 4) mostly likely due to difficulty to find their daily resource requirements in an environment that has been greatly altered. The other factors influencing the home range size are likely to be the presence of human settlements, barriers such as electric fences within its home range as well as harassment by humans, which influenced the direction and speed of movement. The latest Asian elephant home range study was conducted in a fragmented landscape in Sumatra, Indonesia on a single semi-wild female elephant (Sitompul, *et al.,* 2013). This study revealed that the home range of the Sumatran elephant as small, restricted to the river and roads did not appear to affect elephant movements in the study area. The small ranges of the Sumatran elephant compared to Indian and African elephants was suggested to be related to the stability of environmental conditions (annual rainfall is stable and relatively high which is > 3000 mm/year). As a result, the availability of important resources such as water and palatable plants for elephants are consistent throughout the year and there is less need for elephants in Sumatra to increase their home range size in search of water or food.

This current work will improve our understanding of the movement strategies of Asian elephants which are living in highly fragmented habitats, by examining the movement ecology of a population of Bornean elephants. This LKF population is totally isolated from the other populations, which makes immigration and emigration impossible. One of the highest risks faced by an isolated population is the disruption of gene flow within and between populations, leading to inbreeding depression (Moore 2007). Currently, roads and agricultural activities prevent gene flow between the LKF population and other populations of Bornean elephants (Goossens et al. 2016). To maintain the current levels of genetic diversity in this population, we must seek possibilities to secure connectivity with other, spatially distinct populations. The present study also included larger sample sizes than most previous studies and related the positional data from the satellite collars to the latest environmental and anthropogenic conditions of the study area. I also included the most recent analytical methods to facilitate inference about elephants' movement strategies in LKF.

2.3 Objectives and Hypotheses

The overall aim of this study was to gain insights about movements of six collared female elephants in two seasons (wet/flooding and dry/non-flooding), using Global Positioning System (GPS) satellite tracking data. The objectives of this study were to: 1) to calculate and map the utilization distributions (UDs) and core home range areas (CAs) used by elephants within LKF in the flooding and non-flooding seasons, and 2) to elucidate which environmental variables best explain the UDs and CAs of elephants. Based on the existing studies, I anticipated that elephants' utilization distribution and core areas would be smaller in the flooding season than in the non-flooding season. The findings of previous studies (Hedges et al. 2005; Alfred et al. 2012; Sitompul, Griffin, Rayl, et al. 2013) suggest that UDs and CAs will be located primarily in forest habitat, mainly on nearly flat terrain or on slightly to moderately steep slopes. We also expected that the elephants' UDs and CAs lie close to- or within- disturbed areas such as human infrastructures and roads, while restricting their UD and CAs close to the water resources (Srinivasaiah et al. 2012).

2.4 Materials and Methods

2.4.1 Study Area

The Lower Kinabatangan Floodplain (LKF) is located in the eastern part of Sabah, Malaysian Borneo, and is the largest alluvial floodplain in Malaysia (Payne 1997). The area is mostly flat and surrounded by oil palm (*Elaeis guineensis*) plantation estates (Abram et al. 2014). The LKF received an average annual rainfall of 3,000 mm and 3,400 mm during the fieldwork period of this study (Meteorological Department of Malaysia). Each year there is a distinct dry season and a distinct wet season. Flooding usually occurred in LKF between October and March during the northeast monsoon (Azmi 1998; Hai et al. 2001). During the flooding season, certain areas along the main river and tributaries were flooded with water to a depth of 3-4 m (Matsuda, Tuuga and Higashi 2010). Therefore, all data were analysed based on flooding and non-flooding seasons.

2.4.2 Data Collection

Between 2008 and 2013, we collared 14 individual elephants in LKF (male, n=3; female, n=11). We used Xylazine (100-150mg/tonne) to immobilize the elephants and Yoimbine to reverse the effect, with the same dose. During the collaring process, the elephants' heart rate and physiological indicators such as eye movements were monitored regularly to ensure the safety of the animals. Blood samples were also taken to monitor the health status of the individual and for the purpose of disease screening. All elephants were fitted with GPS satellite collars equipped with a built-in VHF transmitter manufactured by Africa Wildlife Tracking. The VHF transmitter allowed the elephants to be located using a VHF receiver and antenna. Geographical location data from GPS collars were sent to the Globaltrack server and data were downloaded from http://www.globaltrack.com. For this study, only six individuals were selected for detailed analysis covering two sets of years (2011-2012, n=3 individuals; 2013-2014, n=3 individuals) to allow for comparison in utilization distribution variation among the elephants (Table 2.1). The collars were programmed to transmit one location every two hours (for individuals tracked in 2013-2014), whereas the sampling interval for individuals tracked in 2011-2012 ranged from 30 minutes to four hours throughout the year. Movement data were extracted for the months of December to March (flooding season) and from May until August (non-flooding season) for each individual. I restricted the UD analysis to these months within the main flooding season and the main non-flooding season (i.e. excluding the transitional months) because I was interested to look at the movement changes and its determinants within these two major seasons. The wet and dry seasons were identified using rainfall data from the Meteorological Department of Malaysia and based on other studies in LKF (Matsuda, Tuuga and Bernard 2010).

Table 2.1 Summary of satellite collars that were fitted on the six adult females use in the study indicating the duration of tracking and group size for each individual.

Individual	Gender	Estimated Age	Start	End	Group size
Aqeela	Female	30-40	5 October 2010	6 July 2013	5
Liun	Female	35-40	15 April 2011	2 November 2013	3
Putut	Female	45-50	26 October 2011	24 August 2012	4
Puteri	Female	30-35	26 October 2011	26 July 2016	4
Ita	Female	>40	3 June 2013	24 July 2014	5
Sandi	Female	30-35	19 June 2013	15 August 2015	Unknown

2.4.3 Data Analysis

2.4.3.1 Utilization Distribution Estimator: dynamic Brownian Bridge Movement Modelling (dBBMM)

In the utilization distribution, animals perform different behavioural activities to maximize their fitness such as finding food, shelter and partners (Kie et al. 2010). For example, the movement path of a dispersing or migrating animal will usually be straighter, longer and less responsive to boundaries than the movement path of a foraging animal (Fahrig 2007). From longitudinal observations, it was evident that elephants changed their movement behaviours over time, particularly as they moved between different habitats in the heterogeneous environment of the study area (Sukumar 2003; de Beer and van Aarde 2008; Fernando et al. 2010; Gaucherel et al. 2010; Srinivasaiah et al. 2012). For example, there are some areas that the elephants actively seek for resources while other areas are used for resting or social interactions (Nair et al. 2009; Ahlering et al. 2011). Therefore, accounting for diversity of behaviour of elephants in their utilization distribution will not only improve the quantification of their landscape use, but at the same time help to infer the importance of different landscape elements for the survival of these elephants (Schick et al. 2008; Gurarie et al. 2009; Kranstauber et al. 2012; Madon and Hingrat 2014).

Some challenges of using movement data gathered by GPS telemetry include the issue of autocorrelation, irregular sampling intervals and error in observed locations (Johnson et al. 2011). Autocorrelation is non-independence of samples collected close together in space or time, which arises due to frequent observations collected using GPS telemetry, and it can cause underestimation of home range size and bias in predictions of habitat selection, core area, and intensity of resource use (Cushman et al. 2005; DeSolla et al. 2010). The physical characteristics of habitats (for example topography and vegetation with high canopy cover) can influence the quality of the data from different habitats, leading to error in observed locations (Withhey et al. 2001).

To determine the annual and seasonal utilization distribution of the elephant in LKF, I used dynamic Brownian Bridge Movement Modelling (Kranstauber et al. 2012). This method was selected mainly because it includes both temporal and behavioural characteristics of movement paths into the estimation of utilization distributions. By including behavioural changes we can understand better the processes that generated the home range in the context of the landscape (Powell and Mitchell 2012). In addition, this method has outperformed the traditional utilization distribution estimators in many ways. For example, it quantifies utilization distribution using the animal paths rather than individual points, it takes into account the location error and importantly, it can work with irregular and autocorrelated movement data (Horne et al. 2007; Shamoun-Baranes, Loon, et al. 2011; Kranstauber et al. 2012; Byrne et al. 2014).

Several aspects of model structure were specified to run the model: window size, location error, margin size and extent. The window size argument is related to the behavioural change-point analysis that is integrated into the dBBMM process (Gurarie et al. 2009). It indicates the size of the window (in number of fixes) that is swept over the data when trying to detect significant change points. The bigger the window, the more stable or accurate the estimates of the Brownian motion variance. We set the window size argument to 2; which represented 24 hours of data for most of the days, allowing us to detect the behavioural changes on a daily timescale. A location error of 2.5, as suggested by African Wildlife Tracking (Sophie Haupt, *pers. comm.*), was used for all locations, and we set the extent argument to 72 after plotting the animal's trajectory and observing that the longest dimension of the track was 72 km. As a result, each raster cell produced by the analysis would be 1 km^2, allowing for a straightforward interpretation. The margin was left at the default setting of 3. Utilisation Distributions for the six individuals were created for each season, and then used to compute the 50% and 95% UD contours. The “core area” represents the areas of concentrated space use within the home range, and was demarcated by the 50% isopleth, whereas the “home range boundary” was delineated with the 95% isopleth (Wilson et al. 2010; Schuttler et al. 2012). These isopleths were then used to determine the area size of the core area and home range from the UD. The movement model was implemented in the R statistical software, version 1.2.475 (R Core Team, 2014), using the “move” package version 1.2.475 (Kranstauber et al. 2012).

2.4.3.2 Generalized Linear Model (GLM)

A GLM was used to determine whether the size of the home range UD and the core area were explained by individual identity and season. The error distribution used in these GLMs was the gamma family with a log link function.

2.4.3.3 Classification and Regression Tree (CART)

I implemented CART analyses to predict which covariates determined both the core and the home range of elephants in different seasons, as these models are suitable for the analysis of complex ecological data and provide easily interpretable results (De’ath and Fabricius 2000; Davis et al. 2013). CART is a non-parametric modelling method that can model the associations between response and predictor variables more flexibly than traditional methods, especially in data sets where the data are limited or incomplete. The methods is also relatively insensitive to outliers (Elith et al. 2008). CART will produce a sequential series of binary splits of the explanatory variables, which is represented as a tree-like structure with the final nodes representing homogeneous subsets of the responses (Lawrence and Wright 2001). The selection of variables, the placement of the variables in the tree model, and the choice of location of the binary split are all data-dependent and determined by the model (De’ath and Fabricius 2000; Lawrence and Wright 2001). In addition to providing predicted classes at terminal nodes, CART analysis reports for each terminal node the probability of misclassification and the probability of membership for each other class (De’ath and Fabricius 2000). This information can be used to assess the quality of the classification, assign fuzzy class memberships, or to conduct Bayesian probability analysis.

In the CART analysis, the response variable was categorical and classified as core area (areas the elephants used intensively), wider area (areas the elephants used but not intensively) and outer area (areas the elephants did not use) (Table 2.2).

Table 2.2 Number of observations for each type of area (core, UD and unused) in each season (flooding and non-flooding).

Area	Flooding Season	Non-Flooding Season	Total
Core (intensive use)	1608	1101	2709
Wider (some use)	4924	4174	9098
Outer (no use)	1245	2349	3594

2.4.4 Preparation of the Predictor Variables

We used 15 predictor variables to explain the elephant spatial distributions observed in LKF, and all the spatial layers were adapted from Abram et al. (2014). Predictor variables were selected based on data availability, the elephants' ecological requirements, and those that are related to anthropogenic activities (Buij et al. 2007; Hien et al. 2007; Fernando, Wikramanayake, et al. 2008; Estes et al. 2012; Srinivasaiah et al. 2012; Sitompul, Griffin and Fuller 2013).

Spatial predictor variables were arranged into three groups; (1) spatial anthropogenic (SA), (2) spatial physical (SP) and (3) vegetation indices (VI). All spatial layers were used to derive raster layers at a resolution of $30m^2$ (Table 2.3). 'Distance to' spatial layers were computed using a Euclidean distance by means of the 'distance to' tool in ArcGIS 10.3. To avoid pseudoreplication (i.e. several points were clustered in the same raster cell) during spatial extraction, all the points that were clipped into the respective polygons were converted to raster format before being converted into points again, producing a single point for each raster cell. At each of these points, I extracted all predictor variables using the "Samples" tool (Abram, *personal communications*).

Table 2.3 Summary of the predictor variables used in the CART analysis to predict whether point location is classified as belonging to the core or UD.

Category	Predictor Variables	Type	Abbreviations
Spatial-Anthropogenic	Distance to buildings	continuous	Dist_Build
	Building density	continuous	Build_Density
	Distance to main roads	continuous	Dist_Road
Spatial-Physical	Elevation	continuous	Elevation
	Aspect	continuous	Aspect
	Slope	continuous	Slope
	Distance to forests	continuous	Dist_Forest
	Habitat type	categorical	LULC
	Distance to river	continuous	River_Dist
	Carbon	continuous	Carbon_TCH
Vegetation Indices	Normalized Difference Vegetation Index	continuous	NDVI
	Normalized Difference Moisture Index	continuous	NDMI
	Tasselled Cup brightness	continuous	TC_BRIGHTNESS
	Tasselled Cup greenness	continuous	TC_GREENESS
	Tasselled wetness	continuous	TC_WETNESS
	Enhanced vegetation index	continuous	EVI

A number of vegetation indices were calculated and used in the model. Vegetation indices, although they do not represent physical quantities, are useful proxies of vegetation/land-cover structure, as well as other biophysical and biochemical properties of land (Jiang et al. 2008). Given the rapid changes occurring in this particular landscape, primarily as a result of land conversion, Spectral Vegetation Indices (SVIs) can form a useful tool for the long-term monitoring of landscape sustainability. All of the calculated indices constitute indirect measures of vegetation quality and vigor, and they differ in their sensitivity to changes in chlorophyll concentration, canopy structure and productivity. Furthermore, they differ in their sensitivity to atmospheric effects and landscape heterogeneity, making it difficult to know in advance which one of them will perform better as a predictor variable in a spatial model, and as a result a large set of indices was calculated and each one of them was evaluated based on its explanatory power in the models (Table 2.3).

The indices were derived from four Landsat 8 images; two for the flooding season and two for the non-flooding season, after converting the original DN values (quantized and calibrated standard product pixel values) to TOA reflectance values using the method described on the U. S. Geological Survey website (http://landsat.usgs/Landsat8_Uisng_Product.php). The acquisition dates of the four images were 15/8/2013 and 12/8/2015 for the non-flooding season, and 25/4/2013 and 31/12/2014 for the flooding season. Above-ground-carbon stocks were calculated based on diameter at breast height (DBH) for trees ≥10 cm, species or genus vernacular/scientific names, habitat type and degradation. The content of carbon per ha was divided into six classes (Class 1 = '<50 MgC/ha'; Class 2 = '50–100 MgC/ha'; Class 3 = '100–200 MgC/ha'; Class 4 = '200–300 MgC/ha'; Class 5 = '300–400 MgC/ha'; Class 6 = '>400 MgC/ha'). Areas with >350 MgC/ha are regarded as high carbon forests. Habitat was classified into 16 forest types (1=beach forest, 2=severely degraded forest, 3=dry lowland dipterocarp forest, 4=dry lowland forest, 5=limestone forest, 6=mangrove forest, 7=nipa palm forest, 8=peat swamp forest, 9=seasonal freshwater swamp forest, 10=freshwater swamp forest, 11=swamp, 12=transitional forest, 13=cleared area/planted/young oil palm plantation, 14=oil palm with good canopy, 15=settlement, 16=oil palm-underproductive <25%) (Table 2.4).

Table 2.4 Definitions of habitat types adapted from Abram et al. (2014).

Forest Types	Description	Annual Flooding Period	Total Forest (ha)
Beach forest	Occurs on sandy substrate along coastal areas. Dominant species includes *Casuarina equisetifolia*.	Tidal	5,327
Severely degraded forest	Areas of severe degradation with unknown previous forest types dominated by shrub/low lying vegetation.	Varied	10,511
Dry lowland Dipterocarp forest	Logged lowland mixed dipterocarp forest, dominated with *Dipterocarp sp.*	Never/rarely	101,878
Dry lowland forest	Previous dipterocarp forest, secondary forest with species including, *Nauclea subdita*, *Neolamarckia cadamba*, *Glochidion rubrum*	<3 months	39,008
Limestone forest	Gomantong substrate association of hill and ridge escarpments. Low human disturbance. Dominant species include *Dryobalanops lanceolata*, *Shorea pauciflora*, *Parashorea malaanonan* and *Dipterocarpus caudiferus*.	Never/rarely	1,679
Mangrove forest	Found in saline coastal sediments. Dominant species include *Rhizophora apiculata*.	Tidal	12,863
Nipa palm forest	Native type of palm (Nypa fruticans) found within the mangrove system either in mono-stands or mixed with *Rhizophora apiculate.*	Tidal	26,618
Peat swamp forest	Oligotropic peat substrate, poorly drained forests exposed to flooding. Common tree species include *Lophopetalum multinerviu*, *Baccaurea*, *Campnosperma coriaceum*, *Syzygium* and *Anisoptera costata*.	>6 months	2,132
Seasonal freshwater swamp forest	Heavy degradation thought to have occurred with many pioneer species. Common species include Macaranga	3-6 months	12,501

	gigantea, Pterospermum elongatum, Cananga odarata.		
Freshwater swamp forest	Formed in backswamps and largely on poorly drained soil. Common species include *Dillenia excelsa*, *Croton oblongus* and *Mallotus muticus*.	>6 months	22,284
Swamp	Open reed, swamp vegetation. Dominant tree species *Excoecaria indica*	>9 months	2,750
Transitional forest	Occurs between mangrove and freshwater swamp forest. Brackish water. Dominant species of *Heritiera littoralis*, *Ilex cymosa*, *Excoecaria agallocha*.	Semi-tidal	13,849
Cleared oil palm plantation	Areas cleared of forest cover with bare earth or grass like vegetation cover. No roads laid nor ground prepared for oil palm planting	NA	NA
Planted out	Areas had roads cut and laid, ground prepared for planting, and in some areas palms planted out (palms would be approximately 2 years or younger)	NA	NA
Young mature	Young mature palms were visible but palm fronds did not overlap. Low-lying (leguminous) vegetation was visible. Palms in this category range from 3–6 years	NA	NA
Oil palm with good canopy	Palms in prime yield (7–24 years) and 'Full stand' (i.e., 76–100% palm capacity). Class had closed canopies i.e., overlapping fronds of neighbouring plants. Canopy closes at 7 years in areas with 136 palms per ha. Homogeneous texture	NA	NA
Oil palm underproductive <25%	Class had ≤25% palms per ha and were largely associated with areas that experience annual flooding and/or daily inundation from tides	NA	NA

The CART models were fitted using the package ‘rpart’ in RStudio, and were based on 5-fold cross validation with strict cost-complexity measures (cp = 0.015, minsplit = 100, maxdepth = 5). Complexity parameters (cp) control the size of the decision tree by selecting the number of splits in the tree, while the minsplit parameters indicate the minimum number of observations that must exist in a node in order for a split to be attempted. In addition, the maxdepth parameter specifies the maximum depth of any node of the final tree. The combination of these parameters pruned the tree to a level where the tree is expected to be robust. Several combinations of cp, minsplit and maxdepth values were investigated by trial and error to identify interpretable results and to provide confidence in the robustness and repeatability of the method.

2.5 Results

2.5.1 Utilization Distributions, Home Range Area and Core Areas of Bornean Elephants

The UD size varied between 77-276 km^2 while the core area size varied between 3.9-53.8 km^2 (Table 2.5) as shown in Figure 2.1 and Figure 2.2 respectively. Our GLM results indicated that the size of the home range UD and core area differed between individuals (Table 2.6). In addition, the size of individual’s home range and core area varied between the two seasons, as most individuals have larger UDs and CAs in the non-flooding season (Figure 2.3) - except for the individual known as “Putut” (Figure 2.4).

