MOVEMENT ECOLOGY OF ASIAN ELEPHANTS IN PENINSULAR MALAYSIA

JAMIE WADEY

Thesis submitted to the University of Nottingham Malaysia for the degree of Doctor of Philosophy

September 2019

Version – inclusive of minor corrections

Statement of word count

Number of pages and words contained in this document including references and appendices:

199 pages and 46,449 words

Abstract

As the largest terrestrial animal on earth, elephants perform important and irreplaceable roles within their environments. However, Asian elephants are facing extinction by the end of the century, with human-elephant conflict and poaching as the main drivers behind their rapid population decline. In Asia, conservation actions rarely take into account the movement ecology of elephants due to the lack of information available. Therefore, conservation actions could be improved by having a deeper understanding of Asian elephant movement ecology. In light of this knowledge gap, this thesis has increased our understanding of Asian elephant movement ecology by generating over 250,000 GPS locations from 51 individuals between 2011-2018, which is equivalent to over 500,000 hours of elephant monitoring in Peninsular Malaysia. In addition, our baseline analysis of elephant movements in Peninsular Malaysia generated information about home range size (up to 600 km^2), movement patterns, habitat selection (avoid steep slopes and preferred secondary forest and open habitats), and how human pressures are affecting elephant movements (decreases home range size). Additionally, a mechanistic modelling framework discovered roads caused strong and consistent barrier effects for elephants, increased mortality, and significantly reduced the permeability (on average by 79.5%) between forest patches. Lastly, post-monitoring of translocated elephants revealed critical patterns in response to translocation. Translocated elephants varied in their responses, with a high proportion of elephants (56%) returning to the original human-conflict area (up to 80 km) or left the protected area, which resulted in translocated movements not settling in the first year. This thesis will contribute to a better understanding of the movement ecology of elephants and provide relevant research for the conservation of the species and their habitats.

Keywords: GPS telemetry, *Elephas maximus*, movement ecology, roads, translocation, habitat selection, home range, human pressure, movement patterns, Peninsular Malaysia

Publications and conferences

A list of publications based on the work of this thesis:

Hii, N., Wong, E.P., Chackrapani, P.R., Solana-Mena, A., Tan, A.S.L., Nagulendran, K.H., **Wadey, J.,** Wyn, L.T., Ong, L., Osman, N.A., Kromann-Clausen, A., et al. (2016). MEME–moving towards a science-based conservation of Malaysian elephants. *Malay Nat J*, *68*,191-197.

Wadey, J., Beyer, H., Saaban, S., Othman, N., Leimgruber, P., & Campos-Arceiz, A. (2018). Why did the elephant cross the road? The complex response of wild elephants to a major road in Peninsular Malaysia. *Biological Conservation*, *218*, 91–98. http://doi.org/10.1016/j.biocon.2017.11.036

Wong, E. P., Loke, V., **Wadey, J.,** Solana-Mena, A., Thuppil, V., Patah, P., et al. (2018). Elephants, roads and drivers: Case study of Gerik-Jeli highway. *Jurutera Bulletin*, *9*, 26–29.

Wong, E. P., Yon, L., Walker, S., Solana-Mena, A., **Wadey, J.,** Othman, N., et al. (2018). The elephant who finally crossed the road – significant life events reflected in faecal hormone metabolites of a wild Asian elephant. *Gajah*, *48*, 4–11.

A list of key international conferences based on work of this thesis:

Conservation Asia, 29 June-2 July 2016, Singapore
Paper: *The Impacts of a major road on elephant movement in northern Peninsular Malaysia.*

Association of Tropical Biology and Conservation, 1-5 July 2018, Kuching, Malaysia
Paper: *How are elephants moving after translocation in Peninsular Malaysia (preliminary findings)?*

International Congress for Conservation Biology, 21-25 July 2019, Kuala Lumpur, Malaysia
Paper: *Movement responses of translocated elephants in Peninsular Malaysia.*

Acknowledgements

I dedicate this doctoral thesis to my parents, Andrew and Jodie Wadey, who have always supported and encouraged me, and instilled in me that it does not matter where you are from or the grades you have received, but rather it is the tenacity and will power from within that makes you achieve in life. Nothing is more evident of that than this PhD – thank you!

I am indebted to Ahimsa Campos-Arceiz for agreeing to take me on as his PhD student. Ahimsa, you have provided me with a fantastic environment to learn, to be curious, and to develop as a professional. Thank you for your support, guidance, and most of all your patience. And to Peter Leimgruber, as co-supervisor, I am grateful for the crucial and valuable technical support throughout the PhD and for providing my technical training at the Smithsonian Conservation Biology Institute.

This doctorate is part of the Management & Ecology of Malaysian Elephants (MEME), a joint research project between the Department of Wildlife and National Parks (DWNP) Peninsular Malaysia and the University of Nottingham Malaysia Campus. I am very grateful to DWNP, and especially to Dato' Abdul Rasid Samsudin and Dato' Abdul Kadir bin Abu Hashim, DWNP's former and current Director Generals, for the permits to conduct this research and for the continuous support in the field. Field activities were generously financed by grants from Yayasan Sime Darby (grant M0005.54.04), Wildlife Reserves Singapore (grant S0002.54.02), and Marinescape (grant M0004.54.04). DWNP's elephant translocation team and elephant unit conducted the elephant capturing and sedation, which was led by Nasharuddin Othman.

My sincere appreciation to all members of the MEME family (in alphabetical order): Alicia Solana Mena, Anders Kromann-Clausen, Ange Tan, Ee Phin Wong, Hii Ning, Husin a/l Sudin, Jon Moore, Khairil bin Othman, Lim Teck Wyn, Lisa Ong, Loo Yen Yi, Mohamad Tauhid bin Tunil (Cherang), Nagulendran A/L Kangayatkarasu, Nur Aida Ab Ghani, Nurul Azuwa, Or Oi Ching, Param bin Pura, Praveena Chackrapani, Rizuan bin Angah, Tan Wei Harn,Vanitha Ponnusamy, Vivek Thuppil and Vivienne Loke. Thank you for your support, advice, ideas, friendship, memorable fieldwork moments, and for welcoming me into Malaysia – terima kasih.