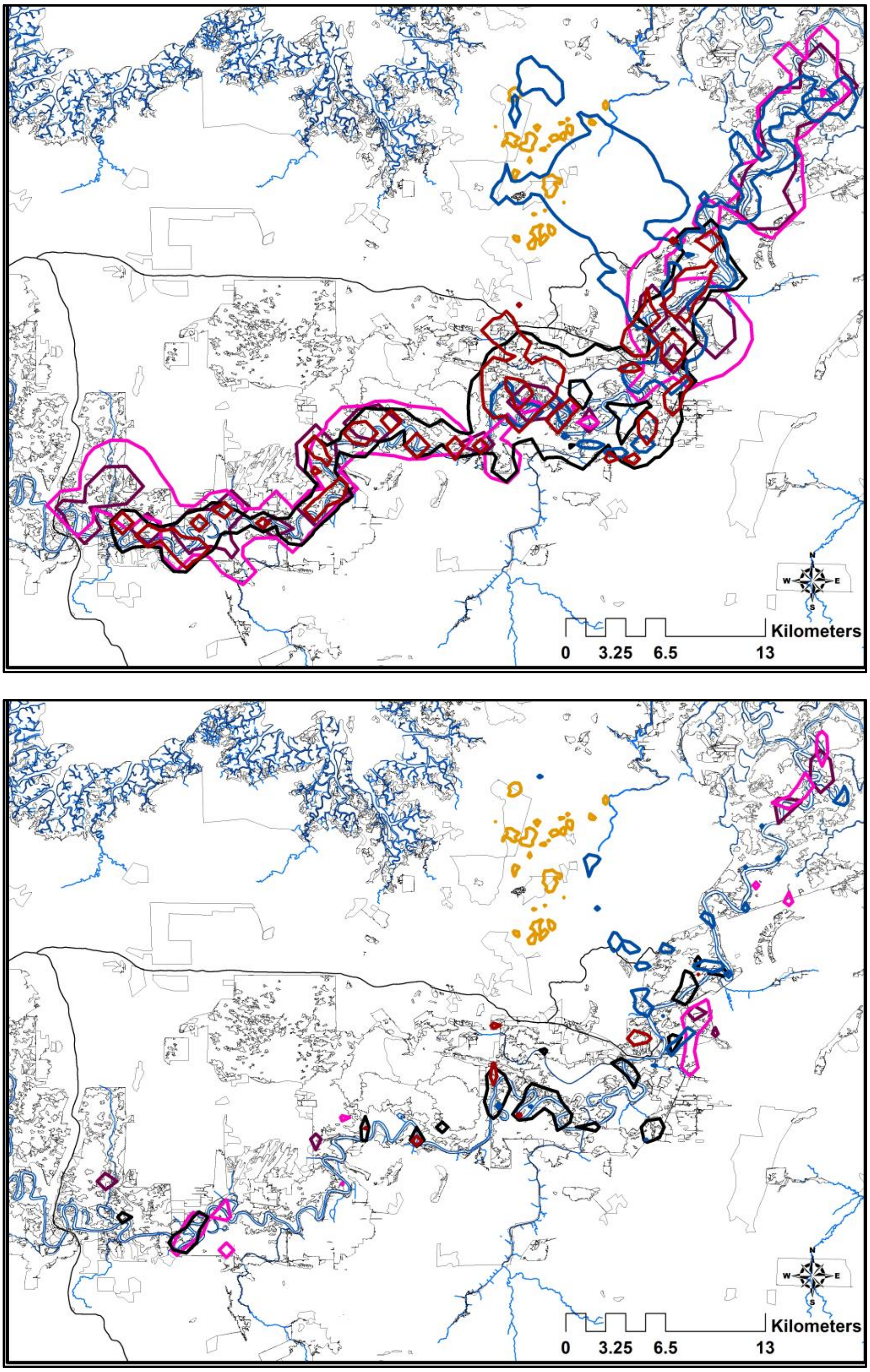
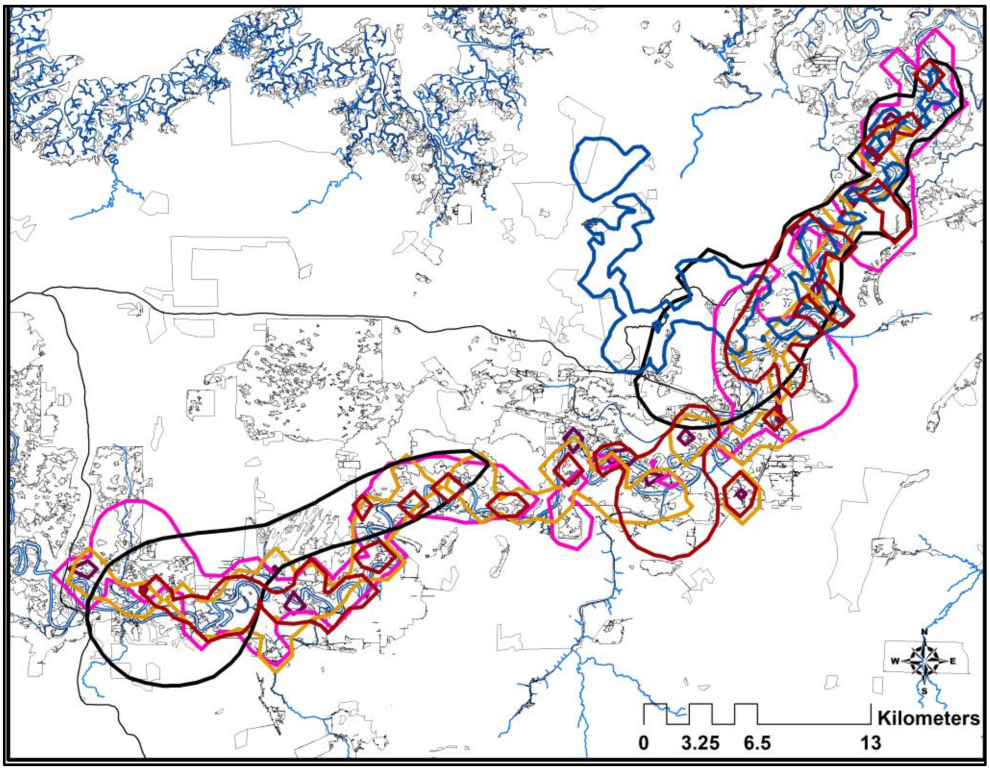


Figure 2.1 These are maps of the overlapping areas used by the six individual elephants showing UD (top) and core (bottom) area in flooding season. Different colours representing different individual (Blue polygon = Liun, yellow polygon = Ita, black polygon = Putut, fushia polygon = Puteri, red polygon = Aqeela, purple polygon = Sandi).



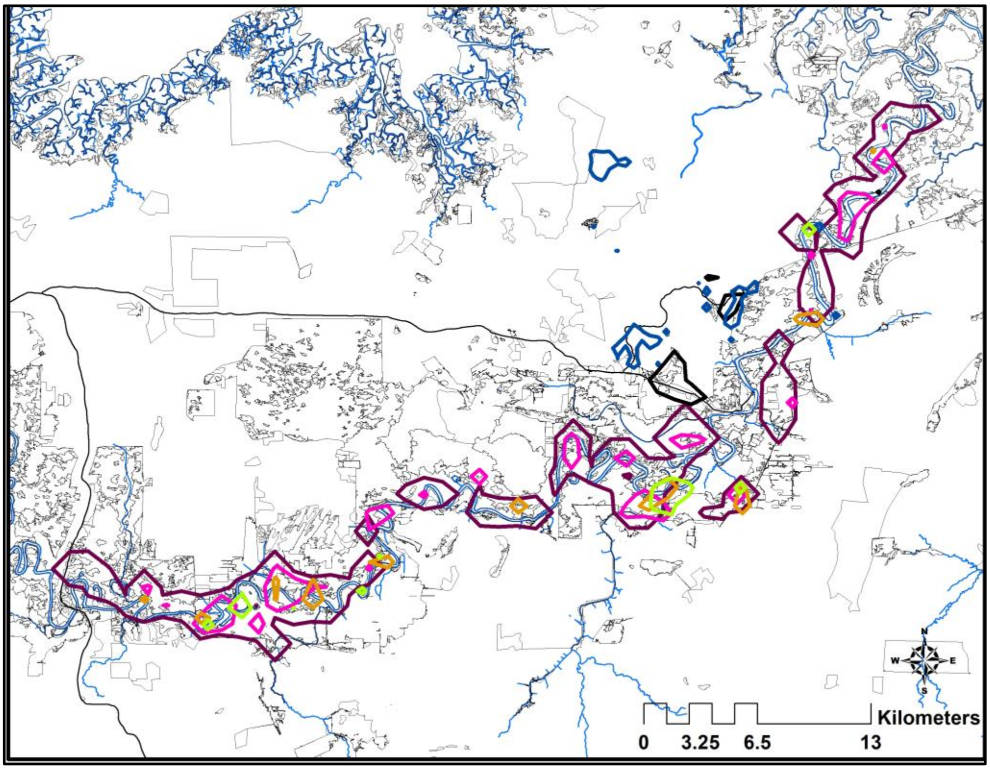


Figure 2.2 These are maps of the overlapping areas used by the six individual elephants showing UD (top) and core (bottom) area in non-flooding season. Different colours representing different individual (Blue polygon = Liun, yellow polygon = Ita, black polygon = Putut, fushia polygon = Puteri, red polygon = Aqeela, purple polygon = Sandi).

Table 2.5 Sampling data and home range size (core = 50% and UD = 95% of observation point locations) for the six individual elephants samples across flooding and non-flooding season.

ID	Sampling period (days)	Fixes	Season	**UD area (km^2)**	**Core area (km^2)**
Aqeela	122	2590	Flooding	65.01	10.63
	123	2039	Non-flooding	330.3	41.29
Liun	122	1115	Flooding	133	14.68
	123	1498	Non-flooding	784.87	55.22
Putut	122	414	Flooding	151.33	29.56
	116	263	Non-flooding	230.1	17.83
Ita	121	1428	Flooding	39.17	6.13
	90	1074	Non-flooding	90.74	20.37
Puteri	120	958	Flooding	124.46	19.76
	88	377	Non-flooding	172.79	25.84
Sandi	121	1431	Flooding	84.76	21.68
	74	892	Non-flooding	87.38	20.45

Table 2.6 A General Linear Model (GLM) analysis to explain the size of area used by elephants in term of the core area or UD area (described by the term "level" and "season" for the six individual elephants tracked. (a) Model 1 includes the main effect of level, season and individual ID and (b) Model 2 includes the two-way interaction between season and ID, showing that different individuals showed significantly difference changes in home range size between the flooding and non-flooding season.

Parameter	**d.f.**	**F**	**p**	**Effect sizes (+/- SE)**
a) Model 1				
Level	1	82.08	<0.001	1.89 +/- 0.194
Season	1	12.67	<0.01	0.73 +/- 0.194
ID	5	3.66	<0.005	
b) Model 2				
Level	1	222.36	<0.001	
Season:ID	5	6.40	<0.01	

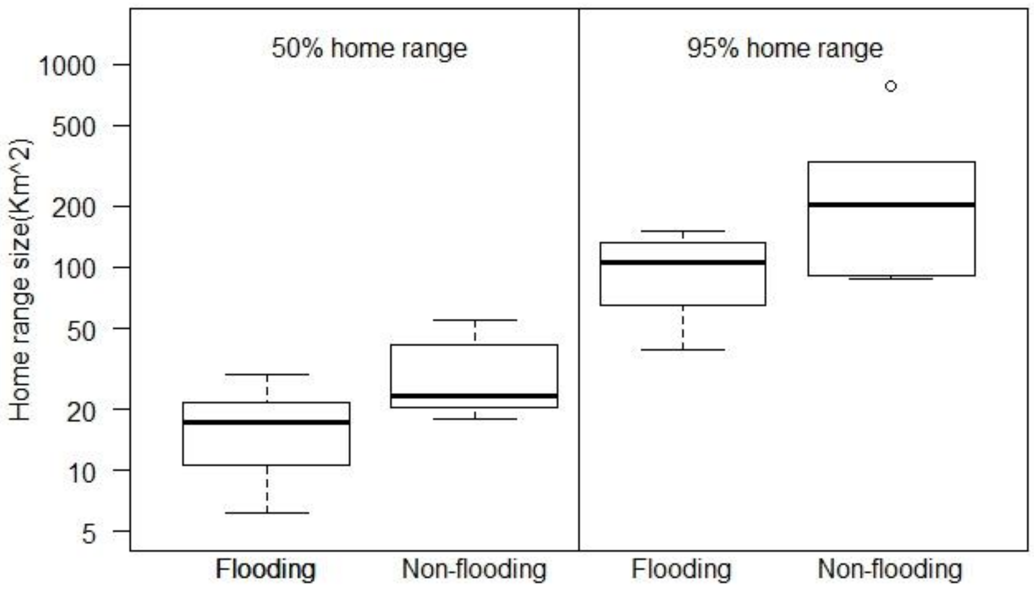


Figure 2.3 The area of core and UD ranges for individually tracked elephant during the flooding and non-flooding season, showing a greater area size for both core and UD ranges during the non-flooding season.

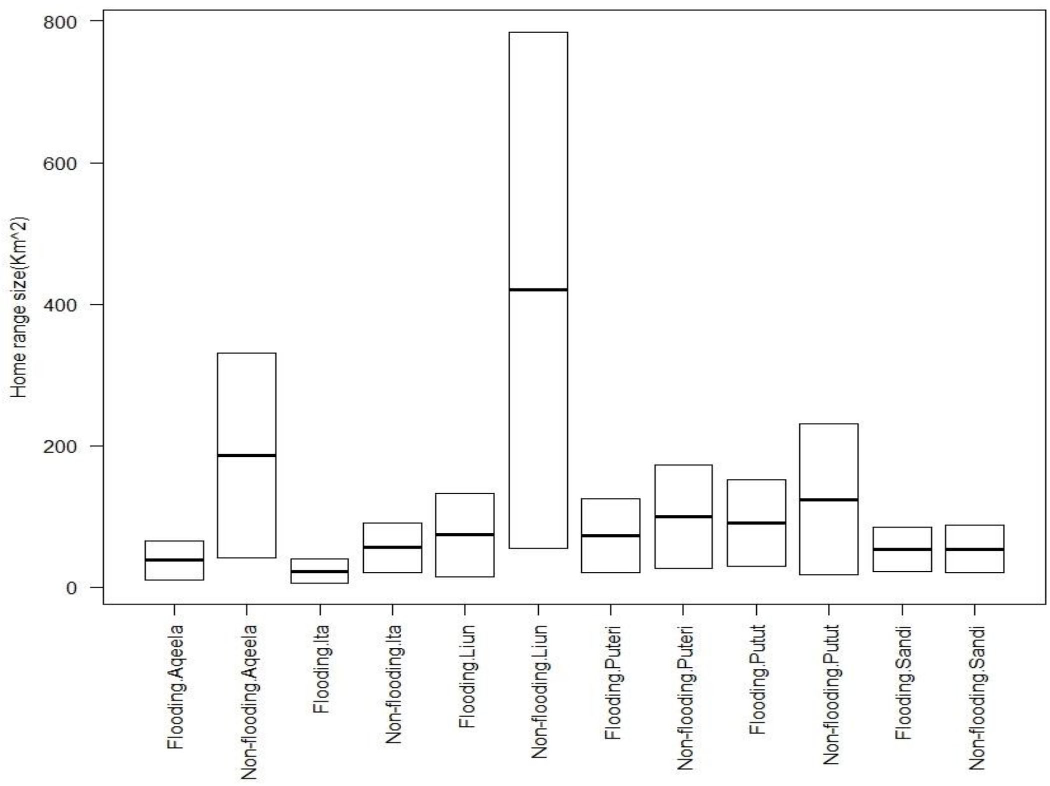


Figure 2.4 Core area and UD area for the six individuals tracked across flooding and non-flooding.

2.5.2 Determinants of elephant home range size and core area size

The classification tree shows the relationships between important variables, and the important levels of those variables, for identifying the home range and core areas of the Bornean elephants in different seasons. During the flooding season, both core area and home range UD were determined by the spatial physical covariates while determinants of both core and UD during the non-flooding season were explained by a combination of both physical and anthropogenic covariates.

2.5.2.1 Space Use during the Flooding Season

The regression tree analysis correctly classified most of the point locations were as elephants' UD (Figure 2.5a), with one sub-group having the highest correct classification (53%) of the data being explained by distance to river, forest carbon stocks and elevation. In general, elephants selected higher ground > 9.2 meters asl, <1.6 km from the river, as well as areas that contain high forest carbon stocks (Classes 3-6) (Figure 2.5a).

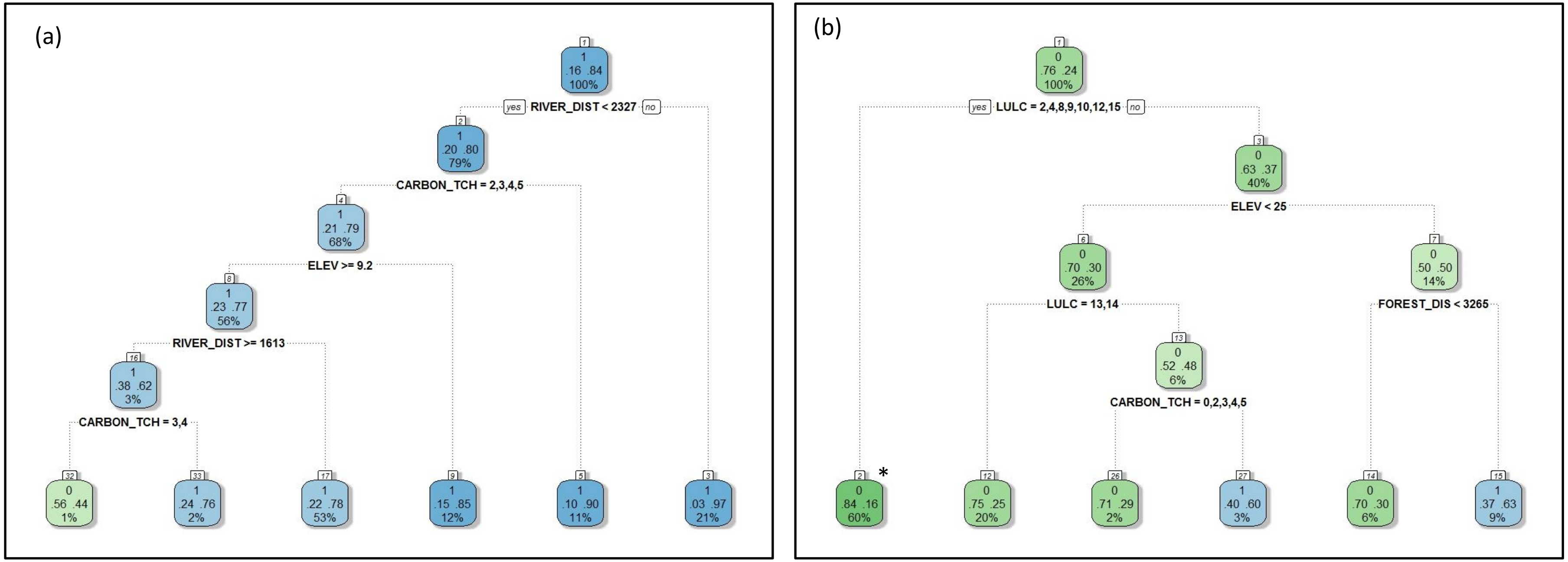
During the flooding season, CART identified habitat type, elevation and distance to forest as the most important variables that determined the core area of elephants (Figure 2.5b). Both natural habitats (beach forest, dry lowland dipterocarp, limestone, mangrove, nipa palm and swamp forest) and non-natural habitats (cleared area/planted/young oil palm, oil palm with good canopy and oil palm-underproductive <25%) are most likely to become the core area during the flooding season. Within these habitat types, two possible sub-group of determinants of the core areas were identified. The first sub-group was elevation <25 meters excluding cleared area and oil palm with good canopy and with carbon class 2 (50–100 MgC/ha). However, this sub-group contains only 3% of the observations, and only 60% of these data were correctly classified as core areas. The second sub-group that explained the core area of the elephants during the flooding season was elevation >25 meters, and in the range of >3.3 km from the forest (excluding oil palm). This sub-group was larger with 9% of total observations and had a better correct classification rate of 63%. The overall correct classification for this tree was 69.7%. These features indicated that the core areas of the elephants during the flooding season were found mostly in unsuitable habitat patches.

It is noticeable that one of the nodes in the CART analysis for core area (labelled as *) has a large proportion of the data (60%) and within that, it contains 16% of misclassifications, so I tried to describe the model better using two approaches. Firstly, I tried to extend the tree and secondly, I created a separate tree just for this group of observations. In both cases, the tree became very complex before it was able to describe the core and non-core areas using the data available.

2.5.2.2 Space Use during the Non-flooding Season

Two possible home range UD types were identified for the non-flooding season; in the first type, the UD was located close to the river (<1.8 km), far from roads (>13 km), and close to settlements as long as they had a low density of buildings. 53% of the observations were in this sub-group, with a correct classification of 74%. The second home range UD type had fewer observations (18%), but a much higher rate of correct classification of the UD (95%). These areas were classified by being far from the river (>1.9 km) and within 8 km from a road (Figure 2.5c).

The core area in the non-flooding season was mainly explained by distance to road, distance to river, distance to building, habitat types and slope (Figure 2.5d). Three possible core area types were identified. The possible core area type with the most observations (12%) was characterized by being close to the road <1 km, and close from the river <4.5 km, in any habitat except for seasonal freshwater swamp, freshwater swamp, swamp and oil palm underproductive and on relatively sloping ground (>0.28°). The percent of the correctly classified core observation areas in this sub-group is 64%. The other two possible core areas contained only 2% and 3% of the total observations respectively.


(a)
1
.16 .84
100%
yes
RIVER_DIST < 2327
no
1
.20 .80
79%
CARBON_TCH = 2,3,4,5
1
.21 .79
68%
ELEV >= 9.2
1
.23 .77
56%
RIVER_DIST >= 1613
1
.38 .62
3%
CARBON_TCH = 3,4
0
.56 .44
1%
1
.24 .76
2%
1
.22 .78
53%
1
.15 .85
12%
1
.10 .90
11%
1
.03 .97
21%
(b)
0
.76 .24
100%
yes
LULC = 2,4,8,9,10,12,15
no
0
.63 .37
40%
ELEV < 25
0
.70 .30
26%
0
.50 .50
14%
LULC = 13,14
FOREST_DIS < 3265
0
.52 .48
6%
CARBON_TCH = 0,2,3,4,5
0
.84 .16
60%
*
0
.75 .25
20%
0
.71 .29
2%
1
.40 .60
3%
0
.70 .30
6%
1
.37 .63
9%

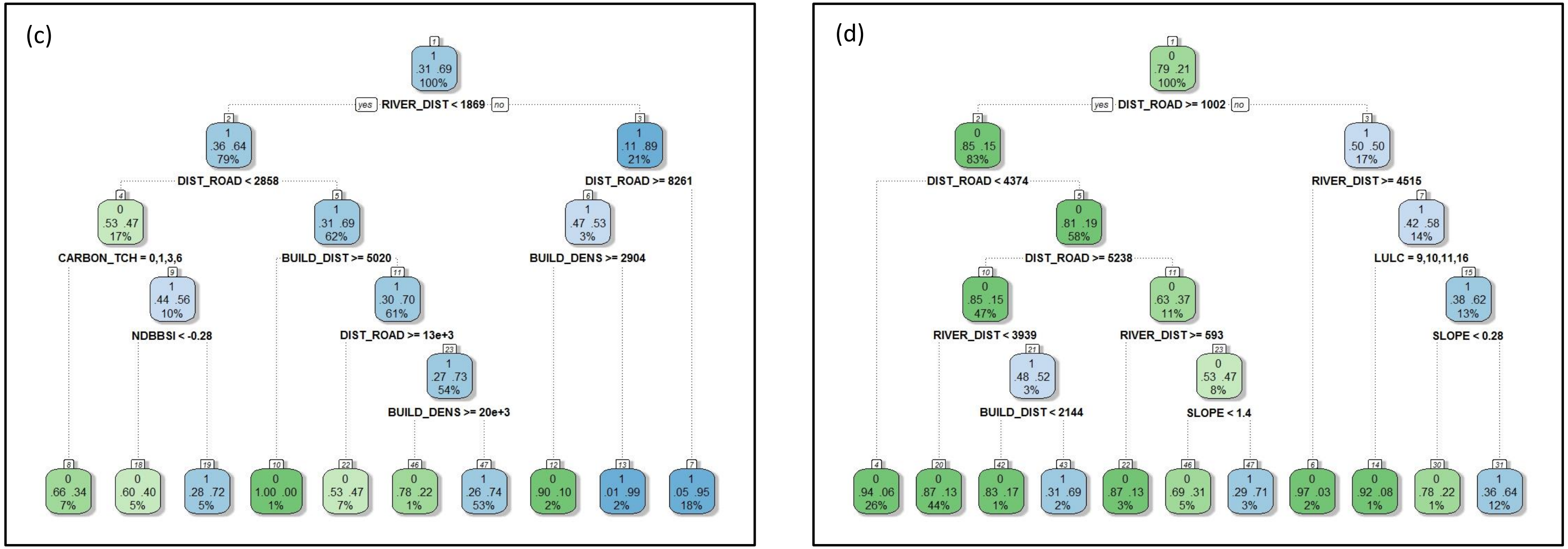


Figure 2.5 Classification tree for UD areas and core areas in non-flooding season and flooding season. At each split, the model selects the variable and the level of that variable that best splits the data in order to predict what areas the elephants will use. For the analysis of UD (a & c), the blue nodes represent both core and wider areas and green nodes represent the outer areas. While for the analysis of core areas (b & d), the blue nodes represent both core areas and green nodes represent the wider areas. On top of the node is a small box with a number that identifies the node; these numbers also show the order in which the nodes were identified by the model. Inside each node is a 0 or 1, indicating UD or core area respectively. Two numbers represent the proportion of observations that were correctly and incorrectly classified by the model in that node, giving a representation of how well the model performed at that stage, and therefore how confident we can be about that result. Darker coloured nodes have more confidence. The percentage number is the percentage of the total data points that fall into that particular node. Nodes with higher percentages represent more data points and are therefore more important to the model.

2.6 Discussion

The Bornean elephant population in Lower Kinabatangan Floodplain exists in a highly fragmented landscape, surrounded by oil palm plantations, and it is currently isolated from the other Bornean elephant populations due to anthropogenic factors (e.g. physical barriers such as a bridge (Estes et al. 2012). By increasing the number of collared elephants from different family units as well as by applying recent analytical approaches to understand their home range and its determinants, I was able to advance our current understanding of elephants' movement behaviour in the LKF. Several previous studies have shown that the size of an elephant's home range is an indication of the availability of essential resources and the degree of disturbance to which the animal is exposed (Baskaran and Desai 1996; Fernando, Wikramanayake, et al. 2008; Williams et al. 2008; Sitompul, Griffin and Fuller 2013).

The dBBMM method applied in this study provides a better representation of space use by elephants in LKF compared to more traditional analysis methods, as it captures the dynamic of space-time processes, such as the elapsed time between the start and ending locations, the speed of movement as well as taking into account the behavioural changes along animal tracks (Horne et al. 2007; Kranstauber et al. 2012). The UDs of several elephants were highly overlapped and this overlapping might be due to high population density as well as high levels of human activities within their UD (Alfred et al. 2010). Currently, LKF sustains the highest elephant density in Sabah (2.15 individuals/km^2) and a high elephant population density will usually result in intraspecific competition between individuals, while flooding events will make such competition even worse as elephants will be compressed into smaller areas (Alfred et al. 2010; Schradin et al. 2010; Estes et al. 2012). In most circumstances, intraspecific competition may force subordinate individuals to move into suboptimal habitats, which could put their fitness at risk (Wittemyer et al. 2007; Fernando et al. 2009).

Resources such as water and food are consistently available throughout the year in the Lower Kinabatangan, and therefore geographically distinct seasonal ranges are not to be expected (Fernando, Wikramanayake, et al. 2008; English, Gillespie, et al. 2014). However, the results show that there was still seasonal variation in the movement of the Bornean elephants, as indicated by the size of their home range UD and core areas. In both seasons, the elephants were observed to maintain their UD close to the river. In the flooding season elephants were less selective about their space use and were more predictable in their movements than in the non-flooding season. Most of the observed data were successfully classified as elephants' UD are areas with higher ground, and these areas appear to be in good quality habitat based on their high carbon density. These determinants identified by the CART analysis fit the criteria of areas which are mostly found near villages and oil palm plantations. These findings support the view of Estes *et al.* (2012) that during the flooding season elephants will likely to be trapped between the villages of Bilit and Sukau until floodwaters recede, which increases the chances of conflicts arising between elephant and the people in this area. Larger home range UDs during the non-flooding season indicated that they could travel further and explore more areas to accommodate their needs in this season (Williams et al. 2008).

Unlike in the flooding season when physical features mostly influenced the elephants UD, during the non-flooding season the elephants' UD was determined largely by anthropogenic factors. Bornean elephants were observed to utilize areas that were close to roads which run through palm oil plantations given there is less human presence in the vicinity of roads. In many circumstances, the development of road will encourage the influx of a large number of people and as a result it will halt elephant movements as seen for the African forest elephant (*Loxodonta africana cyclotis)* in Gabon and the Asian elephant (*Elephas maximus indicus*) in Vietnam (Blake et al. 2008; Varma et al. 2008). In the case of the Bornean elephant in LKF, any new road developments will attract other developments, such as new oil palm estates and human settlements. This may further restrict the elephants' movements, therefore increasing conflicts between people and elephants.

Only oil palm plantations close to the village of Sukau were heavily utilized by elephants and especially by two elephants, Ita and Liun. These plantations might have been part of elephant's traditional routes in Lower Kinabatangan however, presently many of the traditional routes in these areas are denied to the elephants due to anthropogenic activities (Hai et al. 2001). Another plausible explanation is that the elephants ventured into these oil palm plantations to find alternative routes. The village of Sukau has been identified as the one of two major bottlenecks that could hinder the flow of elephants' movement in their UD. Furthermore, the existing network of electric fencing within this landscape has increased the difficulties for the elephants to move between forested areas (Figure 2.6) (Thompson *et al.,* unpublished). In addition, some of these oil palm plantations are defended strongly by people. However, due to lack of coordination in this defence of plantations, the elephants are usually pushed further away into the non-natural landscape instead of going back to the nearest forest. The availability of banana (Musaceae, spp.) in some of the oil palm plantations provided food resources which could also be another reason why the elephants were attracted to the oil palm plantations and lingering in this part of the landscape despite the pressure that they received there from anthropogenic activities (Keeyen Pang, *pers. comm.*). Another route which provides the elephants with access to their habitats, was through Lot 3 of the Wildlife Sanctuary, which represents a narrow corridor of more than nine km in length, but only 0.8 km wide (Estes et al. 2012).

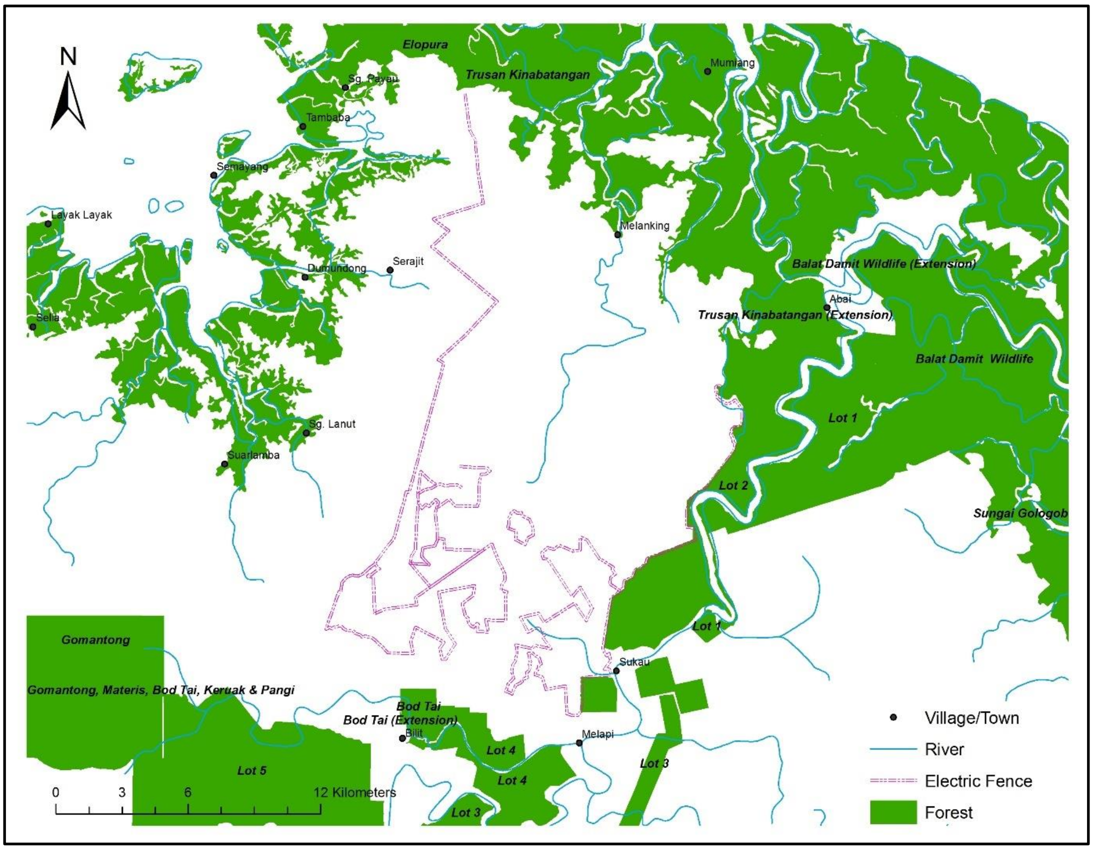


Figure 2.6 Map of the network of electric fences in the oil palm plantations surrounding village of Sukau which might represent barriers to elephants' movement within their home range.

The core areas of elephants in both seasons mostly reflected the need to satisfy their diet and water requirements. In the flooding season, elephants intensively used higher ground areas that were found in these five habitat types; limestone forest, cleared/planted/young mature palm oil, oil palm plantation with good canopy, underproductive oil palm areas, and swamp forests. Oil palm trees that are found in the cleared/planted/young mature areas are usually between two and six years old. Elephants eat the shoots from these young palms because it is easy to knock them down to reach the shoots, especially during the flooding season when the soil is loose and malleable. At the same time, during the flooding season, human presence (i.e. plantation workers) and human activities (i.e. patrolling units) are significantly reduced due to bad weather and constant rain, making those oil palm areas more suitable for elephants to occupy. Meanwhile, there are open grasslands available surrounding swampy areas, which can support the elephants' needs as shown in (Figure 2.7). An expert opinion-based least-cost analysis indicated that limestone forest in LKF can act as barriers to elephants due to steep slopes or cliff edges, creating unsuitable habitat within otherwise suitable habitat for elephants in Lower Kinabatangan (Estes et al. 2012). The same observation was seen in other elephant populations where lower frequencies of elephant occurrence in highly rugged terrain (Rood et al. 2010). However, I believe that during the flooding season, elephants were still utilizing this habitat type due to the high permeability of the limestone bedrock causing water to drain away rapidly, create an area of dry ground that the elephants can use.

Figure 2.7 Aerial photograph showing the grass areas within the swamp forest matrix. These grass areas represent foraging resources for the elephants.

In the non-flooding season, the elephants' core areas were found in severely degraded, dry lowland and transitional forest except for the individual known as "Liun", for which the core areas were found in the cleared areas and oil palm plantation with good canopy cover. This observation provided further evidence that the duration that elephants remain within an area depends on the individual's needs and behaviour (Srinivasaiah et al. 2012). Therefore, it is inappropriate in term of management strategies to suggest a single approach for all elephants, which may not cater to the needs of a particular elephant within the population. Most of the habitats identified by CART provide ample amount of grasses available along the Kinabatangan river that can be consumed by elephants (English, Gillespie, et al. 2014).

The dynamic Brownian bridge movement model has improved our understanding of elephants' movement strategies in highly fragmented areas by estimating relative use of regions within LKF that are intensively (core areas) and non-intensively (utilization distribution) used while CART providing detailed, quantitative information on the main variables that explained these areas. Using the findings from this study, may help prioritize conservation actions and generate flexible management strategies, for example by reducing landscape permeability (e.g. integrated electric fencing) to minimize the recurrence of HEC. Elephants have individual personalities and different individual responses to their fragmented landscape. This chapter illustrates how these individual differences can be investigated by satellite collaring, and a recommendation arising from these findings is for increasing the number and geographical extent of these tracking studies, to investigate further the diversity of elephant responses and the specific behaviour of individuals in areas of potential HEC.

CHAPTER THREE

WHY IS THE ELEPHANT DOING WHAT IT IS DOING? AN EXPLANATORY ANALYSIS OF BORNEAN ELEPHANT BEHAVIOUR IN FRAGMENTED HABITAT

3.1 Introduction

The characteristics of an animal's movement path offer insights into the external influences and internal states of an individual across time and space. Nowadays, movement data are not only useful for monitoring and mapping the details of animal movement, but perhaps equally importantly it now allows us to infer behaviours which previously were difficult to monitor (Wittemyer et al. 2008; Nathan et al. 2012). Specific behaviours such as foraging, escaping predators and searching for prey are the outcomes of several movement types (Bergman et al. 2000). However, to continuously observe behavioural changes along the movement path of individual animals is a great challenge, as many species, including elephants, are sensitive to human presence. The ability to identify different types of behaviours from an elephant's trajectories and how they change, will inform decisions about how to improve landscape connectivity, facilitate elephant movements across the landscape, and to minimise risks of human-elephant conflicts (Baguette and Dyck 2007; Blumstein and Fernandez-Juricic 2010).

Recent technologies such as Global Positioning System (GPS) telemetry now allow researchers to obtain vast amounts of movement data, and provide the opportunity to study behaviour in spatial and temporal detail that is beyond the scope of traditional methodologies such as direct observation (McClintock et al. 2013; Wall et al. 2014; Demšar et al. 2015). Unlike with direct observations, inferring an animal's behaviour from movement data will reduce the interference of the observer with the animal once the animal has been fitted with a tracking device. Concurrently, the development of various statistical methods has increased the effectiveness of inferring animal behaviour using movement data (Patterson et al. 2008; Gurarie et al. 2009; Pedersen et al. 2011; Breed et al. 2012; Kranstauber et al. 2012; Gurarie et al. 2016).

Behavioural analysis is a crucial aspect of movement ecology, especially to understand the process of habitat selection (Holyoak et al. 2008). Animals select habitats that have ample food resources or low predation risk (Martin et al. 2010). However, many flaws detected when habitat selection studies were done without incorporating behavioural aspects as animals select a particular habitat type not only based on external components such as environmental features; but also their internal components particularly their behavioural need (Morales and Ellner 2002; Martin et al. 2009; Byrne et al. 2014; Roever et al. 2014; Abrahms et al. 2016). For example, once behavioural aspects were integrated into the habitat selection studies of African wild dog (*Lycaon pictus*), it became apparent that the wild dogs selected roads when travelling but ignored roads when they were running at high-speed and avoided roads for resting (Abrahms et al. 2016). Meanwhile brown bears (*Ursus arctos*) in Scandinavia prefer to spend their time on steeper slopes, offering a higher relative security during daylight hours (Martin et al. 2010). Both species adopt these strategies to avoid human activities and disturbed areas. Movement data also provide insights into the social ecology of the African elephant (*Loxodonta africana*), which were observed to have maintained similar cyclical movement patterns among higher ranking individuals when resource competition is highest, indicating that higher-ranking individuals were less influenced by competitive interactions then were lower ranking individuals (Wittemyer et al. 2008; Polansky et al. 2013).

The behavioural component could also influence the size of the home range or the utilization distribution of individuals (see Chapter Two for more details). By taking behavioural changes into account in home range estimation, it is possible to reduce uncertainty in the inferred movement path (Horne et al. 2007; Kranstauber et al. 2012).

The Asian elephant (*Elephas maximus*) lives in an exceptional set of circumstances in terms of its proximity to humans; there is one elephant to every 70,000 people living alongside across its geographical ranges and this situation requires a human-focused approach in order to conserve these elephants in the wild (Vivek Menon, *pers. comm.*). Being big, intelligent, nomadic and social animals, elephants require large tracts of land to fulfil their needs, which then creates competition with humans for the same space (Fernando 2010). Consequently, elephants are regarded as agricultural pests, due to crop raiding. Attempts by human to chase off crop raiding elephants are increasingly met with violent responses from them, sometimes resulting in human injury or death (Fernando et al. 2005). Therefore, there is an urgency to understand elephant behaviour to identify effective solutions to human-elephant conflict (Sillero-Zubiri et al. 2007). Direct observation to infer the behaviour of animals is desirable; however, it is highly challenging in practice to continuously follow individuals for long enough to collect observational data, especially in tropical forests, due to limited visibility and accessibility of the habitats to human observers (Beale 2007; Cable 2013; Fernando et al. 2015). As a result of these challenges, there have been only a handful of behavioural studies on Asian elephants to date, based on direct observation (Kumar and Singh 2010; Srinivasaiah et al. 2012; Ahamed 2015). Most of these studies have shown that Asian elephant behaviour was indeed influenced by human presence and human activities, the elephants changed their behaviour and habitat use by avoiding human activity, both spatially and temporally.

Investigation of the role of diel, environmental and anthropogenic features to shape behaviour changes of elephants in their environment is crucial to inform the planning of habitat corridors, as well as the location of electric fences to both control and facilitate the movement of elephants between habitat fragments (Venkataraman 2005; Graham et al. 2009; Estes et al. 2012; Gubbi 2012; Lapoint et al. 2013; Adams et al. 2017). These two methods are so far the most effective way to alleviate conflicts between people and elephants; corridors aid dispersal and movement of individuals between habitat while electric fences act as physical and psychological barriers to reduce elephant depredation of crops and other resources of value to people (Johnsingh and Williams 1999; Fernando, Kumar, et al. 2008). Earlier studies indicated that elephants changed their behaviour while moving through narrow corridors in unprotected areas, either by moving slowly or spending less time there (Douglas-Hamilton et al. 2005; Graham et al. 2009; Adams et al. 2017). Meanwhile, by impeding elephant movements, electric fences can increase the local density of elephants, which could increase the pressure that elephants put on their resources in that area (Loarie et al. 2009).

3.1.1 Statistical Model to Describe Behaviour From Movement Data

A range of different modelling tools are available to describe animal behaviour from movement data (Smouse et al. 2010). These tools are varied in their assumptions, implementation and in the nature of the outputs, and there are some trade-offs to consider (Gurarie et al. 2016). Certain tools examine the physical descriptors of movement, such as speed, direction, acceleration, turning angle and angular speed or the path shape properties such as curvature, sinuosity and tortuosity (Frair et al. 2005; Tremblay et al. 2007; Thiebault and Tremblay 2013; Demšar et al. 2015; Barraquand and Benhamou 2017). Tools such as fractal analysis and first passage time analysis compute a metric of tortuosity or area intensity use along a track (Benhamou 2004; Tremblay et al. 2007). Other tools such as behavioural change point analysis (BCPA), wavelet and decomposition analyses identify the structure or periodicity of movement (Wittemyer et al. 2008; Gurarie et al. 2009). Finally, there are also full model-fitting tools which include the large family of mixed random walk, hidden Markov, and state-space models that estimate transitions between states in a statistical framework derived from the generalized mixed modelling tradition (Breed et al. 2012; Langrock et al. 2012). An investigation of African elephant movement showed that a female herd moved in a consistent direction as indicated by the lacking of correlation between movement angle, turning angle, and movement length, in order to optimize their foraging strategy (Dai et al. 2007).

Of all these stochastic modelling techniques, in the present study I have explored the potential of dynamic Brownian Bridge Movement Model (dBBMM) to understand relationships between variation of motion (referred to as "motion variance") and various predictor variables, to elucidate the Bornean elephant's behaviour in fragmented habitats. dBBMM is a combination of two methods (Brownian Bridge Movement Modelling and Behavioural Change Point Analysis that allow for a simplistic way to identify changes in behavioural states within animal trajectories (Horne et al. 2007; Gurarie et al. 2009; Kranstauber et al. 2012).

To my knowledge, this study will be the first attempt to understand Bornean elephant (*E. m. borneensis*) behaviour using movement data. Previously, BCPA (see above) was successfully applied to determine the response of African elephants to seasonal changes in rainfall, where elephants were observed to make non-random near-simultaneous changes in movements when rainfall was occurring (Garstang et al. 2014). The same species also showed a rapid and highly directional movement behaviour, and consistently chose the nearest waterhole, suggesting a cognitive-based mechanism for these movements (Polansky et al. 2015).

To improve the insight into the behavioural changes provided by dBBMM, I also included the analysis of movement speed. Animal movement speed has been observed to change as a consequence of the activities that the animals are performing (Douglas-Hamilton et al. 2005; Shamoun-Baranes, Bouten, et al. 2011; Abrahms et al. 2016). Low speed is usually related to increased residence time in a certain location, in order to exploit the resources more intensively. For example, elephants moved slowly when they were close to a waterhole (Zollner and Lima 2005; Benhamou and Riotte-lambert 2012; Polansky et al. 2015). In contrast, high speed often reflects risk avoidance by animals. For example, the level of vigilance of the brown capuchin monkey (*Cebus apella*) decreased when the group was traveling faster, while African elephants increased their speed when travelling through habitat corridors (Hirsch 2002; Graham et al. 2009; Chamaillé-Jammes et al. 2013).

3.2 Material and Methods

3.2.1 Study site and focal species

The Lower Kinabatangan Floodplain (LKF) is located in the east of Sabah, Malaysia. It is a highly fragmented landscape, due initially to intensive selective logging followed by conversion to oil palm plantations and an increase in human settlements (Ancrenaz et al. 2004; Abram et al. 2014). Specific forest types in this region are associated with mangrove, flooded forest, and dry (humid) forest systems (Abram et al. 2016). Human presence and agricultural activities have created 20 bottlenecks in the natural habitats throughout the elephants' distribution in the LKF; these bottlenecks are defined as areas which are <1.0 km wide (Estes et al. 2012). Development of the forested land by conversion into human-altered habitat types, is prevalent, especially as there are still significant areas of unprotected forest that remain, outside the protected area (Abram et al. 2014). The Bornean elephant distribution in the eastern part of Sabah comprises five Managed Elephant Ranges (MERs): Lower Kinabatangan, North Kinabatangan, Central Sabah, Ulu Kalumpang and Tabin. The Kinabatangan MER holds between 200-250 elephants (Alfred et al. 2010). Previous work on home range and space use has revealed that movement of Bornean elephant in LKWS is strongly affected by season, distance to river, land use and distance to road (Chapter 2).