Numerous other people (in alphabetical order) have contributed to this PhD in their own way, either through volunteering in the field, carrying out analyses, or simply being generous with assistance, equipment, facilities, services, information, interest, ideas, discussions and advice: Alex Lechner, Carol D'Cruz, Cedric Tan, Chris Flemming, Chris Gibbins, Christine Fletcher, Darashana Wickramasinghe, James Allan, Jared Starbach, Jasmine Lee, Jenny Pastorini, Junn Kitt, Kim McConkey, Lahiru Wijedasa, Laurie Hedges, Lawal Billa, Mariani Ramli, Mary-Ruth Low, Mike Meredith, Mischa Turschwell, Navinder Singh, Ngumbang Juat, Prithiviraj Fernando, Reuben Clements, Sheema Abdul Aziz, Sonya Luz, Susan McGowan, Thary Goh, Wai Yee, Wei Lin Poh,

To my daughter Skyla, you have brought so much joy and happiness into my life and thank you for all the times your little smile, laugh or cuddles got me through those tough days.

Last but far from least, my amazing wife, Natalia Huang - what a journey this has been. First becoming engaged, getting married and then having our first child Skyla. Could I have procrastinated completing this PhD anymore – just joking! Natalia, I could not have done this without your endless support and selfless devotion. And not to mention reading and editing this thesis – I’m forever grateful. This PhD is just as much yours as it is mine. We made it!!!

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Chapter 1: General Introduction

1.1 Introduction

There are three extant elephant species in the world. They are distributed throughout Sub-Saharan Africa, the Congo Basin, and south Asia as *Loxodonta africana*, *Loxodonta cyclotis* and *Elephas maximus* respectively (Blanc, 2008; Choudhury et al., 2008). All species are internationally and locally threatened (Blanc, 2008; Choudhury et al., 2008) and face high extinction risk due to their large body size (Dirzo et al., 2014; Ripple et al., 2016), habitat decline (Chase et al., 2016; Maisels et al., 2013), human-elephant conflict (Fernando & Pastorini, 2011; Perera, 2009; Shaffer, Khadka, Van Den Hoek, & Naithani, 2019) and poaching (Sampson et al., 2018; Wasser et al., 2018; Zhou et al., 2018). As the largest terrestrial mammal in the world, elephants play a crucial role in the function of their ecosystems - they consume a vast diversity and enormous quantify of food (Vancuylenberg, 1977), move large distances (Lindeque & Lindeque, 1991), disperse seeds across the landscape (Campos-Arceiz & Blake, 2011), and have the ability to modify their physical environment with their immense size and strength, for example, by uprooting trees and creating mineral licks (Klaus, Klaus-Hügu, & Schmid, 1998; Lamprey, Glover, Turner, & Bell, 1967).

The propensity of elephants to move large distances makes studying their natural history and landscape usage difficult. This difficulty in studying their movement has resulted in a lack of understanding about elephant movement across the landscape, which can compromise conservation efforts, particularly across human-dominated landscapes or dense vegetation.

Tracking of elephants using GPS technology can provide valuable location data on elephant movement, although such studies are relatively few. The first elephant-tracking studies were conducted in the open savannah of Africa using collars which emitted radio frequencies; these revealed the extent of elephant movement to be up to 10,000 km^2 per year (Douglas-Hamilton, 1973; Lindeque & Lindeque, 1991). However, radio collars are not feasible in tropical rainforests due to the dense forest cover obscuring reception, and as a result the movement of tropical forest elephants remained unstudied for several decades (Olivier, 1978b; Stüwe, Abdul, Burhanuddin, & Wemmer, 1998). The revolutionary development of GPS collars in the 1990s allowed researchers to start collecting more fine-scale location data for both savannah and tropical forest elephants (Stephen Blake, Douglas-Hamilton, & Karesh, 2001; Douglas-Hamilton, 1998).

1.2 Elephant movement ecology

In Africa, movement studies of elephants have increased our understanding of the species. Elephants have been shown to actively move towards areas of rainfall (Garstang et al., 2014) and sometimes demonstrate strong spatial memory when directly moving towards previously-visited watering holes, from distances of up to 50 km (Polansky, Kilian, & Wittemyer, 2015). In seasonal landscapes (for example in southern Africa), home ranges are smaller and movement is more constricted during the dry season (Loarie, Van Aarde, & Pimm, 2009; Ngene et al., 2010). However, in semi-arid environments where the dry season dominates for most of the year, elephants can continue long-distance movements to access remote water holes (Lindeque & Lindeque, 1991). Roads have also been found to reduce home range size and modify movement behaviour by preventing elephants to move between neighbouring areas (Blake et al., 2008; Granados, Weladji, & Loomis, 2012). Lastly, African elephants are able to modify their behaviour by: i) increasing their walking speed when there are high levels of poaching; 2) avoiding human-dominated land use types; and 3) increasing nocturnal foraging to avoid human conflict (Gara et al., 2018; Graham, Lee, Douglas-Hamilton, & Adams, 2009; Ihwagi et al., 2018; Jachowski, Slotow, & Millspaugh, 2013).

Our understanding of elephant response to translocation has improved, with the knowledge that elephants can return to areas up to 300 km from the capture location (Viljoen, Ganswindt, & Toit, 2008), and as a mitigation method, translocation often fails to resolve human-elephant conflict (Slotow & van Dyk, 2001). The translocation process can cause higher rates of mortality and starvation, which is suggested to be the lack of resource knowledge in their new environment (Pinter-Wollman, Isbell, & Hart, 2009).