3.2.2 Statistical Analyses

The Brownian motion variance (σ^2_m) is an important parameter in the estimation of an animal's utilization distribution, as it quantifies how diffusive or irregular the path of an animal is and provides an index of sinuosity of movement (Figure 3.1) (Horne et al. 2007). This parameter is estimated from the animal's mobility based on its speed and direction of movement (Table 3.1) (Horne et al. 2007). However, the σ^2_m values estimated using BBMM are assumed to be constant within the path, but the dynamic Brownian Bridge Movement Model (dBBMM) developed and improved the original BBMM method, by taking into account behavioural changes along the path (Kranstauber et al. 2012). To detect shifts in movement behaviour, an adjustment to the behavioural change point analysis (BCPA) introduced by Gurarie *et al.* (2009) is implemented via a sliding spatial "window" along the path, producing multiple estimates of σ^2_m for each time step, which are then averaged to produce a final, independent σ^2_m for each path step (Kranstauber et al. 2012). The potential for σ^2_m to vary along the path provides provides insights into changes in behaviour along the movement path. High values of σ^2_m are associated with irregular paths and/or increased activity, and lower values of σ^2_m are associated with more regular paths and/or decreased activity.

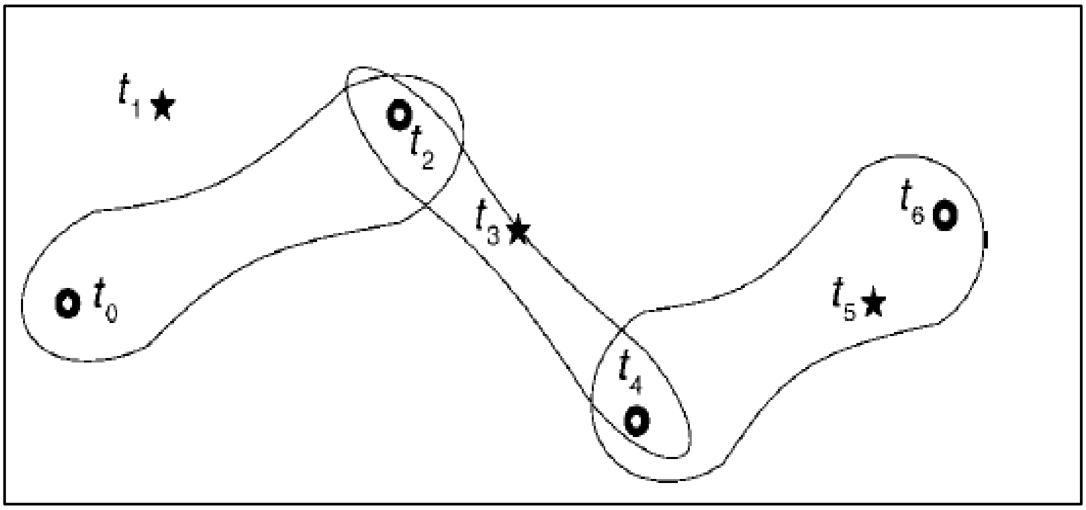
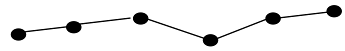
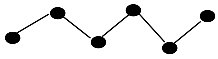
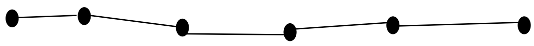


Figure 3.1 A diagram showing how the calculation of the Brownian motion variance (σ^2_m) was made. Using a leave-one-out approach, σ^2_m is estimated from the distances between the actual location (t_0-t_6) and the expected location of the point left out (t_1, t_3 & t_4), under the assumption of a constant movement between the previous and next locations (adapted from Horne et al., 2007).

Table 3.1 Illustration of how the combination of motion variance and speed relate to elephant movements. These movements are made of 5 steps length. 1) MV=4, Speed=5; 2) MV=16, Speed=5; 3) MV=4, Speed=10; MV=16, Speed = 10 (visualisation of ideas presented by Wall et al., 2013; Polansky et al., 2015).

Motion variance	Speed	Examples of movement	Potential mode of movement
Low	Low		Foraging OR vigilance
High	Low		Resting OR searching
Low	High		Forage as you go OR goal-oriented walk

Several arguments were specified when running the dBBMM model: window size, location error, margin size and extent. The window size argument is related to the BCPA that is integrated into the dBBMM process (Gurarie et al. 2009; Kranstauber et al. 2012). It indicates the size of the window (in units of number of location coordinate fixes) that moves across the time/location data, in order to detect significant change points. The bigger the window, the more stable or accurate the estimates of the Brownian motion variance, but the lower the spatial-temporal resolution. We set the window size argument to 2; which represented 24 hours of data (1 location fix every 2 hours) for most of the days, allowing us to detect daily changes in behaviour. A location error of 2.5, as suggested by African Wildlife Tracking (Sophie Haupt, *pers. comm.*) was used for all locations and we set the “extent” argument to 72 after plotting the animal's trajectory and seeing that the longest track dimension was 72 km. The size of each raster cell produced by the analysis was set to 1 km^2, allowing for a straightforward interpretation of results. The margin was left at the default setting of 3, reflecting a medium sensitivity for detecting break-points in movement behaviour. The dBBMM analysis was implemented in the R statistical software (R Core Team, 2014) via the R Studio (https://www.rstudio.com/) graphical user interface, using the "move” package, version 1.2.475 (Kranstauber et al. 2012). All of the predictor variables were extracted by using the “Samples” tool in ArcGIS 10.3, as explained in Chapter 2.

As motion variance is partly derived from speed, I expected that these two variables were not totally independent from each other. To confirm this, I calculated the correlations between these two variables to see if these variables are independent from each other in explaining the temporal-spatial changes in elephant behaviour. Motion variance and speed were calculated from the trajectories of the same set of individuals in Chapter 1.

Generalized Additive Mixed Models (GAMMs) were used to examine the relationships between variation of σ^2_m and speed to the predictor variables, which included season, LULC, elevation, slope, aspect, carbon, distance to river, distance to forest, distance to road, distance to buildings and building density. GAMM models were implemented using the mgcv package (Wood 2011) in R (R Development Core Team, 2015). A smoothing function was applied to the variable “time of day” to allow a flexible non-parametric curve to describe the time of day variation in the response variable. Meanwhile, elephant ID was included as a random variable because repeated observations made from the same elephants, which would otherwise cause pseudoreplication, and to control statistically for any differences between individual elephants.

I further investigated motion variance by examining the interaction between habitat types and time of the day so test whether elephants were active in certain habitat types at different hours of the day. Several habitat types (n=8 habitats) were excluded from the analysis, due to an absence of motion variance data from that habitat including beach, dry lowland dipterocarp, limestone, mangrove, nipa palm, peat swamp, settlement and oil palm underproductive. Seasonal freshwater swamp forest was selected as the reference category for comparisons against other habitat types because it provides significant food resources and connectivity across Kinabatangan landscape. The best models were selected by evaluating the optimal combination of predictor variables, using the Akaike's Information Criterion (AIC) as a measure of model efficiency (variance explained in relation by the number of terms included in the model). The final GAMM model structure included the Gamma error family with a log link function, while the smoothing function was defined using the cyclic cubic spline method with six knots (Thomas *et al.*, 2017). The independent variable data for the GAMM analysis was prepared in ArcGIS 10.3, as described in Chapter Two of this thesis.

3.2.3 Hypotheses

a. Time of day differences

I hypothesised that motion variance and speed would vary significantly over the 24-hr cycle, as elephants are generally observed to be least active during the middle of the day and night and peak in activity at dusk and dawn (Joshi and Singh 2008; Loarie et al. 2009). However, elephant movements and behavioural routines may be affected by land use, we expected to observe habitat differences in the time ofday variation in motion variance and speed (Graham et al. 2009; Alfred et al. 2012).

b. Effect of Environmental Features

The environmental features included as predictor variables are: elevation (m), slope steepness (degree), land use land cover (LULC), season (flooding/non-flooding), carbon stock (MgC/ha), distance to forest (km), building density (people/km^2), distance to buildings and distance to river (km). Water is important for the elephants, mainly to reduce body heat through evaporative cooling (Kinahan et al. 2007; Weissenböck et al. 2012; Dunkin et al. 2013). Lower Kinabatangan region is mostly flat, allowing the elephants to save energy while moving (Pan et al. 2009). Therefore, we expect that the minimal variation in topography (elevation and slope) will not be sufficient to influence motion variance and speed. We hypothesized that distance to river would not be significantly associated with motion variance and speed, because annual rainfall is stable and relatively high (> 3000 mm/year) in the Kinabatangan, providing consistent water availability for elephants (even away from the river and during the non-flooding season); therefore there is no need for the elephants to actively search for that resource (Fernando, Eric D. Wikramanayake, et al. 2008; Sitompul, Griffin, Rayl, et al. 2013). We also postulated that elephants would be less active when they are closer to the forest, because forest could possibly act as a refuge from human activities as well as being a cooler refuge during periods of high ambient temperature (Kumar et al. 2010).

I expected that the motion variance and speed would be higher during the flooding season than during the non-flooding season. This is because flooding reduces and fragments the land area that is available to the elephants and forces the elephants to be constantly travelling to search for food (Estes et al. 2012; Polansky et al. 2013). As habitat selection is a behavioural mechanism by which animals attempt to maximize their inclusive fitness, I predicted that the motion variance and speed would vary between certain habitat types (e.g. less activity and slower movement in open habitats such as swamp and severely degraded forest) as the elephants are utilizing some habitats more for feeding and moving (English, Ancrenaz, et al. 2014; English, Gillespie, et al. 2014; Roever et al. 2014).

Carbon stock was used as a proxy for the quality of the forest, where plots with higher carbon class (i.e. larger diameter at breast height (DBH) were able to act as a better sink of atmospheric carbon (Foody et al. 1996; Morel et al. 2011; Abram et al. 2016). We predicted that motion variance and speed would be low in areas with low carbon stocks (between 0-400 MgC/ha). I postulated this because regardless of the season; elephants in LKWS were observed to prefer grazing on grasses such as *Phragmites karka* and *Dinochloa scabrida* which are available mainly in riparian areas (English, Gillespie, et al. 2014). When they are actively feeding on these grasses, the elephants commonly remain in the same location and only infrequently change their movement direction (*pers. obs.*).

c. Effect of Anthropogenic Activities

I predicted that human presence and activities would increase the likelihood of vigilance-related behaviours. Therefore the motion variance and speed were hypothesised to be lower when the elephants were close to buildings and roads, as well as in higher building density (Blake et al. 2008; Srinivasaiah et al. 2012).

3.3 Results

3.3.1 Motion Variance

Motion variance provides a simple index to identify potential behaviours of a moving animal (Kranstauber et al. 2012). Estimates of the Brownian motion variance for individual Bornean elephant ranged from 0.362 m^2 to 8121.512 m^2, with a mean of 984.947 m^2 (Figure 3.2). The GAMMs fitted with and without a random effect for 'individual elephant' provided a similar result. Therefore, the random effects were excluded in the final models, which were thus GAMs with individual identity fitted as a fixed factor habitat types, season, distance to road, distance to river and distance to building were the best predictor variables to explain the motion variance indicated by the best fit model (Table 3.2).

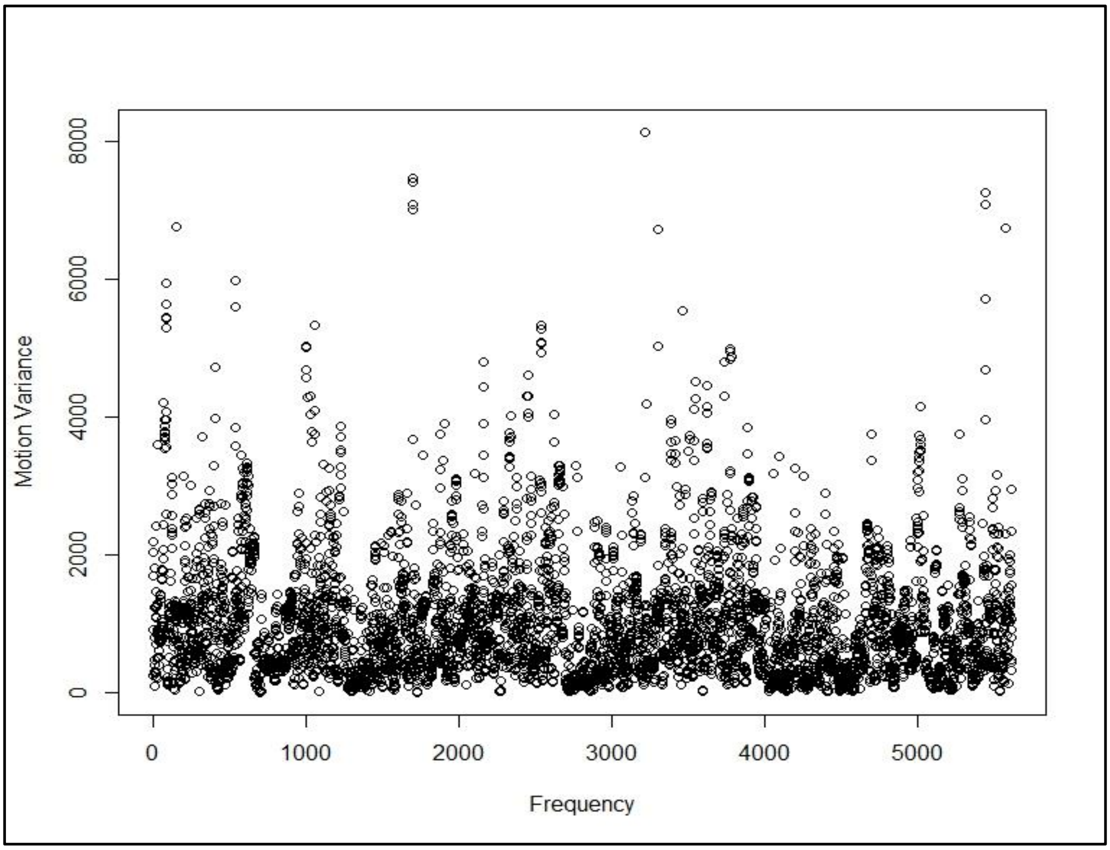


Figure 3.2 Distribution of motion variance values across the whole dataset, showing the zero limited but highly skewed distribution of values which was modelled using a gamma error distribution in the analysis.

Motion variance differed significantly between habitat types; when compared to seasonal freshwater swamp, two habitats showed significant differences in motion variance; motion variance was significantly lower in dry lowland forest, but was significantly higher in swamp (Table 3.2). Motion variance was significantly higher in the non-flooding season than in the flooding season (Table 3.2). Furthermore, the GAMM identified that the covariates of distance to building (Figure 3.3a), distance to river (Figure 3.3b) and distance to road (Figure 3.3c) significantly explained the motion variance. Higher motion variance was observed when the elephants were close to roads, but the motion variance decreased when the elephants were closer to buildings and the river (Figure 3.3).

There was also a significant interaction between motion variance, time of the day in two habitats which are freshwater swamp forest (Figure 3.4a) and transitional forest (Figure 3.4b), respectively.

Table 3.2 Summary statistics for covariates tested in the GAMMs fitted to the relationships between variation of σ^2_m and the predictor variables. Individual ID was also included as a term in the model to account for between-individual differences.

Independent variables (Time): Habitat	**F-test**	**edf**	**p-value**
Freshwater swamp forest	3.528	2.285e+00	<0.001
Transitional	2.759	2.086e+00	<0.001
	Estimate	**S.E**	**p-value**
Dry lowland forest	-8.737e-02	4.102e-02	< 0.05
Swamp	2.039e-01	7.674e-02	<0.01
Season (Reference category = Non-flooding)	1.828e-01	2.429e-02	<0.001
Distance to Road	-1.594e-05	4.800e-06	<0.01
Distance to Building	3.223e-05	1.245e-05	<0.05
Distance to River	2.459e-05	1.253e-05	<0.05

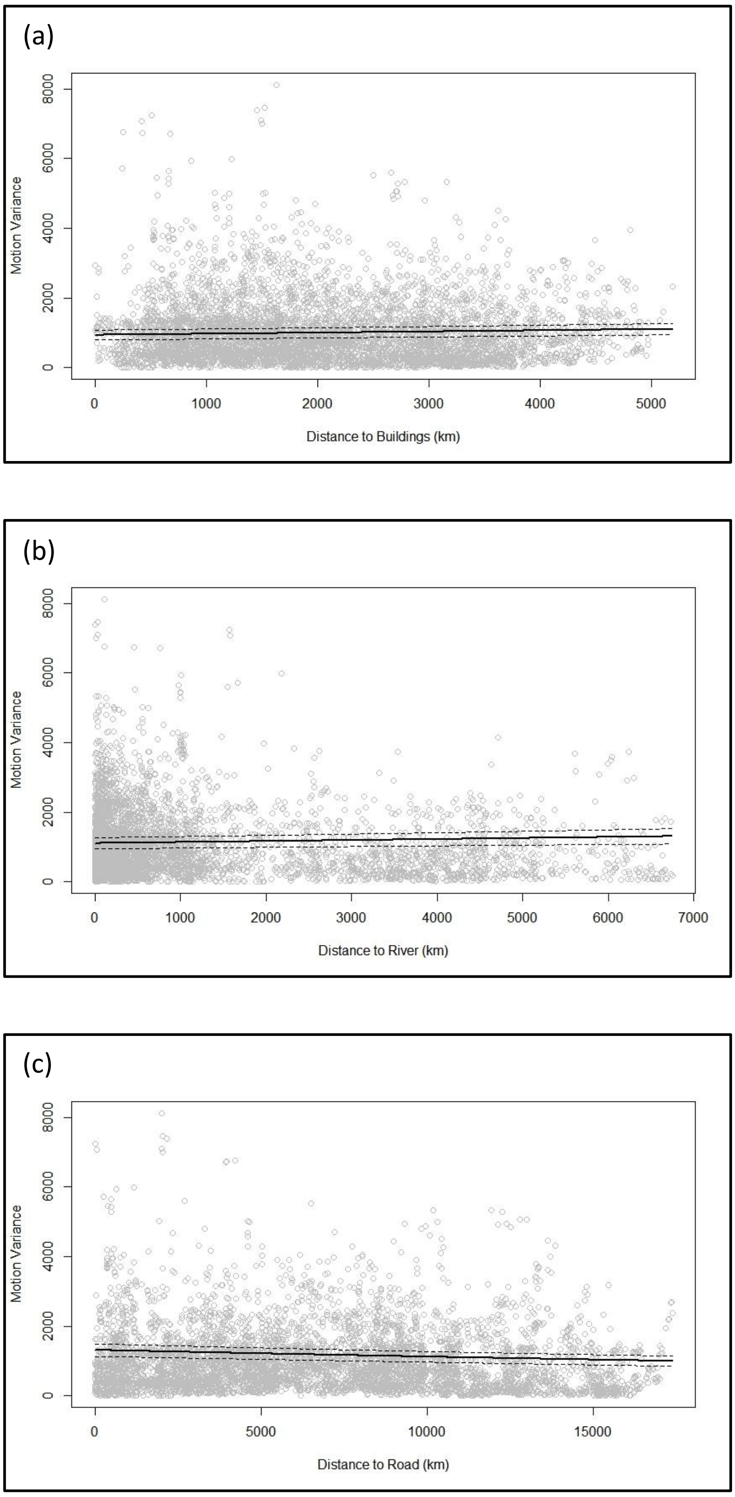


Figure 3.3 Association between motion variance of elephants, and physical features of their environment: a) Distance to buildings, b) distance to river and c) distance to road. Fitted lines represent model predictions (controlling statistically for all other terms in the model), +/- 1SE.

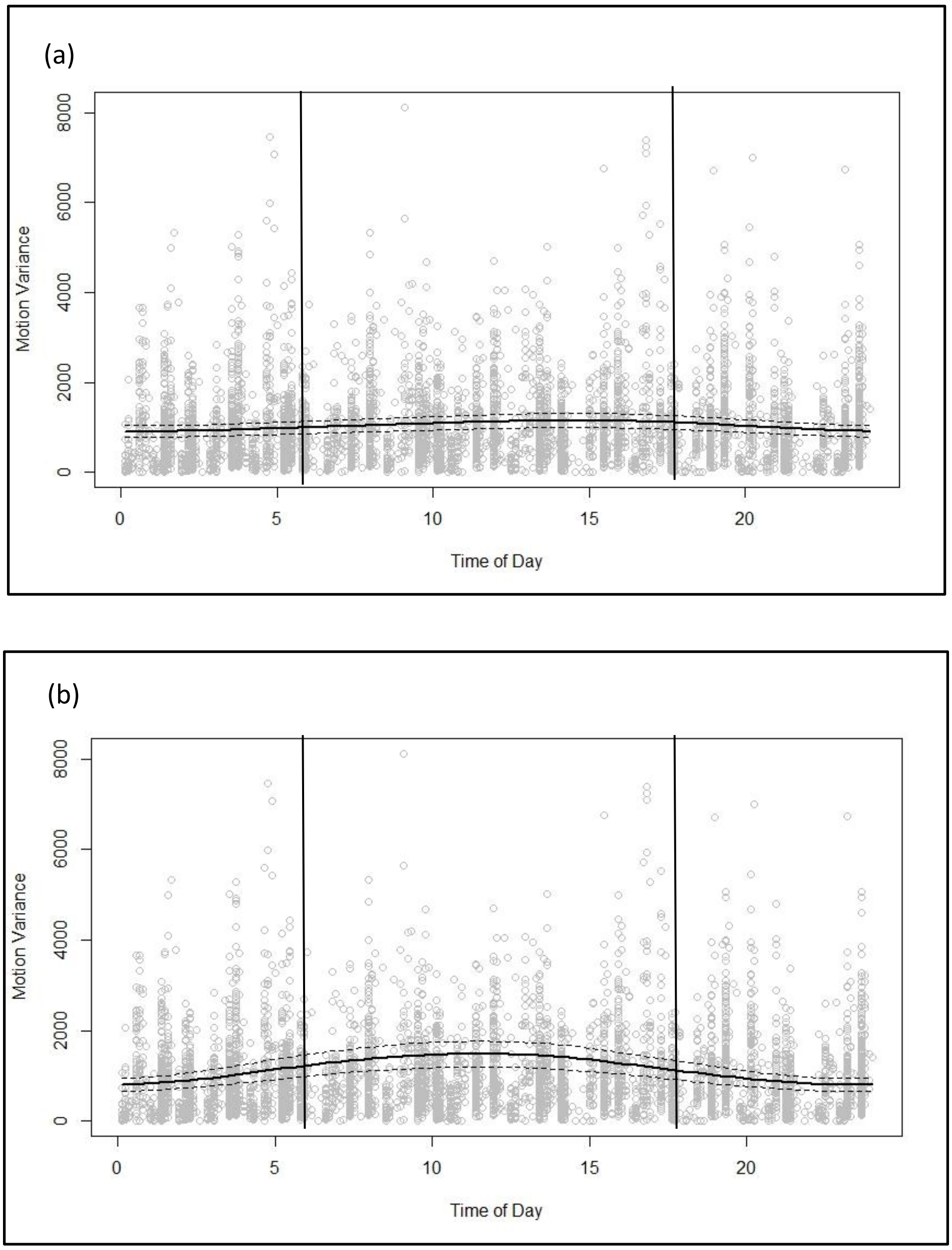


Figure 3.4 Time of day variation in motion variance of elephants in a) freshwater swamp forest and b) transitional forest. Fitted lines represent model predictions (controlling statistically for all other terms in the model), +/- 1SE.

3.3.2 Speed of Elephant Movement

On average, the monitored elephants moved at a speed of 0.17 km/h (n = 8460 point locations) although this varied significantly between different land-use types specifically in severely degraded forest, dry lowland forest, freshwater swamp and transitional forest (Table 3.3). Elephants had a significantly lower speed in all these habitat types compared to the speed in the seasonal freshwater swamp forest. The time-of-day variation in elephants' movements also changed depending on which land-use type they were in, as the interaction between time and habitat was significant (Figure 3.5). In all land-use types, elephants moved more slowly in the early morning (between 12 am until 8 am), and they moved at a higher speed at night (between 4pm-12am).

Meanwhile, in the oil palm plantation elephants moved at a lower speed during the day compared to their movement speed at night (Figure 3.6). There was no significant difference in movement speed between the flooding and non-flooding seasons (Table 3.3). Elephants significantly increased their speed when they were close to the river (Figure 3.6a) and they significantly reduced their speed when they were close to buildings (Figure 3.6b). There were four habitat types where speed was significantly lower than in seasonal freshwater swamps these were severely degraded forest, dry lowland forest, swamp and transitional forest (Figure 3.6c). Overall, this GAMM model explained 0.0473 of the deviance.

Table 3.3 A GAM model to explain elephant's speed in relation to time or day, spatial physical and spatial anthropogenic covariates.

Covariates (Time): LULC	**F-test**	**edf**	**p-value**
a) Severely degraded	5.339	3.125	<0.001
b) Dry lowland forest	9.157	3.684	<0.001
c) Seasonal freshwater swamp	12.877	3.220	<0.001
d) Freshwater swamp	9.439	3.476	<0.001
e) Swamp	17.568	3.444	<0.001
f) Transitional	1.276	1.618	<0.05
g) Cleared area/planted/young	3.850	2.162	<0.001
h) Oil palm with good canopy	12.657	3.709	<0.001
	Estimate	**S. E**	**p-value**
Season:non-flooding	-2.596e-02	2.675e-02	0.3319
Distance to building	5.220e-05	1.204e-05	<0.001
Distance to river	-6.071e-05	1.271e-05	<0.001
Severely degraded	-2.589e-01	5.451e-02	<0.001
Dry lowland forest	-2.473e-01	4.412e-02	<0.001
Swamp	-6.698e-01	7.448e-02	<0.001
Transitional	-1.951e-01	7.797e-02	<0.05

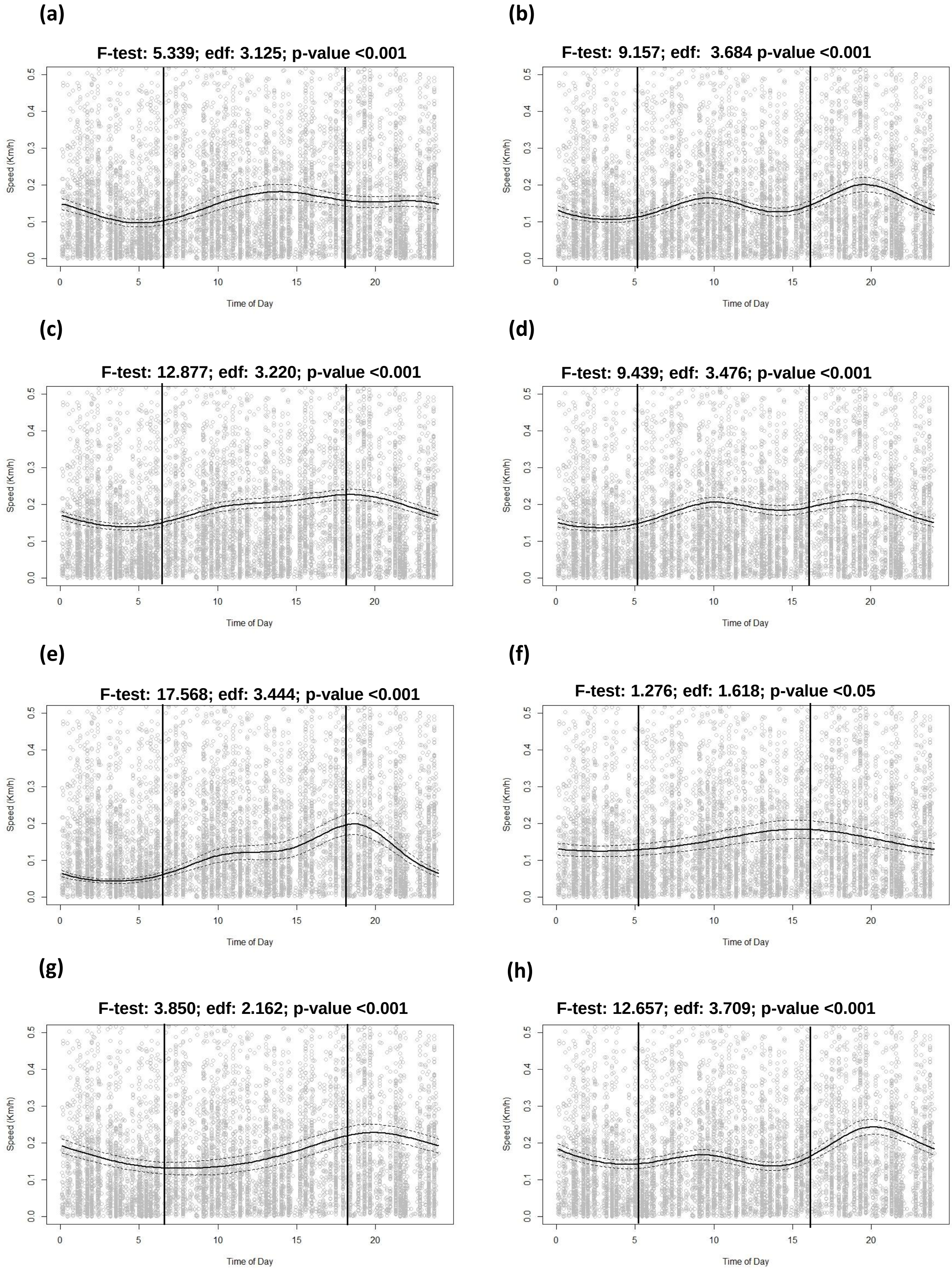
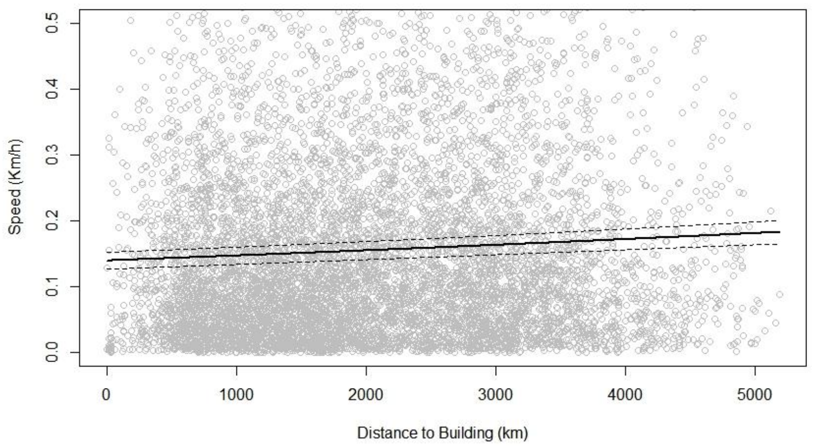
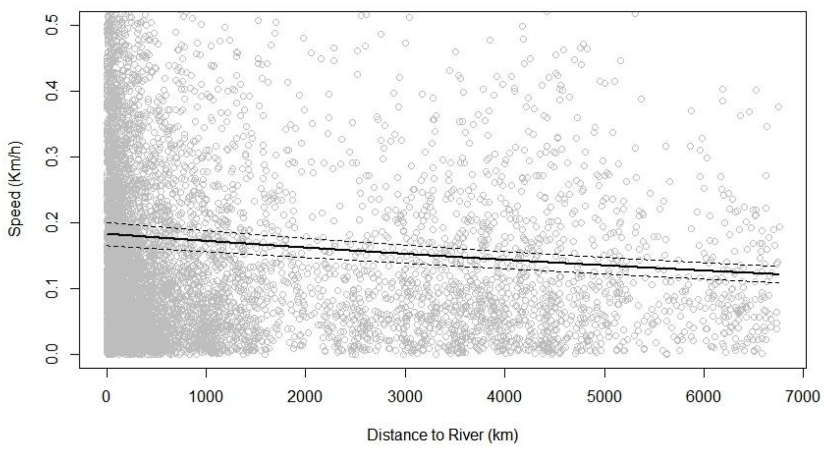


Figure 3.5 a) severely degraded; b) dry lowland forest; c) seasonal freshwater swamp; d) freshwater swamp; e) swamp; f) transitional; g) cleared area/ planted/young OPP trees; h) OPP with good canopy. Black line is the dusk and dawn.

(a)



(b)



(c)

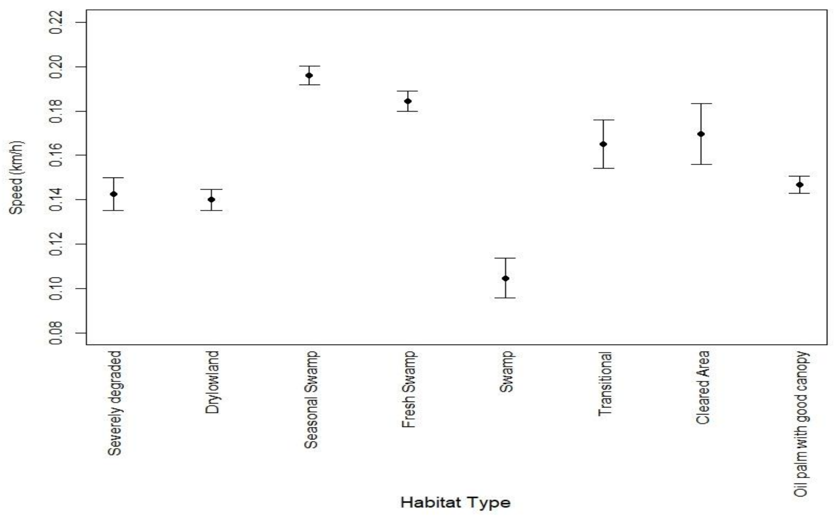


Figure 3.6 GAM model predictions of the relationship between speed and a) distance to building; b) distance to river and c) habitat types.

Table 3.4 Comparison of four models to explain elephants' movement 1) dependent variable = motion variance and 2) dependent variables = speed.

a) Models without habitat X time of the day interaction

	Dependent variables	
Predictors	**1) Motion Variance**	**2) Speed**
Close to road	High	-
Close to river	Low	High
Close to buildings	Low	Low
Season: Non-flooding	High	Low*
Dry lowland forest	Low	Low
Swamp	High	Low
Severely degraded forest	-	Low
Transitional	-	Low

b) Models with habitat X time of the day interaction

Predictors	**1) Motion Variance**	**2) Speed**
Interaction TOD: LULC		
Severely degraded		*
Dry lowland forest		*
Seasonal Freshwater swamp		*
Freshwater swamp	*	*
Swamp		*
Transitional	*	*
Cleared area/planted/young OPP		*
Oil palm with good canopy		*

3.4 Discussion

Motion variance is a composite measure of animal movement which integrates information about a range of movement dynamics (velocity, changes in direction etc.). In contrast, speed is a simple and readily understood component of movement. As there was no apparent correlation between motion variance and speed, it was thus informative to use both motion variance and speed to explain the shifting behavior in elephant's movement.

There are four possible combinations of motion variance and speed that we expected to see (Table 3.1). A combination of high motion variance and low speed would indicate that elephants are in an "encamped" state in which step lengths are small and turning angles are high. A combination of low motion variance and high speed indicated that elephants are in an 'exploratory' state, in which step lengths are large and turning angles small (Morales et al. 2004). Some studies show that certain animals such as elk (*Cervus elaphus*) alternated between encamped and exploratory modes, possibly linked to changes in motivational goals from foraging to social bonding (Fryxell et al. 2008). Meanwhile, woodland caribou (*Rangifer tarandus caribou L.*) make frequent short-distance movements within patches, as they search for terrestrial and arboreal lichens (Johnson et al. 2002). In a study of a lowland tapir (*Tapirus terrestris*), the individual exhibited a faster and more variable movement, likely related to travel and food searches (González et al. 2017). For African savanna elephants, encamped behaviour usually occurred near locations with abundant resources, whereas they moved faster and more linearly in locations without resources or when migrating (Roever et al. 2014). Cougars (*Puma concolor*) tended to have straighter movements and moved faster through urbanized areas (Dickson et al. 2005).

Animal trajectories are a succession of different types of movements corresponding to specific activities. However, the habitat they are living in, and their movement patterns within those habitats, makes it difficult to observe directly the behavioural states or the shifts between different behaviours.

Using location data from satellite collars to identify and categorise changes in behaviours will reduce the disturbance caused by the observer and provides an opportunity to analyse aspects of behaviour that remain beyond the capability of traditional methodologies. One of the crucial behavioural requirements of Asian elephants is to be able to move across extensive tracts of land in order to fulfil its needs. However, due to habitat loss and fragmentation in most parts of its range, the species often comes into conflict with humans over resources (Leimgruber et al. 2003; Fernando 2010). It is therefore one of major interest to understand how elephant behaviour changes in response to various stimuli, providing insights into the mechanisms which mediate the elephants' movement trajectories and consequently determined their immediate success or failure in these modified environments (Caro 1999; Sih 2013). Using the measures of motion variance and speed produced by dBMM, in the present study I have used both motion variance and speed to identify the modes of movement of Bornean elephants in a highly fragmented area of the Lower Kinabatangan Floodplain.

Variation in motion variance and speed between land use types may indicate both the resource availability in different habitats, and the resistance to movement that elephants are facing as they moved across this highly fragmented landscape. When the elephants were approaching the river, they moved in a highly directional movement and with high speed (e.g. goal-oriented walking). Water availability was not seen as an important determinant of elephant ranging patterns for the African forest elephant (*L. a. cyclotis*), Sri Lanka elephant (*E. m. indicus*) and Sumatran elephant (*E. m. sumantrensis*) because there is consistent water availability in their habitats (Buij et al. 2007; Fernando, Wikramanayake, et al. 2008; Sitompul, Griffin and Fuller 2013). As the same circumstances are expected in Lower Kinabatangan, it is likely that elephants are orienting their movements by walking directly towards the river to exploit riparian vegetation along the river such as *P. karka* and *D. scabrida*, which could be found mainly in the riparian area. This observation would suggest that the Bornean elephant has strong spatial awareness of crucial resources, as has been shown for the zebra (*Equus burchelli antiquorum*) and the African savanna elephant (Brooks and Harris 2008; Polansky et al. 2015).

Two covariates which are the distances to buildings and to dry lowland forest were significantly associated with the elephants moving in a directed manner and reducing their speed. In Lower Kinabatangan, there are four main villages (Batu Puteh, Bilit, Sukau and Abai) that are found within the elephant population's range, and many of the dry lowland forests are either located close to these villages or bordering oil palm plantations. The development of these human settlements has created a spatial bottleneck to elephant movements, limiting movements between areas of natural habitat. The two longest habitat bottlenecks (6.5 and 9.0 km respectively) are the only options for elephants to pass by Sukau village (Figure 3.7) (Estes et al. 2012). Therefore, for the elephants to be able to move across the landscape through these areas, a trade-off must exist by either adjusting their behaviour to tolerate the situation or to totally abandon the area. Unlike the African forest elephant and the Indian elephant, which were observed to increase their speed of movement rates in highly disturbed areas, the Bornean elephant reduced its speed of movement (Buij et al. 2007; Blake et al. 2008; Srinivasaiah et al. 2012). This unexpected movement strategy may assist Bornean elephants to maintain their vigilance as seen on a few occasions when elephants spent between 2-5 days in the Bukit Melapi-Yu Kwang Corridor, located behind Melapi lodge near the village of Sukau, before they left this area (Figure 3.8).

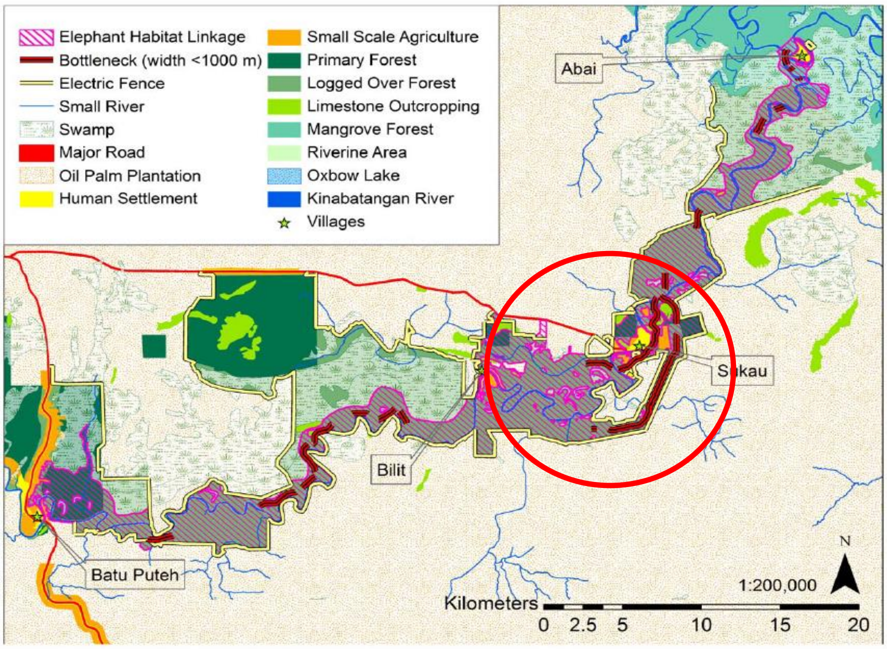


Figure 3.7 The red circle higlights the location of the two longest habitat bottlenecks (6.5 and 9.0 km respectively) which serve as the only options for elephants to pass by Sukau village.

Figure 3.8 Elephant herds were stranded near Bukit Melapi-Yu Kwang Corridor due to the presence of a lodge and oil palm plantations impeding their movement pathway.

Both motion variance and speed were significantly different when the elephants were in swampy areas compared to seasonal freshwater swamps. When elephants moved in swampy areas, they were walking slowly (short step lengths) and in a meandering path (with high turning angles). Speed was low, which is an indication of intensive searching within a small area (Fauchald and Tveraa 2003; Martin et al. 2009; Knell and Codling 2012). When the elephants concentrated their foraging effort in areas which could maximize their energy intake, their efficiency of foraging would also increase. Similar observations were made on another herbivore, the domestic goat (*Capra hircus)* moving within patches with higher plant density (De Knegt et al. 2007). Although swampy areas caused resistance to elephant movement (Estes et al. 2012), the elephants could potentially use swaps as a natural refugee from human disturbance.

Unexpectedly, elephants were more active or frequently moving in an undirected manner (characterized by short step length and high turning angles) in the non-flooding season rather than in the flooding season, as indicated by higher motion variance in this season. However, their speed did not vary significantly between these two seasons. During the non-flooding season, the elephants were observed to use areas that were close to roads which run through palm oil plantations given there is less human presence in the vicinity of roads (Chapter 2). One plausible explanation for this finding is that the road network within the elephants' home range could act as a barrier to their movement. This assumption is strongly supported by another covariate (distance to building) which was also found to significantly influence the motion variance. Motion variance was significantly higher when elephants were close to the road. Figure 3.9 illustrates the situation where in many circumstances elephant movements were disrupted by unnecessary human harassment. This is illustrated by the case shown in Figure 3.8, where two vehicles were sounding their horns and revving their engines, to scare the elephants away from the road. Elephants were probably most affected by heavy vehicles due to their size, and continuous pressure from human populations would likely alter elephant tolerance towards people (Fernando 2010; Vidya and Thuppil 2010).

Figure 3.9 Examples of disturbance to elephants by traffic passing along the road network through oil palm plantation.

Elephant motion variance varied significantly interacted with time of the day, especially in freshwater swamp forest and transitional forest. Speed varied significantly with time of the day in all of the land-use types; elephants moved more rapidly at night than during the day. Elephants are facing elevated risks in the oil palm plantation due active efforts by plantation workers to defend their oil palm estates from encroachment by elephants. During the day, among the active techniques to push away elephants from the oil palm plantations is by making noise using vehicles such as motorbikes or 4W drive vehicles. Areas of oil palm present more risks and therefore tend to be used more by night than by day, which suggests that this is a risk-avoidance strategy (Graham et al. 2009; Kumar et al. 2010).