In Asia, elephant movements are less-extensively studied (Fernando & Pastorini, 2011). There is evidence to suggest that elephants are selecting secondary and disturbed habitat (Aini, Sood, & Saaban, 2015), however, majority of these habitats are outside protected areas (Aini, Husin, Sood, & Saaban, 2017). Asian elephants are known to have smaller ranging areas from 9 to 800km^2 (Alfred et al., 2012; Bahar, Hidayah, & Hambali, 2018; Fernando et al., 2008; Olivier, 1978b; Williams, Johnsingh, & Krausman, 2008) compared to 10 to 10,000 km^2 in Africa (Douglas-Hamilton, 1998; Galanti, Preatoni, Martinoli, Wauters, & Tosi, 2006; Lindeque & Lindeque, 1991; Ngene et al., 2010). The higher human pressure in Asia than in Africa could be one reason behind the smaller home ranges of elephants as human activities may restrict their movement (Tucker et al., 2018), or it may be the consistency of food and water resources in the tropical jungles of Asia which require shorter distances to cover their energetic requirements. This is discussed further in the following chapters.

Despite technological advancements, our understanding of elephant movement can still be improved upon. For example, the strength of inferences made from elephant movement studies have been limited by small sample sizes and the duration of studies being relatively short compared to the lifespan of an elephant. Additionally, majority of elephant movement studies are from Africa comprising open savannahs and savannah forests which is a very different physical landscape to that of tropical Asia comprising dense jungle (Fernando, Leimgruber, Prasad, & Pastorini, 2012; Pinter-Wollman et al., 2009). Furthermore, in Africa, most studies have been of translocated or reintroducing elephants into small fenced reserves, which has limited the movements of free-ranging elephants to a few studies (Pinter-Wollman et al., 2009; Slotow, Garai, Reilly, Page, & Carr, 2005). In addition, African elephants may be expected to behave differently to their Asian counterparts, with similar but different natural histories (for example, African elephants being larger in size and weight), different physical environments and different pressures (for example, African climate being hotter, with greater seasonal variation in food and water, and higher poaching pressure).

The Asian elephant is an endangered species and population trends are decreasing across all range states (Choudhury et al., 2008). In Peninsular Malaysia, the most recent population estimates range from 1223 and 1677 individuals (Saaban, Othman, Yasak, Burhanuddin, & Campos-Arceiz, 2011). The landscape in Peninsular Malaysia has drastically changed due to agricultural and urban expansion. Forest cover has been reduced from nearly 80% in the 1940s (Aiken, 1994) to less than 37% in 2010, with a more open and human-dominated landscape replacing the original closed canopy forests (Miettinen, Shi, & Liew, 2011). Asian elephants are edge specialists, preferring open areas and disturbed habitats compared with mature rainforest where fodder is less abundant (Yamamoto-Ebina, Saaban, Campos-Arceiz, & Takatsuki, 2016). This means they often forage along roads or on agricultural crops in human-dominated landscapes. As a result, there has been a drastic increase in human-elephant conflict (HEC). Human-elephant conflict and the resulting actions taken to address this conflict are now the main threat to elephant survival in Peninsular Malaysia (Saaban et al., 2011).

1.3 Aims and objectives

The general aim of this thesis is to gain a better understanding of the movement ecology and the movement responses to roads and translocation for elephants in Peninsular Malaysia. More specifically, our objectives are to estimate (Chapter 2):

- i) home range size;
- ii) movement patterns; and
- iii) explore the impacts of human pressure.

By meeting these objectives, we hope to understand how much area elephants require, how they move throughout their home range, and how human pressures are impacting their movements.

We also aim to increase our knowledge of the movement responses to roads and translocation; our additional objectives are to:

- i) describe the spatial and temporal patterns in road-crossing behaviour (Chapter 3);
- ii) quantify the effects of a road on movement behaviour and estimate the permeability (Chapter 3);
- iii) quantify the proportion of translocated elephants that remain at the release site (Chapter 4); and

iv) estimate the amount of time translocated elephants take to settle after being released (Chapter 4).

This thesis will fill essential research gaps for elephant movement research which can be used to advocate and formulate efforts to conserve elephants in Peninsular Malaysia and other elephant range countries.

1.4 How do Asian elephants move? (Chapter 2)

GPS telemetry research has increased our knowledge of space use and movement patterns of wide-ranging species and in turn benefited their conservation and management actions (Allen & Singh, 2016). For example, migrating wildebeest have been protected by better understanding their habitat use and movements across corridors (Thirgood et al., 2004), while spawning sites have been identified and protected for Atlantic bluefin tuna which has assisted in harvesting and management of the species (Block et al., 2005). In Africa, GPS telemetry studies have contributed to improved governmental cooperation between neighbouring countries that share elephant populations (Graham et al., 2009).

In Peninsular Malaysia, the dense forest has meant landscape usage and movement patterns of elephants to remain largely unknown, which makes conservation and management of the species challenging. Therefore, in my first chapter I use GPS telemetry to ask: **What is the space use and movement patterns of Asian elephants in Peninsular Malaysia?**

1.5 Response of wild elephants to a major road in Peninsular Malaysia (Chapter 3)

Roads are known to have adverse effects on a number of movement aspects. For example, through edge effects which modify habitat preference (Benítez-López, Alkemade, & Verweij, 2010; Fortin et al., 2013), and being barriers to movement by reducing permeability and connectivity across the landscape (Beyer et al., 2014; Laurance & Gomez, 2005; van Strien & Grêt-Regamey, 2016), which over time can result in the fragmentation of populations (Dunson & Travis, 1991; Laurance, Goosem, & Laurance, 2009; Said et al., 2016). Roads can also affect movement behaviour (Blake et al., 2008; Dussault et al., 2007; Eftestøl, Tsegaye, Herfindal, Flydal, & Colman, 2013) by altering the ability of wildlife to move between neighbouring areas and utilise resources within the available habitat (Johnson, Wiens, Milne, & Crist, 1992).