Elephants are highly cognitive animals and for us to able to understand better their behaviour from movement data, tool such as activity sensors (e.g. accelerometers) that are attached to the radio collar could assist to describe the activity level of an animal (Shepard et al. 2010; Nathan et al. 2012; Soltis et al. 2012; McClintock et al. 2013; Nams 2014). Accelerometers are motion-detection devices that, when attached to animals, are capable of detecting body orientation, overall activity levels, and specific behaviour patterns. However, in the absence of activity sensor on the radio collar, analysis such as behavioural change point analysis (BCPA) would produce more compelling results in distinguishing between different types of behavioural mode. The results in this chapter demonstrate that individuals may adjust movement behaviour spatially and temporally to deal with trade-offs between resource acquisition and risk avoidance, at the landscape scale. However, the pressure caused by human activities can lead to conflicts between humans and elephants. Understanding behavioural states, and their important role in the process of habitat selection, will help us to prioritize action for conservation and management. These applications to specific conservation issues are identified in the Chapter 5: General Discussion.

CHAPTER FOUR

DAILY AND SEASONAL BEHAVIOURAL PATTERNS OF BORNEAN ELEPHANTS IN NATURAL HABITATS AND OIL PALM PLANTATIONS ADJOINING THE KINABATANGAN RIVER, SABAH

4.1 Introduction

Natural forests are rapidly being lost, degraded and fragmented, particularly in the tropics, by conversion to agricultural and other types of land uses and human development (Leimgruber et al. 2003; Sodhi et al. 2004; Songer et al. 2012). The impacts of these environmental changes are particularly acute for large mammals such as elephants, which have low population densities and slow life histories leading to a high risk of population extinction (Purvis et al. 2000; Cardillo et al. 2005). As an immediate response to these rapid changes in their environment, animals may have to modify their behaviour (Vidya and Thuppil 2010; Wong and Candolin 2015). An understanding of behaviour can thus improve assessments of whether a species is capable of surviving in a particular habitat, and how it will cope (or fail to cope) with habitat modification.

Comparisons of the activity patterns of a species in different habitats can reveal how habitat changes can impact individual behaviour (Fiore and Rodman 2001; Kumar and Singh 2010; Vidya and Thuppil 2010; Srinivasaiah et al. 2012). Activity budgets of highly social animals with well-developed cognitive abilities, such as elephants, depend primarily on the availability of various resources; namely water, minerals, and food as well as habitat conditions like temperature (Holdo et al. 2002; Sukumar 2003; Blake et al. 2008; Baskaran et al. 2010; Pastorini et al. 2010; Fernando and Leimgruber 2011). In many circumstances, elephants altered their behaviour to minimize anthropogenic threats and these behavioural changes can have profound impacts on the elephants' welfare and fitness (Blake et al. 2008; Shannon et al. 2008; Kumar and Singh 2010; Vidya and Thuppil 2010; Srinivasaiah et al.

2012; Cable 2013; Fishlock and Lee 2013). For example, body condition of elephants has deteriorated when they were confined only to certain habitat types and faecal glucocorticoid metabolite concentrations during translocation of elephants by wildlife managers indicate elevated stress levels as elephants are relocated to novel areas (Fernando et al. 2009; Jachowski et al. 2012).

Most studies on activity budgets of elephants were conducted in zoos or wildlife parks, to better understand stereotypic behaviours and improve their welfare (Rees 2009; Freeman et al. 2010). Behavioural studies of elephants in the wild have primarily focused on sexual segregation and behavioural response by elephants (Shannon et al. 2008; Srinivasaiah et al. 2012; Ahamed 2015). These studies showed that under natural conditions, elephants were observed to spend a lot of the time eating and to move relatively little (Evans and Harris 2008; Baskaran et al. 2010; Srinivasaiah et al. 2012). Whereas in human dominated landscapes, major elephant activities are both foraging-related and moving, which occurred mostly in more natural habitat types within the landscape mosaic (Kumar and Singh 2010). Elephants partitioned their activities temporally, feeding in the early hours of the morning and evening, and resting during the middle part of the day (Shannon et al. 2008; Joshi 2009; Baskaran et al. 2010). In areas with high human disturbance, elephants reduced their effective feeding time, and increased the amount of time moving and standing alert (Kumar and Singh 2010; Srinivasaiah et al. 2012). In Borneo, the loss of natural forest habitat due to habitat conversion has led elephants to increasingly use oil palm plantations, even though this habitat may be suboptimal for them (Alfred *et al.* 2012, Othman *et al.* 2013). In these plantations, elephants are more likely to encounter people and human infrastructure (roads, oil processing mills, villages, buildings, etc.) compared to natural habitats, which can result in human-elephant conflict (Othman et al. 2013; Ancrenaz et al. 2015).

In the present study, I examined the behavioural patterns of Bornean elephants across riparian habitat, seasonal freshwater swamp forests, and for the first time in the highly artificial habitat of oil palm plantations. The goal was to better understand the ecological requirements of this charismatic but endangered taxon in a rapidly changing and already highly modified environment. Only one study has systematically examined the extent to which elephant behaviours may differ between habitats. Kumar and Singh (2010) found that Indian elephants (*E. m. indicus*) showed more feeding behaviour and less vigilance in natural habitats than in human-altered habitats. Based on these findings, I hypothesized that Bornean elephants may differ in their behaviours with dependence on the habitat types. It is important, however, to note that Kumar and Singh (2010) did not further distinguish between habitat types. For instance, rainforest fragments and riparian vegetation along the river were combined into a single category of "natural habitat". Therefore, research is needed to compare elephant behaviours between different natural habitat types (such as riparian areas and seasonal freshwater swamp forests), but also further comparisons between natural versus human-altered habitats to better understand how they might alter the behaviours of elephants in oil palm plantations.

The current study focused on the behaviours of adult females since female elephants seem to be particularly responsive to environmental and social stressors in human dominated landscapes (de Silva et al. 2011; Lee and Moss 2012; Srinivasaiah et al. 2012) . Furthermore, variable group sizes and behavioural patterns (both daily and seasonally) of the Bornean elephants were assessed in this study. It was hypothesized that the elephant group sizes are larger in oil palm plantations, due to the expected lower quality of available food (Alfred et al. 2012; English, Gillespie, et al. 2014) and the greater human-conflict risks associated with this landscape (Othman et al. 2013). It was also expected that the elephants would temporally partition their activities throughout the day in each habitat, with active behaviours (e.g. feeding and moving) most frequent in the mornings and evenings, and inactive behaviour occurring mostly during the middle of the day (Rees 2002; Rees 2004; Shannon et al. 2008; Kumar and Singh 2010; Srinivasaiah et al. 2012; Ahamed 2015). Lastly, I tested if there is seasonal variation in the activity budget of elephants. The present work will help to improve our understanding of the use of oil palm habitat by elephants, and their behaviour in this habitat compared to more natural parts of the landscape.

4.2 Materials and Methods

4.2.1 Study Area and Focal Species

The study focused on the three habitat types most commonly used by the elephants in LKF, namely riparian areas, seasonal freshwater swamp forest, and oil palm plantations. Riparian areas (also known as riverine areas) are commonly found <20 m from the river bank and characterized by moist soil and open grassy areas (Estes et al. 2012). Among the dominant plants in riparian habitat are herb species from the Poaceae (specifically *Phragmites karka* and *Dinochloa scabrida*) and trees like *Ficus racemose* (Payne 1997; English, Gillespie, et al. 2014). Seasonal freshwater swamp forest is inundated between three to six months annually and is comprised of mixed dipterocarp species tolerant to high water levels and periodic flooding, such as *Malotus muticus*, *Macaranga gigantea*, *Pterospermum elongatum* and *Cananga odarata* (Payne 1997; English, Gillespie, et al. 2014). Conversion of land to oil palm plantations has been the main driving force for forest loss in Sabah: about half of the land area of the lower-middle Lower Kinabatangan Floodplain (LKF) is now covered with oil palm plantations (Hai et al. 2001; Abram et al. 2014).

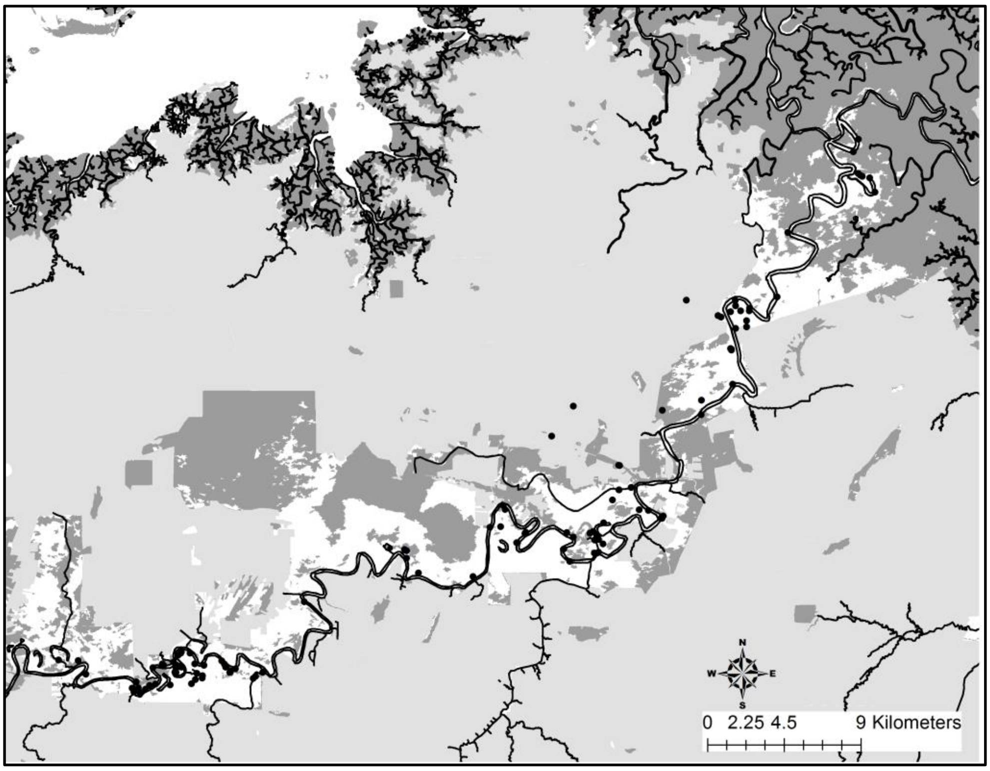


Figure 4.1 Map of the study area in the Lower Kinabatangan floodplain, Sabah, Borneo. The three habitat types compared in the study are demarcated; (i) Riparian forest (blackline along the river), (ii) Freshwater swamp forest (white), and (iii) Oil palm plantation (light grey). Black dots indicate the behavioural sampling points.

The Bornean elephant is a subspecies of the Asian elephant, endemic to the island of Borneo (Fernando et al. 2003; Cranbrook et al. 2007). The taxon is endangered and continuously declining, with threats including human-elephant conflict, habitat degradation and fragmentation (Elephant Action Plan 2012-2016). The LKF is inhabited by an estimated 200-250 wild Bornean elephants (between 10% and 20% of the total estimated population size), and has been designated as one of the five Managed Elephant Ranges (MERs) in the Malaysian state of Sabah (Elephant Action Plan 2012-2016). Bornean elephants are “Totally Protected” under Schedule I of the Sabah Wildlife Conservation Enactment 1997, which is the highest level of protection available. Consequently, any person caught killing or hunting an elephant will receive a mandatory six months to five years jail sentence and/or a fine of RM50,000 (estimated USD11,000) (Elephant Action Plan 2012-2016).

The elephant population in LKF harbours the highest genetic diversity of all of Sabah's elephant populations (Goossens et al. 2016) but has become isolated from other populations due to increasing fragmentation of their habitat. This isolation is likely to lead to a reduction in genetic diversity within the population, making it more vulnerable to natural or man-made catastrophes (Sharma et al. 2012; Goossens et al. 2016). The migratory range of the elephant population in LKWS is restricted between the two villages of Batu Puteh and Abai by roads, oil palm plantations, mangrove forests and human settlements. With only 184 km^2 of land within these limits available to the elephants, the density of this population (2.5 elephants per km^2) is exceptionally high when compared to other Asian elephant population throughout it ranges (Sukumar 2003; Alfred et al. 2012; Estes et al. 2012).

4.2.2 Data Collection

Data were primarily collected each day for two weeks every month from February 2011 to September 2013, using fresh feeding signs, elephant footprints and vocalizations. While in the oil palm plantations, elephants were tracked partly based on information provided by the oil palm workers. In addition, 12 individuals living in the Kinabatangan population were tagged with Very High Frequency (VHF) and satellite collars, which provided an accurate location every two hours. Radio signals emitted by the VHF collars aided in locating the elephants for observation.

Behavioural data were obtained from adult females within a group using instantaneous scan sampling (Altmann 1974). A group was defined as a set of individuals who were within a five-meters radius from the matriarch, i.e., the largest female of the group (McComb et al. 2001; Fishlock and Lee 2013), an approach that is consistent with previous research (de Silva et al. 2011). The scans were carried out every five minutes for one hour or until the group or matriarch was out of sight for more than 10 minutes. During the scans, the behavioural activity was reported for each visible female of the group as either feeding, resting, moving, vigilance, social interactions or bathing (for the definitions of these mutually exclusive activities, see Table 4.1) (Rees 2009; Kumar and Singh 2010; Vidya and Thuppil 2010). Data were collected opportunistically from one group at a time. The data collection was carried out across the seasons from 06:00 to 18:00 hours (daylight period), limited in duration only by logistic constraints such as habitat visibility and accessibility. All data were obtained by the same researcher (NO), who had years of experience observing these elephants. The observations were usually made from a distance of 10-30m, to minimise the impact of the observer presence on the elephant behaviour. Altogether, behavioural data from 40 individually-identifiable adult females were included in this study.

Table 4.1 Definitions of behavioural activities reported in this study.

Behaviour	Definition
Feeding	Inserting any kind of vegetation into the mouth
Resting	Standing passively or lying down, without interacting with other individuals in the herd
Moving	Moving from one place to another, resulting in a change in spatial position at any speed
Vigilance	Looking straight at potential threat, stretching both ears wide apart, smelling by lifting the trunk in the direction of potential threat, or showing aggression to nearby objects, such as uprooting vegetation or pulling out tree branches
Social interactions	Interacting with other individuals of the herd, such as playing, reassuring and greeting.
Bathing	Standing/lying in the water or squirting water over the body with the trunk

Prior to the data collection, each elephant was photographed, identified and named, based on combinations of characteristics such as tears, nicks and holes in the ears as well as tail shape (Vidya et al. 2014). Some of the elephants also had wounded legs due to snares. The best opportunity to learn to identify the elephants and their family members was when they were swimming across the Kinabatangan River.

4.2.3 Statistical Analyses

Generalized additive mixed effect models (GAMMs) was constructed to explain each behaviour (dependent variable), using the ‘mgcv’ library (Wood 2011) implemented in R v3.2.1 (R Development Core Team 2015). All the scans that were less than 20 minutes of observation were discarded from the analysis in order to improve the confidence in the quality of the observational data. GAMMs are a relatively new class of models that are especially useful for analysing daily and seasonal routines of behaviour based on repeated measures of the same set of individuals over time. GAMMs identify smoothed lines of best fit, and include random effects which was used to account for the repeated measurements from the same individual elephants. These models do not use a standardised relationship (e.g. a straight line or a parametric function) between the dependent variable and the independent variable(s). Instead, a non-parametric ‘smoother’ is chosen to fit a smooth curve through data, and thus to maximise the goodness of fit of the model to the data (Thomas 2017). This approach is particularly effective at handling the complex non-linearity commonly associated with behavioural changes across days and seasons. To my knowledge, this is the first study to use GAMMs to explain the daily activity budgets of elephants.

GAMMs was used to analyse the likelihood of observing each behaviour in relation to habitat type (categorical; riparian, seasonal freshwater swamp forest, oil palm plantation), group size (integer count data) and season (categorical; flooding / non-flooding) as fixed independent variables, with hour of the day, fitted as a non-parametric smoothed function. A binomial error family and a complimentary log-log (‘cloglog’) link function were used, following Zuur et al. (2009) and Thomas (2017), to minimise the residual deviance and/or AIC values. Elephant ID was used as the random term in each model, to account for individual variability and repeated measurements of the same individuals over the study period (Zuur et al. 2009).

I used a further GAMM to analyse variation in group size (dependent variable) in relation to the fixed independent variables of habitat type (categorical) and season (categorical), with hour of the day, fitted as a non-parametric smoothed function and elephant ID as the random term. A Poisson error family and a log link function was applied to model the dependent variable as integer count data.

4.3 Results

A total of 2,015 instantaneous scans were used in the analysis. The largest number of scans was recorded in riparian (n=1,653) followed by seasonal freshwater swamp forest (n = 245) and oil palm plantations (n = 117). There was significant variation between habitats in the likelihood of observing the different behaviours (Chi-squared = 115.08, d.f. = 10, $p < 0.0001$, Figure 4.2). Within individual habitats, the most common activities in the natural habitats were feeding (34% in riparian and 33% in freshwater swamp forest), resting (27% in riparian and 29% in freshwater swamp forest) and moving (23% riparian and 28% in freshwater swamp forest), whereas in palm oil plantations the most common activities were moving (52%) and feeding (41%). The least common overall behaviour was bathing (3%), which was the only behaviour of this study that was excluded from further statistical analysis. Comparing between natural and oil palm habitat, feeding behaviour was more likely to observe in the oil palm plantation (41%) than in the riparian (34%) and swamp (33%) habitats.

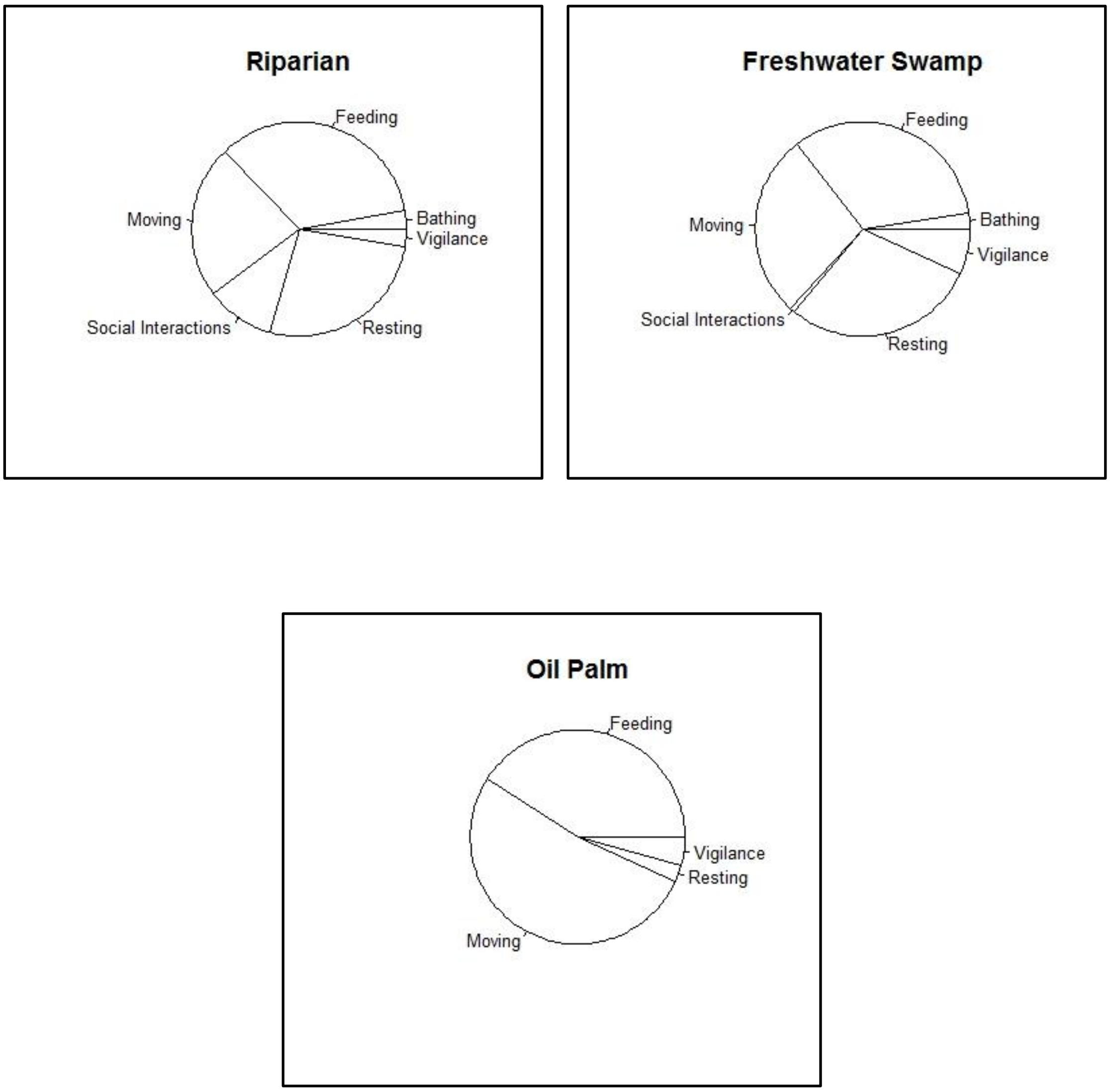


Figure 4.2 Relative proportions of elephant behaviours calculated for the three habitat types of this study; (i) Riparian habitats, (ii) Freshwater swamp forest, and (iii) Oil palm plantations.

4.3.1 Associations between behaviour and habitat type, time of day, season, and group size

4.3.1.1 Feeding

Significant differences between habitats were observed in the frequency of feeding activity, with higher feeding frequency in freshwater swamp forest than in riparian ($p < 0.03$), but not significantly higher than in oil palm plantation ($p = 0.07$, Figure 4.3a). There was significant non-linear variation in foraging activity across the daytime period (edf = 6.986; p-value < 0.0001); elephants fed most intensively in the morning between 6 am and 9 am, and late afternoon between 2 pm and 6 pm (Figure 4.4a). Elephants tended to feed more when they were in small groups than when in larger groups, although the difference was marginally not significant ($p = 0.06$). My results did not show any significant seasonal variation in foraging behaviour ($p > 0.05$).