In addition to affecting movement patterns, roads are known to facilitate a plethora of threats to wildlife. Such direct threats include vehicle-wildlife collisions (Clevenger, Chruszcz, & Gunson, 2003; Trombulak & Frissell, 2000) which can create population sinks and lead to local extirpation (Woodroffe & Ginsberg, 1998). Arguably it is the indirect effects of roads that affect wildlife the most, where regions that were once protected by inaccessibility are now exploited for natural resources (Suárez et al., 2009) leading to further habitat loss and degradation. Furthermore, roads can elicit a whole suite of environmental impacts that include soil erosion and landslides (Bruijnzeel, 2004), disease transfer (Dutta et al., 1998; Eisenberg et al., 2006), invasive species (Brown, Phillips, Webb, & Shine, 2006; Walsh et al., 2004), poaching (Wilkie, Shaw, Rotberg, Morelli, & Auszel, 2000) and forest settlements (Laurance et al., 2009).

Studies in Africa have demonstrated the negative impacts of roads on elephants: forest elephants in Central Africa have exhibited a strong barrier effect to roads with no records of road-crossings (Granados et al., 2012), and increased home range size was linked to road-free habitat (Blake et al., 2008). These results have important implications for elephant management and conservation in regard to improving connectivity and habitat protection for sustaining future populations. There is no study in Southeast Asia that directly investigates the impact of roads on elephant movement. In northern Peninsular Malaysia, the Belum-Temengor landscape is ideal to investigate the impact of roads on elephant movement, as it consists of two large forest blocks that are bisected by a single major road with known elephant herds in the area. Therefore, in my second chapter I ask: **What is the impact of roads on elephant movement in the Belum-Temengor landscape?**

As human presence increases in previously-forested landscapes and elephants exploit open disturbed areas, contact between humans and elephants will inevitably increase. The development of roads generally results in further land-use change, and what usually follows is forest clearance for human purposes. The resultant conflict often demands translocation of individuals by the public which involves physically removing elephants from the conflict area. In Peninsular Malaysia, translocation is one of the main elephant management tools to mitigate HEC, with over 600 elephants translocated to protected areas between 1974 and 2010 (Saaban et al., 2011).

1.6 Movement responses of wild elephants to translocation (Chapter 4)

Little is known about the impacts of translocation on Asian elephants. Only a few studies in Asia have monitored translocated elephants with telemetry - one elephant in India (Roy et al., 2010), 16 elephants in Sri Lanka (Fernando et al., 2012) and two elephants in Malaysia (Stüwe et al., 1998). Even from these few studies, it is clear that translocation does not achieve elephant conservation or HEC mitigation goals. Instead, translocation has resulted in high rates of mortality, returning to the capture site, and leading to wider propagation and intensification of HEC (Fernando et al., 2012).

There has been only one study on movement responses to translocation in Peninsular Malaysia - this was conducted in 1995 and involved satellite-collaring two elephants (Stüwe et al., 1998). They found large differences in ranging areas, where one individual ranged around 350 km^2 from the release site and stayed within the protected area, while the other left the protected area ranging across an area of 7,000 km^2 (Stüwe et al., 1998). This disparity highlights the importance of studying a larger sample size to better understand the range of responses between different individuals.

A major gap in our knowledge is how elephants respond to translocation, in particular, how they move and use the landscape following translocation. Understanding where and how elephants respond to translocation would be invaluable information for the future management of HEC in Peninsular Malaysia. Therefore, in my third chapter I ask: **What is the movement response of elephants to translocation in Peninsular Malaysia?**

1.7 Conclusions

In conclusion, this thesis will generate knowledge that is relevant for the conservation and management of a threatened species, by understanding where and how Asian elephants use their environment (general movements) and the extent to which human infrastructure (roads) and management actions (translocation) impact their movements. It will fill essential research gaps for elephant movement research which can be used to advocate and formulate efforts to conserve elephants in Peninsular Malaysia and other elephant range countries.

Chapter 2: How do Asian elephants move in Peninsular Malaysia? A pioneer study on home range, movement patterns and human pressure

Authors: Jamie Wadey[1, *]; Hawthorne Beyer[2]; Jared Stabach[3]; Salman Saaban[4]; Nasharuddin Othman[4]; Christen Fleming[3]; Peter Leimgruber[3]; Ahimsa Campos-Arceiz [1,5]

Affiliations:

[1] School of Environmental and Geographical Sciences, The University of Nottingham Malaysia Campus, Jalan Broga, Semenyih 43500, Selangor, Malaysia; [2] School of Biological Sciences, University of Queensland, Brisbane, Qld 4072, Australia; [3]Smithsonian Conservation Biology Institute, Front Royal, Virginia, United States of America; [4] Department of Wildlife and National Parks Peninsular Malaysia, Km. 10, Jalan Cheras, 56100 Kuala Lumpur, Malaysia; [5] Mindset Interdisciplinary Centre for Tropical Environmental Studies, The University of Nottingham Malaysia Campus, Jalan Broga, Semenyih 43500, Selangor, Malaysia.

[*]**Corresponding author.** Email: jamie.wadey@nottingham.edu.my

2.1 Abstract

Understanding the movement ecology and spatial requirements of threatened species can provide numerous benefits for conservation and management. Here we apply the optimal foraging theory to make predictions about different movement strategies between sexes and the impacts of human disturbance. In short, optimal foraging theory predicts individuals to acquire food at the lowest energetic cost. As males are larger than female elephants, they will have larger energetic budgets. Therefore, we predict male elephants to increase their home range and movement rates to balance their larger energetic requirements with reproductive opportunities. Additionally, we hypothesize that increases in human disturbances will decrease home range size among elephants due to the increase in food availability. We used GPS telemetry from 15 wild Asian elephants in Peninsular Malaysia and found elephants to have large area requirements, with home ranges of up to 600 km^2. Additionally, human pressures decreased home range size and modified behaviour by increasing straight-line movements. We also found sexual differences, with males generally having larger home ranges, greater home range overlap, taking longer to cross their home range and exhibiting more straight-line movements than females. Our results are relevant for landscapes throughout Asia and Africa, where managers are planning to link elephant movement ecology with wildlife management and conservation. We suggest future conservation and management approaches to be tightly linked to movement ecology research for: a) determining the importance of different management options; and b) evaluating how management is affecting movement and area use by large mammals.

Keywords: *Elephas maximus*, movement ecology, home range, turning angles, daily distance, Peninsular Malaysia, habitat selection

2.2 Introduction

Movement is a fundamental characteristic of life that profoundly influences the structure and dynamic of ecosystems, populations, and communities, and the evolution and diversity of all species on earth (Nathan et al., 2008). The four mechanistic components of animal movement are: (1) why move (internal state); (2) how to move (motion); (3) when and where to move (navigation); and (4) external factors affecting movement (Nathan et al., 2008). The movement path of an animal is the result of the interplay between these four components, which reflects the different decisions and behaviours made by an animal (Gurarie, Andrews, & Laidre, 2009; Morales, Haydon, Frair, Holsinger, & Fryxell, 2004). As such, different optimal movement strategies can arise, which can be a reflection of different goals between individuals (Polansky, Douglas-Hamilton, & Wittemyer, 2013).

Megafaunal species, e.g. species larger than 15 kg (Ripple et al., 2016) and their movements have disproportionally high impacts on the environment, with their removal reducing plant-animal interactions and affecting ecosystem functions and services (Dirzo et al., 2014), which can lead to trophic cascades (Terborgh, 2015). In a human-dominated world, there are few places animals can move without coming into contact with human activities (Allan et al., 2017). This has resulted in a global restriction in megafauna movements (Altizer, Bartel, & Han, 2011; Tucker et al., 2018), rapid declines in populations and increased species extinctions (Dirzo et al., 2014; Ripple et al., 2016).

Human pressure, e.g. infrastructure development, land-use change, and human population density (Kareiva, Watts, McDonald, & Boucher, 2007; Venter et al., 2016), can negatively affect megafaunal movements. For example, jaguars have increased their home range size with increases in human density (Morato et al., 2016), while in Europe urbanisation has simultaneously decreased home range size of wild boar and increased their daily movements (Podgórski et al., 2013). Additionally, path tortuosity and home range overlap of wolves and coyotes increase near infrastructure (e.g. roads) where prey species are known to congregate (Riley et al., 2006; Whittington, St Clair, & Mercer, 2004). The long-term implications of species persisting in high levels of human pressure are strongly correlated with species extinction (Di Marco, Venter, Possingham, & Watson, 2018).

Researchers estimate home range size of animals in an attempt to understand what environmental resources or factors are important for an animal's fitness (Powell & Mitchell, 2012). Broadly speaking, a home range is an area that is routinely used by an animal to meet its daily needs (Burt, 1943). The increase in size and weight of a species, and in turn their metabolic demands, is expected to be reflected by a larger home range (Dahle & Swenson, 2003; Harestad & Bunnell, 1979). Therefore, as the largest terrestrial animal, elephants are expected to have large home ranges; and as a sexually dimorphic species, males too are expected to have even larger home range sizes than females. However, few Asian elephant studies can support these predictions (Fernando et al., 2008). Key factors that drive home range sizes of elephants are food and water, with elephants needing to find and consume around 150 kg of fresh vegetation per day and drink up to 190 litres of water every few days (Vancuylenberg, 1977). This results in elephants devoting large amounts of time feeding - up to 17 hours a day (Sukumar, 1990), and moving large distances - up to 64.7 km (Rowell, 2014; Wall, Wittemyer, Klinkenberg, LeMay, & Douglas-Hamilton, 2013).

Movement patterns can reveal finer-scale decisions that are made within an animal's home range. For example, home range overlap of elephants can reveal important social and reproductive strategies between males and females (Wittemyer, Getz, Vollrath, & Douglas-

Hamilton, 2007). Home range overlap between elephants occurs because elephants are non-territorial species (Fernando et al., 2008; Wittemyer et al., 2007). Much less in known about the extent to which males overlap their home ranges with female herds - presumably male elephants would overlap their home ranges with females to increase mating opportunities.

Home range crossing time is a movement metric that indicates how much time an animal requires to cross their home range (Morato et al., 2016). Understanding the temporal scale in which elephants move around their home range can provide insights about the use of resources throughout a home range. At a finer scale, the distribution of resources is known to affect how animals move throughout a home range – areas with high density of resources result in higher tortuosity (more twists and turns), while low density of resources can result in lower tortuosity (more straight-line movements) between resource patches (Bartumeus, 2009; Bartumeus, da Luz, Viswanathan, & Catalan, 2005). Elephants with straight-line movements have been linked with good spatial memory of resources to allow more efficient use of time between sparse resources (Polansky et al., 2015; Wato et al., 2018).

Southeast Asia is the region of the world with the largest number of threatened megafauna (Ripple et al., 2016; 2017). It is also a region where threatened megafauna face some of the highest levels of human pressure (Allan et al., 2019). Furthermore, the region is experiencing rapid economic growth, road expansion, forest loss, and human population increases (Dulac, 2013; Miettinen et al., 2011; World Bank, 2016). The continual increase in human pressure will further threaten the region's megafauna, including Asian elephants, the largest terrestrial animal in the region. Asian elephants are endangered due to the rapid decline of their populations, mostly as a consequence of habitat loss and the resulting human-elephant conflict (HEC) in the form of crop-raiding (Choudhury et al., 2008; Fernando & Pastorini, 2011).

Within Southeast Asia, Peninsular Malaysia remains a stronghold for megafauna (Ripple et al., 2016), including Asian elephants (Saaban et al., 2011). The dense tropical rainforest and steep terrain in Peninsular Malaysia makes it difficult to study elephant movement ecology and spatial requirements. Previous studies have been limited to using early telemetry technology (e.g. VHF and ARGOS collars), which provided valuable but limited information with high rates of collar failure (Jamieson, Zubaid, & Husband, 2012; Stüwe et al., 1998). Technological advancements in telemetry technology (e.g. GPS collars), have allowed detailed tracking of elephants in Peninsular Malaysia, with higher accuracy and for longer periods. However, few studies have been conducted and only three elephants in total were tracked (Aini et al., 2015; 2017; Bahar et al., 2018). Despite low sample sizes, these studies found elephants to prefer disturbed habitat outside protected areas; which is invaluable information as wild elephant numbers in Peninsular Malaysia have plummeted from ~ 6,000 to ~ 1,200 individuals (Olivier, 1978a; Saaban et al., 2011).