4.3.1.2 Moving

Elephants had a higher likelihood of moving in oil palm plantations than in the riparian and freshwater swamp habitats (Figure 4.3b, $p < 0.01$). However, no significant difference in the likelihood of movement was identified between the two types of natural habitat ($p > 0.05$). Movements were significantly associated with time of the day (edf = 8.449, $p < 0.0001$, Figure 4.4b) but not with season or group size (p-values > 0.05).

4.3.1.3 Vigilance

Vigilance behaviour was significantly more frequent in seasonal freshwater swamp forest ($p < 0.0001$) and in oil palm plantation ($p < 0.01$) compared to riparian (Figure 4.3c). There was no significant variation in vigilance with time of the day, season or group size (p- > 0.05, Figure 4.4c).

4.3.1.4 Bathing

Bathing behaviour couldn’t be analysed in the same way as other behaviours due to sample size constraints (bathing is a rare activity) leading to lack of a stable model.

4.3.1.5 Resting

Resting behaviour was significantly less frequent in oil palm plantation compared to riparian and seasonal freshwater swamp forest ($p < 0.01$, Fig 4.3d). No significant differences were observed between riparian and seasonal freshwater swamp forest for resting activity. Resting behaviour varied significantly with both time of the day (edf = 7.718; $p < 0.0001$) and group size ($p < 0.0001$). Overall, elephants were most likely to rest between 9 am and 1 pm, coinciding with the lower incidence of feeding (Figure 4.4d). Resting was more likely to be observed when the elephants were in a larger group ($p < 0.001$).

4.3.1.6 Social Interactions

Social interactions occurred significantly more frequently in riparian than oil palm plantation ($p < 0.0001$) and semi swamp forest ($p < 0.0001$) (Figure 4.3e). In riparian areas, the peak periods for social interactions coincided with the peak periods for feeding activities (morning and evening; Figure 4.4e). Social interactions were significantly negatively associated with group size ($p < 0.01$) in the model in which all of the other independent variables are controlled for statistically.

4.3.1.7 Group Size

Group size was significantly associated with time of day (larger group size later in the day, $p < 0.0001$) (Figure 4.5a), habitat (larger groups in riparian habitat compared to seasonal freshwater swamp forest and oil palm plantation, $p < 0.0001$) (Figure 4.5b) and season (larger groups during the flooding season, $p < 0.0001$) (Figure 4.5c).

(a)

(b)

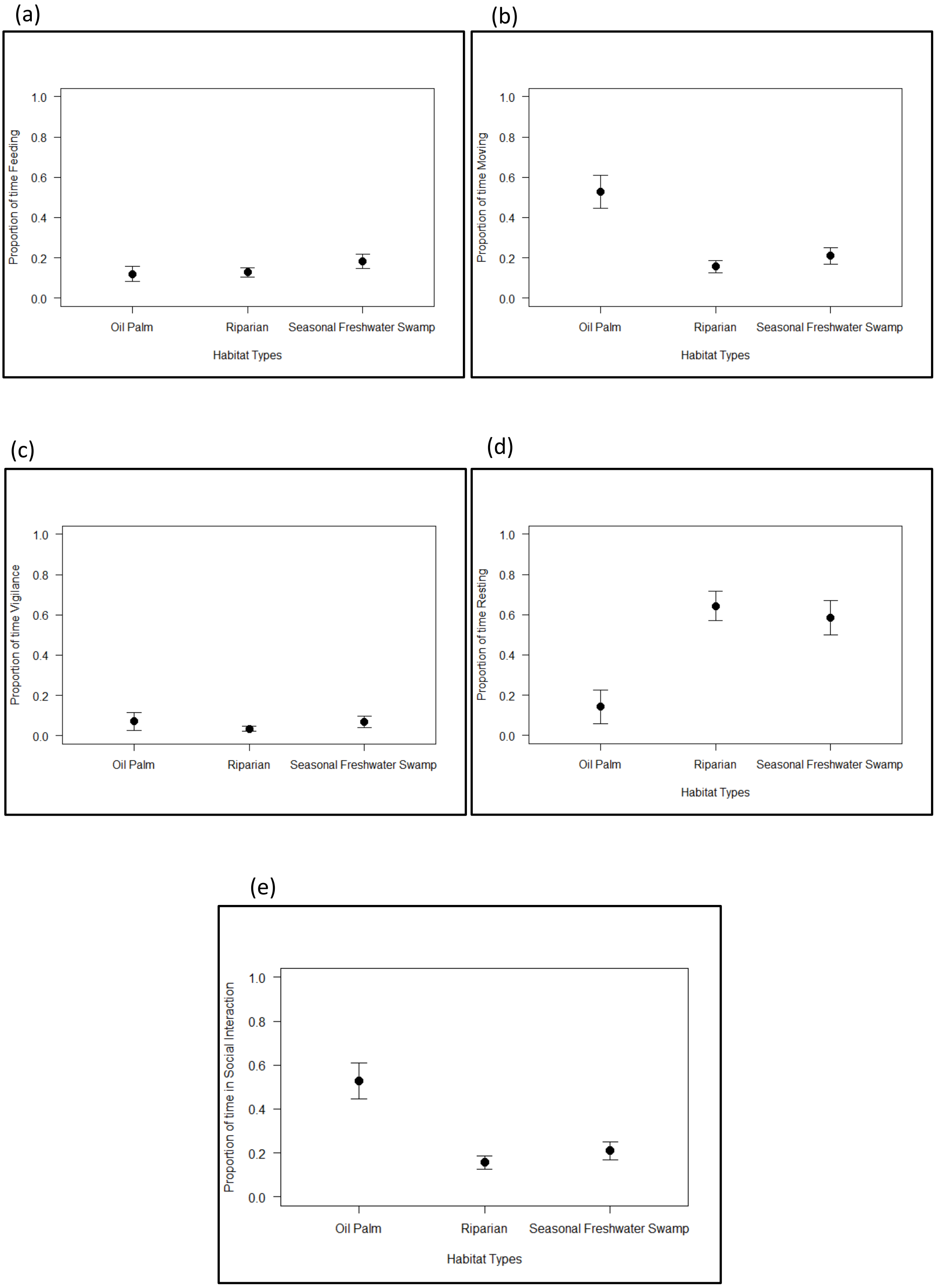


Figure 4.3 Likelihood of behavioural activities in each of the three habitat types used by elephants in this study; (i) Riparian habitats, (ii) Freshwater swamp forest, and (iii) Oil palm plantations.

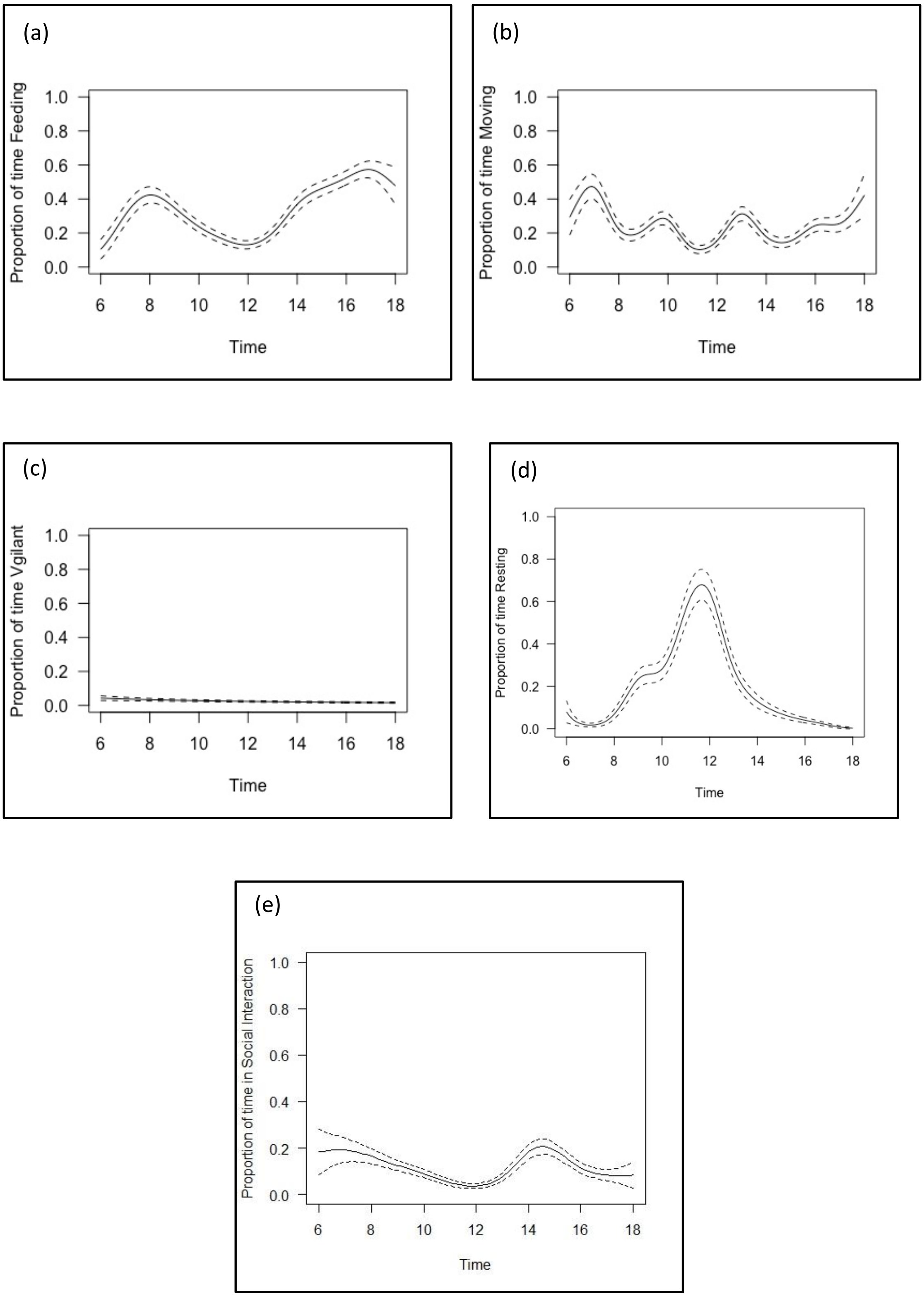


Figure 4.4 Diurnal variations in the likelihood of observing different behaviours (solid lines). Dashed lines indicate +/- 1SE.

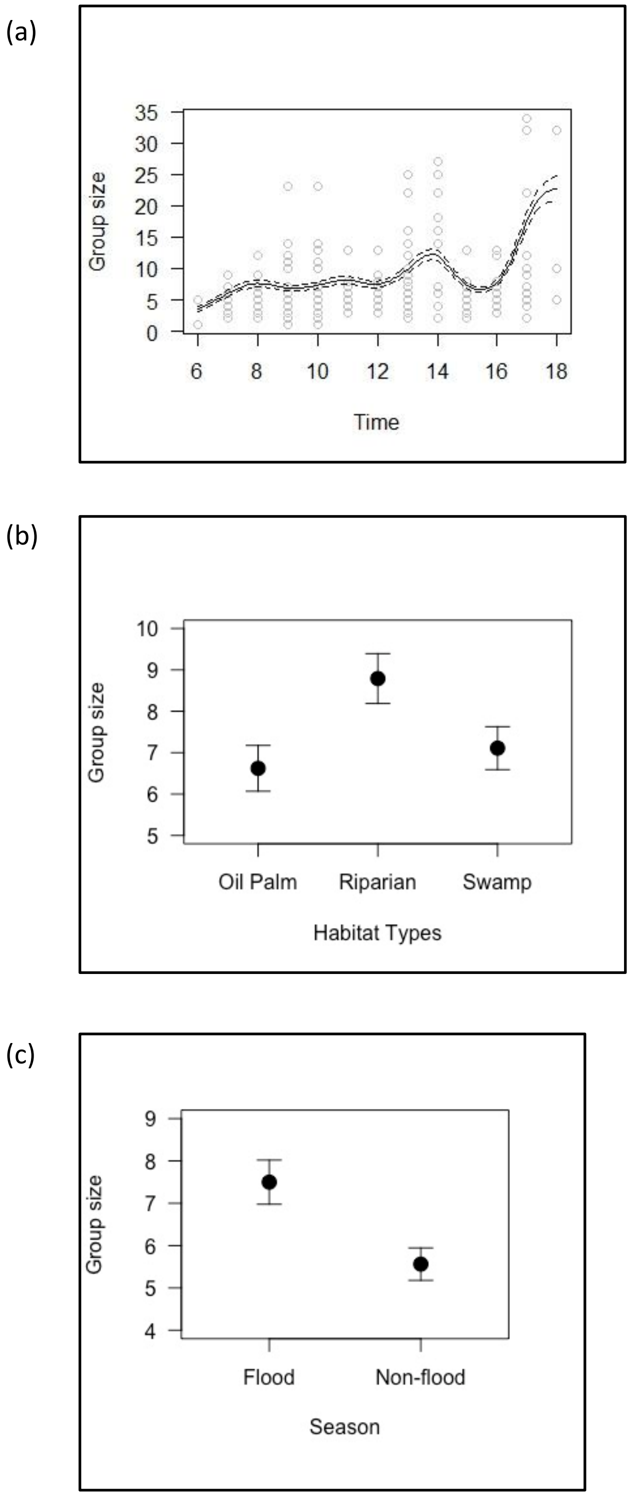


Figure 4.5 Variation in group size in relation to three temporal and spatial variables (a) Variation in group size between dawn (0600) and dusk (1800) (b) Variation in group size in each of the three major habitat types used by elephants in this study; Oil palm, riparian habitats and freshwater swamp forest. (c) Variation in group size between flooding and non-flooding seasons. Error bars indicate +/- 1SE.

4.4 Discussion

Due to the rapid and ongoing transformation of their natural habitat throughout their ranges, there is a need to understand how elephants can adapt to human-altered landscapes, to manage increasingly fragmented elephant populations and to minimize the occurrence of human-elephant conflicts (Leimgruber et al. 2003; Fernando 2010; Songer et al. 2012). It is crucial to take behaviour and habitat use into consideration in conservation management, especially for species like elephants that are highly social, utilize large home ranges, and have well-developed cognitive abilities (Sukumar 2003; Plotnik et al. 2006; Cable 2013). This study, therefore, examined the behavioural activities of Bornean elephants in riparian areas, seasonal freshwater swamp forest, and oil palm plantations adjoining the Kinabatangan River in Sabah, Malaysia, and compared the behaviours across the two natural habitat types as well as between the natural and the human-altered habitat types.

This study provided the first empirical evidence that elephants may adjust their behaviours in different natural habitats, i.e., riparian areas versus seasonal freshwater swamp forests, based on data on feeding, vigilance, and social interactions. Furthermore, the findings of this study showed that the elephants may carry out some essential activities predominantly in these natural habitats, particularly resting and social interactions, while living within a largely human-dominated landscape. I found that in Kinabatangan, elephants moved more in oil palm plantations than in natural habitats. Previously, Kumar and Singh (2010) found that Indian elephants adjusted their behaviours when they were in a human-altered habitat, but thus far such adjustments were not known for comparisons across natural habitats nor for other elephant taxa.

In this current study, behavioural data were obtained only from females elephants since this sex class seems to be more affected in human-dominated environments than male elephants (see de Silva et al. 2011, Lee and Moss 2012; Srinivasaiah et al. 2012). It is possible that Bornean elephant males do not adjust their behaviours in accordance to habitat types and further research is needed here. However, female groups with their offspring are the most sensitive cohort in population dynamics and therefore by closely monitoring them it will help us to understand the effect of anthropogenic disturbance to the population.

The elephants of this study were feeding in all three habitat types, predominantly in the natural habitats tested (riparian; seasonal freshwater swamp forest). Previous studies in Kinabatangan showed that riparian habitat offers large quantities of good quality food to the elephants and that these resources were used intermittently and following a recursion pattern by the animals (English, Ancrenaz, et al. 2014; English, Gillespie, et al. 2014). Unlike grasses (*Phragmites karka* and *Dinochloa scabrida*) that are readily available in the riparian habitat, elephants spent more time processing their food in the seasonal freshwater swamp forest; they needed to peel off the bark of the plants such as *Dillenia excelsa* and *Mallotus muticus*, trees consumed frequently in this habitat. I also observed that elephant would wrap their trunk around the tree bark and branches to debark the plant and have access to its cambium, as previously described in India (Mohapatra et al. 2013). I also observed that elephants would also spend more time chewing and swallowing vegetation in the seasonal freshwater swamp forest than in other habitats because of the fibrous structure of most of the food exploited in this particular habitat (mostly fibrous vines and climbers or barks). Meanwhile, in the oil palm plantations, elephants consumed different parts of oil palm tree particularly the shoots. Most of the damages occurred when oil palm trees especially the young or underproductive trees were pushed down by elephants to get access to the shoot. These underproductive oil palm trees are mainly found in the areas that experience annual flooding and/or daily inundation from tides (Abram et al. 2014). I also observed the elephants pull the leaves to get access to the fruit as well as pluck on epiphytes that grow on the oil palm trunks.

Interestingly, my results showed a significant larger group sizes as well as significantly more social interactions in riparian habitat compared to the other two habitats. Open area such as forest clearing or bais in Africa provides opportunities to animals to meet and the elephants in particular utilized these opportunities to enhance and maintain their social bonding and status through aggregation and social interactions (Fishlock and Lee 2013; Turkalo et al. 2013). African forest elephants (*Loxodonta cyclotis*) were observed to maintained a close distance to certain conspecifics during their visitation to the bai while forest buffalos (*Syncerus caffer nanus*) performed agonistic behaviour such as driving from other individuals to displace them from the best resting sites (Melletti et al. 2007; Fishlock and Lee 2013). The results suggest a view of riparian along the Kinabatangan River may also act as social arenas for Bornean elephants such as the bais in Africa. Elephants are attracted to this habitat types as it is close to the river which provides the water resources as well as providing large quantities of grasses (English, Gillespie, et al. 2014). My view is further support by the frequent observation on their social interactions particularly trunk-to-mouth placement behaviour, which occurs when two elephants extend their trunks into each other's mouths. It arguably functions to help recognize the other better when it is darker or to assess foods eaten by group members (Lee and Moss 2012; Makecha et al. 2012). Maintaining close bonds within a social group is essential for acquiring various types of information for these highly sociable animals (van Schaik and Griffiths 1996; Sukumar 2003; Dunbar et al. 2009; Pinter-Wollman et al. 2009).

The results of this study also showed that the natural habitats were key areas for the resting where the time spent for resting increased towards the middle of the day. By reducing movement and activities under full sun, it could facilitate their thermoregulatory strategy (Kinahan et al. 2007; Weissenböck et al. 2012). The elephants moved markedly more and showed more vigilance in the oil palm plantations than in the two natural habitat types. High vigilance and locomotion levels could mean that elephants may be avoiding direct and frequent contact with people in oil palm plantations, as suggested in previous studies (Kumar and Singh 2010; Srinivasaiah et al. 2012). It is very rare to see the adult females of this study lying down while resting in the oil palm plantation unlike when they are in their natural habitat. The differences in behaviours associated with the oil palm plantations, thus, infer of the readjustments in the female groups of the Kinabatangan elephants, which often have offspring.

On the contrary, the elephants stayed in the smallest groups when they were in these plantations and their groups were largest in the riparian areas. Elephant like some other animal species such as proboscis monkey (*Nasalis larvatus*), African buffalo (*Syncerus caffer*) and bottlenose dolphins (*Tursiops* sp.) live in fission–fusion societies where the composition of group members changes over the course of hours, days or seasons (Cross et al. 2005; Lusseau et al. 2006; Matsuda et al. 2009). The advantage living in this social system is that it allows individuals to respond adaptively to changing resources or threats by altering the number and identity of animals with which they associate (Wey et al. 2008). Among the three habitat types, food resources exploited in oil palm plantations may be of the lowest quality for elephants (Alfred et al. 2012; English, Gillespie, et al. 2014). Therefore, by living in smaller group size the elephants are expected to reduce the level of within-group food competition (Dammhahn and Kappeler 2009). In addition, I noticed that elephants were very secretive when in oil palm plantation. I believed by reducing communication via vocalization and stayed closed very close to each other will facilitate them to minimize encounters with people. I also found that group size increased significantly during the flood season. This is the opposite from what is seen in African elephants in dry areas which are more dispersed during raining seasons (Wittemyer et al. 2005). This may be explained by the findings in Estes et al. (2012) where habitat modelling suggested only 6500 ha of habitat fragments remained which could be causing a grouping of elephants.

Caution is, however, required when making species- and population level interpretation of the results as the data were collected only on female elephants in LKF. Interestingly, the females of this study spent less time feeding (only 34% of the time) than Indian elephants in previous studies, which were observed to spend between 40% to 75% of their time in feeding in their natural habitats(Sukumar 2003; Kumar and Singh 2010; Srinivasaiah et al. 2012). While there are numerous factors that could account for such differences that cannot be properly examined here (representation in the sample, habitat infrastructure, phylogeny, etc.), it is important to report such differences for future research that might systematically compare elephant populations or species from this perspective.

The results show that natural habitat like riparian are essential to sustain elephant populations in Kinabatangan. I concur with English et al. (2014) that some open areas should be set aside to allow for grasses to grow naturally because elephants attracted to these open areas for food as well as to maintain their social bonding. I highly believed that land-use planning is the key to sustain balanced elephant groups in LKF. Elephants also use natural habitats to find food source: it is thus important to allow elephants to get access to this habitats via forest corridors or else. Lastly, although elephants spend increasing amount of time in OPP, my data show that they are highly alert and stressed in this man-made landscape. Providing connectivity and corridors of natural habitat across an entire landscape as well avoiding unnecessary provocation to the elephants which might alter elephant's behaviour in the long run would certainly reduce the stress level of the elephants and reduce HEC significantly.