Here we apply the optimal foraging theory to make predictions about different movement strategies between sexes and the impacts of human disturbance. In short, optimal foraging theory predicts individuals to acquire food at the lowest energetic cost. As males are larger than female elephants, they will have larger energetic budgets. Therefore, we predict male elephants to increase their home range and movement rates to balance their larger energetic requirements with reproductive opportunities. Additionally, we hypothesize that increases in human disturbances will decrease home range size among elephants due to the increase in food availability. This study is a pioneer study in describing Asian elephant movement ecology and spatial requirements from GPS telemetry and it has important implications for all Asian elephant range countries. Locally, our research has implications for Malaysia’s CFS and NECAP policies which can inform management recommendations and support conservation of elephants and other large mammals in the country.

2.3 Materials and methods

2.3.1 Study area

Our study was conducted in four locations across Peninsular Malaysia (Figure 2-1):

(1) Belum-Temengor, located in northern Peninsular Malaysia with a large mature primary dipterocarp rainforest to the north (~ 1,200 km^2) and a secondary, previously logged forest to the south (~ 3,000 km^2);

(2) Siput-Lenggong, an area 75 km south of Belum-Temengor within the main mountain range which runs along the central part of the country, and is comprised mostly of mature secondary forest (~ 2,000 km^2);

(3) Gua Musang, a mosaic of oil palm and rubber plantations with small patches of fragmented regrowth forest (~ 300 km^2), located 10 km north of Peninsular Malaysia's national park, Taman Negara (Kelantan); and

(4) Temerloh Forest Reserve, an area that is a mixture of logging concessions, Acacia plantations, and regrowth forest (536 km^2), located in central Peninsular Malaysia on the west side of the central mountain range.

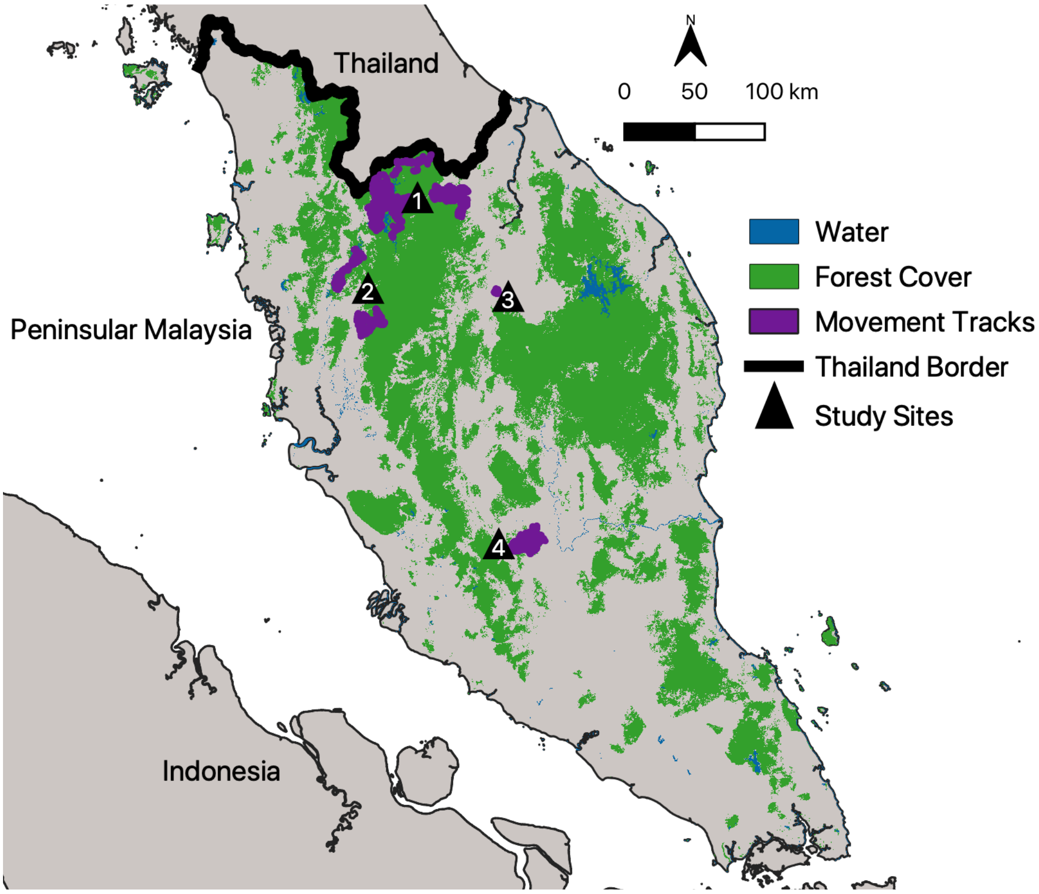


Figure 2-1. Study areas in Peninsular Malaysia included: (1) Belum-Temengor; (2) Siput-Lenggong; (3) Gua Musang; and (4) Temerloh Forest Reserve. Extent of each study area are denoted by the movement tracks.

Throughout our study sites, primary and secondary forests consisted of dipterocarp and montane forest, with an altitudinal range of zero to 2187 metres above sea level (Saw & Chung, 2015). Our study sites represent the main vegetation and land-use types where elephant populations remain in Peninsular Malaysia: Belum-Temengor is a mature old growth forest and contains one of the largest elephant populations remaining in Peninsular Malaysia; Siput-Lenggong represents mature secondary forest with historical logging activity; and Gua Musang and Temerloh represent agricultural plantations in human-dominated landscapes.