CHAPTER FIVE

GENERAL DISCUSSION

5.1 Why is this study needed?

Habitat fragmentation, and conflicts between elephants and humans, are the major issues in the conservation of the Asian elephant. There are four specific factors which have contributed to the escalating conflict between humans and elephants: (1) habitat change, including destruction, degradation and fragmentation of natural habitats, (2) people contributing to initiating, escalating, or sustaining HEC, (3) elephant population size, and (4) elephant behavior (Leimgruber et al. 2003; Fernando, Wikramanayake, et al. 2008; Fernando 2010; Kumar and Singh 2010; Alfred et al. 2011; Songer et al. 2012; Othman et al. 2013; Desai and Riddle 2015). The latter factor, elephant behaviour, has received the least attention, mainly due to the type of habitats that Asian elephants inhabit, which are characterized by low visibility, high variability of terrain, making it difficult to locate individuals at a safe distance and to study their behaviour. Until now, there are only a handful studies on Asian elephant behaviour, limiting our ability to use behavioural insights to solve management issues (Vidya and Thuppil 2010; Srinivasaiah et al. 2012). The present study has aimed to fill the existing knowledge gaps, to better understand how elephant behavior mediates their interactions with their human-altered habitats, and in particular how elephants are changing their behavior in response to anthropogenic pressures and habitat fragmentation in the wild.

The conservation of the Bornean elephants started to get increased attention from different stakeholders at both national and international level after a publication by Fernando et al. (2003) which highlighted the urgent need to conserve these populations based on their distinctive genetic status. More recent genetic studies have confirmed that the Bornean elephant is a distinct sub-species of Asian elephant, although it is not entirely consistent with a combination of historical and paleozoological evidence (Fernando et al. 2006; Cranbrook et al. 2007; Goossens et al. 2016), which supported the view that the population of Bornean elephant are of remnant survivors of the extinct Javan elephant (*Elephas maximus sondaicus*) (Cranbrook et al. 2007; Payne and Davies 2013). Indeed, a more complete description of the Bornean elephants' endemic status is highly recommended as it will strongly influence the conservation priorities for this population (but see Sharma *et al.* under revision).

It is concerning that the Bornean elephant population in Sabah is threatened by its very low genetic diversity compared to the other Asian elephant populations and subspecies across Asia (Fernando et al. 2006; Sharma et al. 2012; Goossens et al. 2016). With such low genetic diversity and inadequate connectivity to facilitate gene flow (i.e. migration from population to another), local extinction of fragmented sub-populations may occur because of deleterious effects of inbreeding (Moore 2007), placing the long-term survival of the Bornean subspecies in serious jeopardy.

How can the study of elephant behavior assist in the management of conflicts between humans and elephants? Elephants have large brains and are highly cognitive, making them capable of rapid learning and adjustment to environmental changes (Hart et al. 2001; Srinivasaiah et al. 2012; Mutinda et al. 2014). On the other hand, their behavior may not change in ways that might be predicted. For example, the elephants in the present study did not avoid "risky" areas which may have been part of their historic home range, instead they change their behaviour by moving at a slower speed, or may adjust their behaviours in different habitats at different times of the day.

While I was doing my fieldwork, there were several occasions when I got to speak to local people regarding the elephants' behaviour; many of these people had experience of direct contact with elephants during a conflict event. I found that in many cases, people were misinformed or ignorant about elephant biology and behavior. For example, some people assumed that removing (by translocating or killing) the oldest or biggest female (i.e. the matriarch of the group) will make the other elephants leave the area, whereas this action will leave the other members confused and likely to act more aggressively (McComb et al. 2011; Shannon et al. 2013). Another behavioural issue of concern is the biological condition of male elephants known as "musth", which local people often treat lightly, but which is a period when males may be particularly dangerous. Musth is a period of reproductive readiness that occurs at least once a year, when the male's temporal gland is swollen, and there is secretion, dribbling of urine or wet hind legs (Lee 1996; Fernando et al. 2012; Koirala et al. 2015). During this period of musth, the males tend to be more aggressive (Figure 5.1) due to the hormonal changes as they are ready for breeding and usually their ranging patterns are larger than females (Fernando, Wikramanayake, et al. 2008). Certain male elephants shown elevated stress hormone when they passed through settlement areas (Ahlering et al.,2011). Therefore, unnecessary provocation towards these elephants can cause serious consequence to both people and elephants.

Figure 5.1 A bull elephant, Raja was in musth and regularly checking for females in estrous by smelling at the female's genital area or urine. The calf got kicked as it was standing in the way betweenRaja and the female (photo credit to John Nair Rajan).

5.2 Overview

This thesis examines the behavioural and spatial ecology of the Bornean elephant in the Lower Kinabatangan region of Sabah, in Malaysian Borneo. I tested a range of hypotheses that were designed to address the gaps in the knowledge of the species that are essential for conservation and management of the Bornean elephant. I presented the aims, hypotheses and a brief summary of my findings in Table 5.1. Although it is a common practice now of using with global positioning system (GPS) technology to obtain accurate locations of elephants (Fernando, Wikramanayake, et al. 2008; Williams et al. 2008; Alfred et al. 2012; Sitompul, Griffin and Fuller 2013), this current works will improve our understanding of the movement strategies of Asian elephants which are living in highly fragmented and isolated habitats (specifically the Bornean elephant) by including larger sample sizes (Chapter 2) and applying appropriate analytical models to understand elephant's behaviour both indirectly (Chapter 3) and directly (Chapter 4).

Table 5.1 A summary of the aims and hypotheses and the results and implications for the conservation of Bornean elephant which are detailed according to each chapter in this thesis.

Chapter	Objectives	Hypotheses	Results
Chapter 2	To gain insights about seasonal movements of six collared female elephants	1) The size of elephants' UD and core areas were explained by individual identity and season. 2) To predict which covariates determined both seasonal UD and core areas of elephants.	1) The UD and core area size differed between individuals and seasons. 2) During the flooding season, both core area and UD were determined by the spatial physical covariates while determinants of core and UD during the non-flooding season were explained by a combination of both physical and anthropogenic covariates.
Chapter 3	To understand elephant behaviour using movement data (motion variance and speed)	Motion variance and speed were influenced by time of the day, environmental features and anthropogenic activities.	1) Both motion variance and speed are informative to explain the shifting behavior in elephant's movement. 2) Motion variance were explained habitat type, season, distance to river, distance to building and distance to road. 3) Speed were explained by time of the day, habitat types, distance to river and distance to building.

Chapter 4	To examine the behavioural patterns of elephants across riparian habitat, seasonal freshwater swamp forest and oil palm plantations	1) Elephants would temporally partition their activities throughout the day in each habitat. 2) There is seasonal variation in the activity budget of elephants	1) Elephants carried out some essential activities predominantly in the natural habitats (riparian and seasonal freshwater swamp forest). 2) Elephant's activities varied in relation to time of the day, season and group size.

This thesis answered the question of where, when, and why the Bornean elephant move in highly fragmented habitats of Lower Kinabatangan. The movement behaviour of the Bornean elephants in LKF were mainly determined by food, water and human activities. However, the six elephants adjusted their behaviour to tolerate to anthropogenic activities rather than abandon the area such as palm oil landscapes. I further discussed the implication of these findings in term of the future of elephant conservation locally, nationally and internationally.

5.3 How Can the Findings of this Study be Applied to Conservation?

5.3.1 Local Scale: Lower Kinabatangan

In the most ideal situation, Bornean elephants should be living in landscapes where large protected areas are surrounded by buffer zones, connected by corridors, and integrated into a national-scale network of natural ecosystems. But unfortunately, that is not the case for the Bornean elephant in Lower Kinabatangan. Other Asian elephant populations are linked using habitat corridors, to mitigate the effects of habitat fragmentation by protecting strips of forests connecting two larger habitat "islands" (Johnsingh and Williams 1999; Cushman et al. 2010; Sitompul, Griffin and Fuller 2013), but for Bornean elephants in Lower Kinabatangan there are no "islands"; only narrow corridors of suitable habitats are left for elephants to live in (Alfred et al. 2012; Estes et al. 2012). Given that the current human population increases, and the very limited extent of natural habitat available, I believe that complete separation of humans and elephants in Lower Kinabatangan is impossible, and that interactions between humans and elephants are inevitable, and becoming much more common.

The seasonal and diurnal spatial distribution and movements of six female Bornean elephants (both the utilization distribution and core area), demonstrated by Bornean elephants can be seen as a response to the landscape's resistance to the free movement of elephants (roads, oil palm plantations and anthropogenic activities) and availability of resources (habitat types) to maximize their fitness. Through further investigation of their behavior which was gathered both directly (data on different activities gathered via direct observation) and indirectly (from elephants' movement trajectory), the elephants demonstrated their ability to modify their behavior to avoid risk in human-dominated landscapes. In Chapter 5, I found elephants carried out some essential activities predominantly in these natural habitats, particularly resting and interacting socially while higher mobility in oil palm plantations than in natural habitats. High vigilance and locomotion levels could mean that elephants may be avoiding direct and frequent contact with people in oil palm plantations. I recommended that further investigation should be carried out to better understand the behavioral traits of individuals that consistently use oil palm plantations as part of their utilization distribution, because individual animals differ in their average level of behaviour displayed across a range of contexts (animal 'personality'), and in their responsiveness to environmental variation (plasticity) (Börger et al. 2006; Dingemanse et al. 2010; Srinivasaiah et al. 2012; Merrick and Koprowski 2017). Individual perception and responses to landscape structure will be influenced by their state and motivation, which will then dictate their movement decisions.

In Lower Kinabatangan, mitigation activities are too often decided and implemented opportunistically by individuals, groups of people or organisations, without prior consultation with neighbours or adjacent communities, and without considering what medium to long-term impacts these mitigation measures will have on the elephant herds and their movements. This lack of coordination creates a very complex and highly fractured landscape throughout the floodplain that becomes unsuitable for elephant movements (Estes et al. 2012). In mainland Asia, electric fencing is particularly popular as a mitigation method as it has been highly effective at preventing intrusion and crop damage by elephants (Doyle et al. 2010; Davies et al. 2011). However, in areas where the elephants depend critically on access to resources such as food, water, or minerals, elephants can become habituated to electric fences and have been known to learn how to get around this barrier (Figure 5.2). I strongly agree with the statement that: "*fencing for conservation is an acknowledgement that we are failing to successfully coexist with and, ultimately, conserve biodiversity*" (Hayward and Kerley 2009). Electric fencing in Lower Kinabatangan effectively reduces the permeability of the landscape to elephants, as well as forcing the elephants to revisit the same places more often, creating problem areas for HEC. Thus, fencing does not provide the most effective solution, particularly for the area surrounding the village of Sukau (Alfred et al. 2012; Estes et al. 2012).

Figure 5.2 Sandi, one of the elephants that is a permanent resident in the oil palm plantations stepping careful over an electric fence after he initially received a shock to his trunk.

At this point, the ultimate way of reducing the cases of human elephant conflict in Lower Kinabatangan is firstly by accepting the fact that the wildlife in general, and elephants existed before human encroachment on natural habitats, and that we are sharing the land with them, so that a total separation is not possible to achieve. We could improve the tolerance of people towards elephants and conservation by identifying correctly those species that cause the greatest amounts of crop damage (i.e. rodents from the Muridae family, long tailed macaques (*Macaca fascicularis*) and bearded pigs (*Sus barbatus*) and assess the perception of conflict among people (i.e. fear of encountering elephants, economic loss or the view that elephants belong to the government, therefore government agencies are responsible for their management) (Figure 5.3). Awareness of people on the behavior and biology of elephants will help them to have a better understanding on why, when and how to deal with a conflict situation.

Figure 5.3 Bananas were planted to provide food for the people but attracted crop-raiding elephants leading to HEC.

The next step in the conservation of Bornean elephants within the LKF is to create an elephant-friendly landscape in the floodplain, by stopping further human intrusion into elephant's habitat. New developments such as bridges, roads, agricultural activities and human settlement – especially near the spatial bottlenecks (e.g. the village of Sukau see http://dailyexpress.com.my/read.cfm?NewsID=2518), should be avoided. Communication among stakeholders (local community, local administration, local politicians, palm oil sectors, government agencies, NGOs and tourism businesses) should be encouraged, to ensure the development and implementation of an integrated management strategy. For example, a well-planned and integrated electric fencing strategy within the oil palm plantations surrounding Sukau, which is jointly managed by different oil palm plantation owners, would allow the elephants to pass rapidly through the area instead of preventing them from entering the area. By doing this, we will reduce the disturbance to the elephants, and thus reduce the time spent by the elephants lingering around the area before they can pass (*pers. comm.* with Alexandra Zimmermann). Further investigation should be carried out to better understand the elephants' behavior and ecology in the oil palm plantations before we can be certain of the value of this mitigation approach (Thompson *et al.*, in preparation).

5.3.2 National scale: Sabah

The Bornean elephant contains the least genetic diversity compared to the other Asian elephant subspecies and populations (Fernando et al. 2003; Goossens et al. 2016). The question of whether or not Sabah holds a unique subspecies of Asian elephant should not lead us astray from the fact that the Bornean population deserves conservation efforts (Goossens and Ambu 2012). At the national (Sabah) scale, strategic land-use planning must be implemented to create connectivity between the few remaining blocks of semi-natural forest (Goossens and Ambu 2012). As Sabah is the major oil palm producing region in Malaysia (MPOB, 2012), intense HEC that is impacting both elephants and people in Lower Kinabatangan will become typical of Sabah in the near future if we still pursue our current development trajectory in ignorance of the impacts on elephants. A worrying trend is that the new oil palm plantings often target degraded forest (unprotected/native lands), once commercial exploitation of the primary forest has ceased, and that incentives provided by the government facilitate smallholders to convert their land into oil palm and rubber (*Hevea brasiliensis*) plantations (Othman et al. 2013; Martin et al. 2015).

Currently, at Danau Girang Field Centre, we are assisting the Sabah Wildlife Department (the local wildlife authority), to identify connectivity corridors, to ensure elephant migration while minimizing human-elephant conflicts throughout Sabah. So far, we have tagged 35 elephants throughout Sabah with satellite collars, and I am planning to use the experience and training that I have received while completing my thesis, to analyze these movement data further, and at the same time to explore other issues of direct conservation relevance, such as the effectiveness of the elephant translocation program within Sabah and the design of the best corridors for elephants. Movement data may be the simplest, yet most powerful, approach to inform decision-making processes. The map of movements of one of our collared elephants, Puteri, in Lower Kinabatangan provided an explicit visualization for politicians and local people to acknowledge the implication to both people and elephants of building a second bridge across the Kinabatangan in the village of Sukau (Figure 5.4). As a result of different strategies by local organisations, and focused attention from an international audience, the government of Sabah has recently decided to scrap the construction of a bridge in Sukau across the Kinabatangan river (see https://www.nst.com.my/news/nation/2017/04/233759/sabah-gets-thumbs-conservationists-cancelling-kinabatangan-bridge-plan) . This has provided conservationists with a huge motivation to keep fighting to conserve Kinabatangan and other important land in Sabah as a safe refugee to wildlife and others.

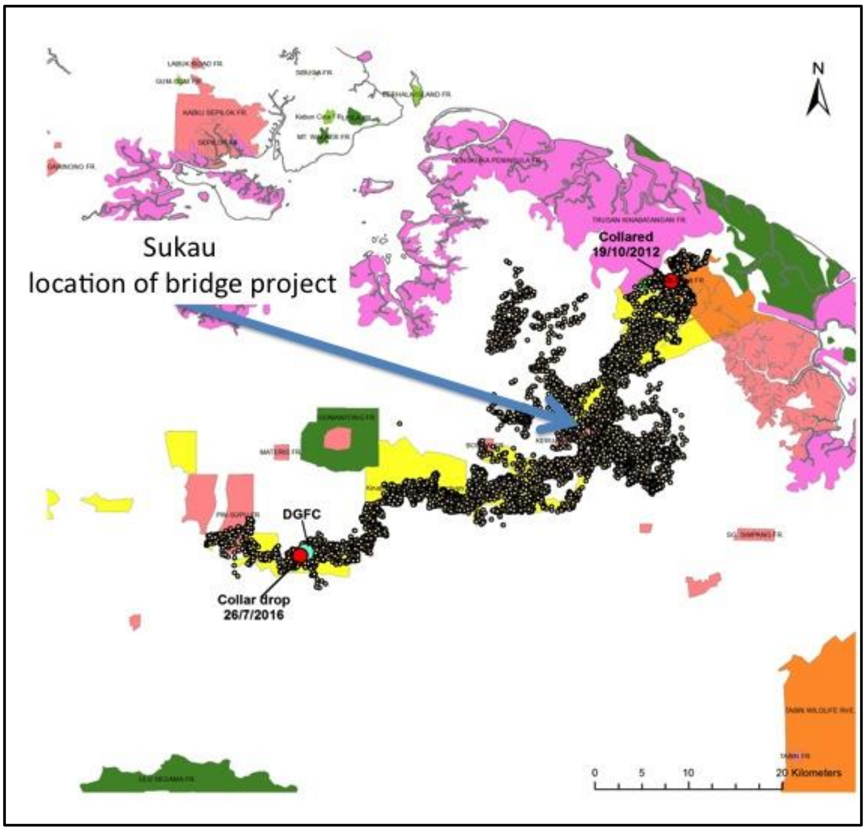


Figure 5.4 A map is showing Puteri's movement within her home range in LKF between October 2012 to July 2016. Puteri's movement provides strong scientific evidence that if the plan to build a second bridge in the village of Sukau is carry out, this will further disrupt elephant's movement and consequently increase the HEC cases in this area.

A permanent conservation response team or unit which is committed to respond to the presence of a wild elephant or a herd near a village, and effectively drive the elephant or herd back into the forest/natural habitat, will help to reduce fear among local communities and foster coexistence between people and elephants (Riddle et al. 2009). The existence of the Elephant Conservation Unit (ECU) in Lower Kinabatangan has successfully reduced the number of such conflicts between smallholders and elephants. The team was created 15 years ago and since then ECU has acquired a lot of experience in survey and research techniques. The ECU has designed simple and cost-efficient ways to mitigate conflicts and trains other groups to deal with elephants. Now, we can disseminate the knowledge that the team has gathered, to reach into new districts (i.e. the district of Telupid) that are currently experiencing the same type of HECs that Kinabatangan District has experienced over recent years.

5.3.3 Global scale: All elephants (Asian subspecies and African elephants)

Asian elephants are found in the continent with the largest number of human beings, as well as the highest diversity of wildlife and plants (Bloom 2011). Unfortunately, Asia is losing its diversity at an unprecedented rate (Sodhi et al. 2004). There are a lot of lessons that the world can learn from the situation in Lower Kinabatangan, a place which, despite being heavily impacted from past commercial timber exploitation and extensive forest conversion resulting in significant forest loss, severe fragmentation and degradation within the forest ecosystem, still strives to be the home of several endemic and iconic species in Sabah. The present study has demonstrated that conservation can succeed by adopting appropriate peer-reviewed survey and monitoring methods which explicitly provides evidence, improved integrated cooperation, and data sharing. This study has also shown that investment into long-term projects is valuable to make sure we have a sound understanding of population trends and dynamics which are important for making recommendations for conservation actions (Sutherland et al. 2004; de Silva 2016). The advantages of satellite tracking are obvious, including the ability to collect fine-scale spatio-temporal location data on many animals that had previously been impossible to study in such detail. However, without a field-based understanding of animal ecology to support these data we would not be able to interpret these insights into the ecology and conservation of these animal species (Hebblewhite and Haydon 2010). Only through a long-term project can the combination of these two approaches produce meaningful and robust scientific evidence to assist conservation efforts. Using the scientific data collected from the last 15 years and through a civil society partnership, we will continue our efforts to make Lower Kinabatangan "*a floodplain with large tracts of forests, riparian vegetation, wildlife corridors, clean river, and viable wildlife populations, where local communities benefit through ecotourism and compatible land-uses*" (Campaign "Save Kinabatangan", 2017).

There is still an ongoing debate about what a habitat corridor should look like for elephants, in terms of width, length and its functionality (Johnsingh and Williams 1999; Chetkiewicz et al. 2006; Lapoint et al. 2013). Theoretically, a corridor is "*a narrow strip of forest connecting two larger forest areas, to connect fragments of wildlife habitat*" (Belisle 2005). In reality, the elephants in Lower Kinabatangan only have a narrow habitat corridor to live in (Alfred et al. 2012; Estes et al. 2012). These corridors were gazetted as Lower Kinabatangan Wildlife Sanctuary (LKWS) in order to increase connectivity between the remaining forest reserves found in Kinabatangan (Payne and Davies 2013). So far, there is no documented intraspecific competition among the elephants inhabiting this confined area, over space use and resources (e.g. agonistic interactions including charges, chases, pokes, pushes and displacements (Archie et al. 2006). At the same time, informal assessments of the elephant's body condition (assessment of the degree of concavity around the elephant's lumbar depression and scapular area) indicate that there is no nutritional stress among Bornean elephants (Fernando et al. 2009). Does this suggest that Lower Kinabatangan is the best example of how should a corridor for elephants look like? The evidence presented in this study shows that the elephants are willing to adapt, the question is, are we human ready to adapt, and to tolerate elephants too?

5.4 Impacts and Recommendations

I respectfully recommended, based on my extensive field experience of elephant behavior and research findings, that the Sabah state government and/or the Malaysian federal government must act proactively to conserve the Bornean elephants, and to address related conservation issues in Malaysia. A specific fund should be allocated during the next Malaysia Plan, to revise and implement policies regarding environment issues and wildlife conservation, as well as to nurture our younger generations in the concepts and actions of conservation (i.e. capacity building). We must take advantage of the work of different NGOs (both local and international), as well as the IUCN-Species Specialist Commission (IUCN-SSC), to provide scientific advice to help the process of decision-making. We must also listen to the local communities, as they are the frontline during any conflict events and have an important voice that must be listened to. Indeed, the conservation of the elephant in Malaysia, and in Sabah specifically, is now critically dependent on level of tolerance and appreciation of elephants by the local people who interact with the elephants on a regular basis.

My PhD studies have placed me in a valuable position to act as a bridge between different stakeholders involved in elephant conservation, conflict resolution and environmental policy. Being a Malaysian national, with a formal training in research and conservation, I am in the fortunate position of being able to facilitate communication and cooperation between different stakeholders; both locally, nationally and internationally.

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