2.3.2 Elephant tracking

We captured, collared and released wild elephants at the same location, with the process completed within the same day. The total number of elephants tracked, sex ratio, and their distribution across the country could not be decided *a priori* because it was dependent on the success of collaring operations. We used Inmarsat and Iridium GPS collars specifically designed for elephants (Africa Wildlife Tracking, Pretoria, South Africa), programmed to record one location every two hours. We collected GPS data until the collar battery was exhausted. All elephants were immobilised by the Department of Wildlife and National Parks (DWNP) as described in (Daim, 1995). We complied with research and ethics requirements by the Malaysian government (permit #JPHL%TN(IP): 80-4/2) and the Smithsonian National Zoological Park Institutional Animal Care and Use Committee (NZP-IACUC #10-32).

2.3.3 Statistical software

All calculations in this thesis were made in the *R environment for statistical computing*, hereafter termed "*R*" (R Core Team, 2016). Functions and packages used in *R* are indicated in the text in italics where relevant.

2.3.4 Home range size

We estimated home range size for all elephants. We used two home range estimators: 1) the autocorrelated kernel density estimator (AKDE), which was applied to 'resident' elephants, i.e., elephants which resided in a defined area over the tracking period (Fleming et al., 2015a); and 2) minimum convex polygon estimator (MCP estimator), which was applied to 'non-resident' elephants, i.e., elephants which continued to move across the landscape showing no preference for a defined area (Bekoff & Mech, 1984).

We selected the AKDE as our primary home range estimator because it accounts for the autocorrelation that is present in all animal tracking data, i.e., one location being dependent on another (Worton, 1987). However, the main assumption of the AKDE is that it can only estimate the home range of ‘resident’ animals (Fleming et al., 2015a). Therefore, for ‘non-resident’ elephants we selected the MCP estimator, which contains no autocorrelation assumption but lacks any underlying probabilistic model (unlike the ADKE). We chose the MCP estimator because the majority of other probabilistic estimators violate autocorrelation assumptions which result in underestimating home range size (Fleming & Calabrese, 2017). An elephant was categorised as ‘resident’ when the squared distance (function *variogram*) reached an asymptote as a function over time (Figure 2-2) which denoted a defined home range (Fleming et al., 2015a). Conversely, an elephant was categorised as ‘non-resident’ when its squared distance did not reach an asymptote (Figure 2-2), indicating there was no defined home range (Fleming et al., 2015a).

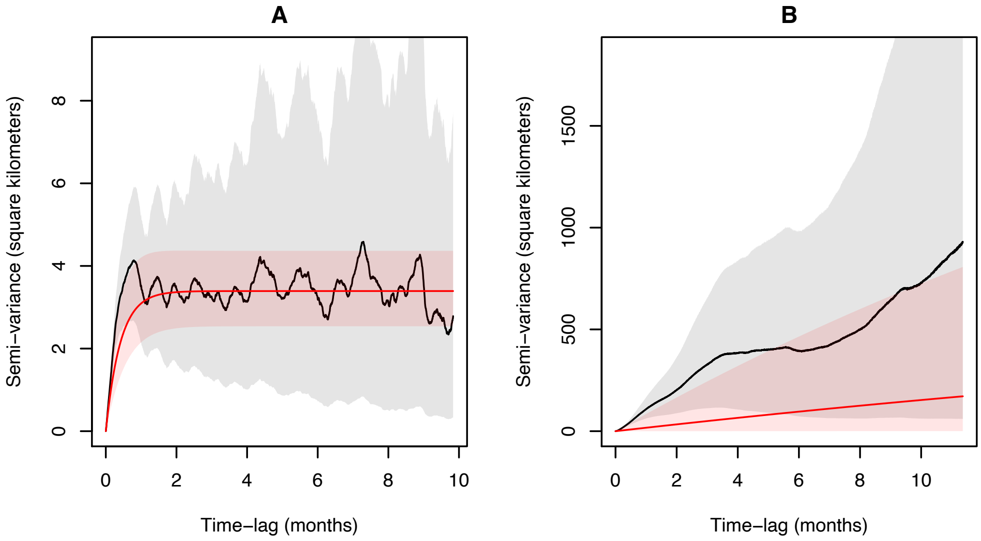


Figure 2-2. (A) Variogram of a resident elephant (ID = 9;Table 2-1). The semi-variance reaches asymptote within the first month, roughly representing the time to cross its home range. The fitted movement model is represented by the red line and the red shading denotes

the 95% CI. (B) A non-resident elephant (ID = 15; Table 2-1). Notice that the semi-variance is increasing over time and does not reach an asymptote. The AKDE home range estimator requires animals to be range resident and thus all non-range resident animals need to be excluded. For A, 50% of the elephant track length is displayed while B is 70%.

We calculated home range size of ‘resident’ elephants using the AKDE from the *ctmm* package (Calabrese, Fleming, & Gurarie, 2016). The AKDE uses continuous-time movement models to estimate home range size (Fleming, Subaşı, & Calabrese, 2015b). We used four different commonly used continuous-time movement models on ‘resident’ individuals: (1) Ornstein-Uhlenbeck (OU); (2) Integrated Ornstein-Uhlenbeck (IOU); (3) Ornstein-Uhlenbeck with Foraging (OUF); and (4) Independent Identically Distributed (IID). Models were fitted using a maximum likelihood approach with function *ctmm.fit* (Fleming et al., 2014) and consequently ranked based on the corrected Akaike’s Information Criterion (AICc) to select the best model using function *ctmm.select* (Calabrese et al., 2016). The function *akde* was then applied to the best model to estimate home range size and the 95% confidence interval. For more details on continuous-time movement models see Calabrese et al. (2016).

Home range size for ‘non-resident’ elephants was calculated using the MCP estimator from the *rhr* package and the *rhrMCP* function (Signer & Balkenhol, 2015). We calculated the 95% minimum convex polygon (MCP), which is calculated as 95% of the area (square kilometres) bounded by the furthest GPS coordinates. Historically the 95% threshold has been the most commonly-used threshold in animal tracking data analyses (Laver & Kelly, 2008; Worton, 1987). In addition, for more appropriate comparisons between individual home range estimates and track lengths We also calculated annual home range size (at 12-month track lengths and 2-hour fixes) and using one home range estimator - the 95% MCP.

2.3.5 Movement patterns

We calculated the following movement patterns for each elephant: 1) home range overlap (percentage of overlap between two elephant home ranges; km^2); 2) home range crossing time (time each elephant took to cross the maximum distance of its home range; km); 3) daily distance (maximum distance each elephant travelled daily, measured as track length, not straight-line distance or displacement; km); 4) path tortuosity (the proportion of turns in a movement path; low tortuosity indicate more turns, while high tortuosity indicates more straight-line movements; hours); and 5) turning angles (change in angular direction between successive locations; degrees). Movement patterns were calculated in *R* (R Core Team, 2016) using continuous-time movement models from the *ctmm* and *adehabitatLT* packages (Calabrese et al., 2016; Calenge, 2006; Winner et al., 2018).

Home range overlap was defined as the percentage overlap in home range area (km^2) between two animals. It was calculated using the *ctmm* package and *overlap* function (Winner et al., 2018). We calculated home range overlap for all combinations of unique elephant pairs. The main assumption behind the *overlap* function is that it can only estimate the home range overlap of ‘resident’ animals, since ‘non-residents’ by definition lack a home range for an overlap to be calculated (Winner et al., 2018). Therefore, we used the AKDE home ranges that were previously calculated above with the addition of applying the function *overlap* which produced a mean and 95% confidence interval for home range overlap (Winner et al., 2018).

As described in the previous section, while home range estimation of 'non-resident' elephants is not suitable for the AKDE, continuous-time movement models of movement patterns have been found to be accurate for 'non-resident' animals (Noonan, Fleming, et al., 2019a; Noonan, Tucker, et al., 2019b). Thus, for estimates of home range crossing time, daily distance and path tortuosity, we fitted and selected the best continuous-time movement model for each elephant (functions *ctmm.fit* and *ctmm.select*). We then calculated the movement parametres (mean and 95% confidence interval) by using the *summary* function on the best model.

Finally, we calculated the turning angles in degrees (ranging from -180 to +180) using the *adehabitatLT* package and function *as.ltraj* (Calenge, 2006). Turning angles were calculated from three successive locations, which was estimated as the change in angular direction between the first and third successive location (Calenge, 2006). Successive locations were two hours apart.

2.3.6 Sex response

We tested whether home range and movement patterns (with the exception of turning angles) varied with sex by using hierarchical Bayesian fixed-effect one-way ANOVAs (Kery, 2010; McCarthy, 2007). Normality was tested using the Shapiro-Wilk test (function *shapiro.test*) and by visually inspecting Q-Q plots (Royston, 1992). Data were transformed if distributions did not meet model assumptions. We used the Markov chain Monte Carlo (MCMC) algorithm to estimate marginal posterior distributions of home range and movement patterns estimates. The MCMC algorithm was fitted with 100,000 iterations and a 20% burn-in period (i.e., 20,000 iterations). As recommended, we assessed convergence of the MCMC algorithm by visually inspecting trace plots and by checking the scale reduction factor was less than

1.02 for home range and movement patterns estimates (Gelman & Rubin, 1992). We calculated the probability (here after as 'Prob') that the mean of one group was greater than the other by sampling (10,000 iterations) from each of the resulting posterior distributions (Gelman & Hill, 2007). Analyses were completed in *R* using the *jagsUI* and *rjags* packages (Kellner, 2019; Kery, 2010; McCarthy, 2007; Plummer, 2018; R Core Team, 2016). For turning angles, we calculated the percentage overlap of turning angle distributions between males and females using the *overlap* function from the package *overlapping* with a *von Mises distribution* (Pastore, 2018).

2.3.7 Human pressure

We used human footprint and human density (both data sets were one km^2 pixel resolution) as indicators of human pressure on the landscape. The human footprint is an index of human pressure ranging from 0 to 50 (Venter et al., 2016). Human footprint values of zero indicate areas with no significant human pressure, whereas a value of four corresponds to low pressure levels (e.g. agricultural lands), and values above 20 represent densely populated semi-urban and urban areas (Venter et al., 2016). Human density is the number of resident humans per unit of land area (number of humans/km^2) from the LandScan dataset (Bright, Colman, Rose, & Urban, 2011). We examined the relationship between human pressure and home range size and movement patterns by creating linear regressions in a Bayesian framework using *R*. Firstly, we plotted the intersect between the independent variable (which was either human footprint or human density) and the dependent variable (home range size or movement pattern) for each elephant (Table 2-1;Table A2-1; Table A2-2).

Human footprint and human density values were calculated for each elephant with respect to their home range size. For human footprint, we took the average value within the home range. For human density, we divided the total number of humans by the size of the home range (i.e., number of humans/km^2; Table A2-2). We calculated 95% confidence intervals around our linear regressions to assess the strength of our relationships. Confidence intervals were modelled using the *rjags* package (Plummer, 2018) by following commonly-used methods that are described in (Kery, 2010; McCarthy, 2007; Morato et al., 2016). We assessed model fit by calculating the Bayesian *p*-value, which is the proportion of times the posterior dataset is greater than the actual dataset (Gelman & Hill, 2007; Kery, 2010). Values close to 0.50 indicate a good model fit (i.e., no difference between the two datasets). The posterior dataset was created by randomly sampling (10,000 times) from the posterior distribution.

2.4 Results

2.4.1 Elephant tracking

We collared a total of 15 wild Asian elephants between 2011 and 2017, comprising ten female and five male individuals (Table 2-1). Elephants were tracked for an average (± SD) of 428 ± 343 days (range 70 – 1,005 days; Table A2-3), while the number of recorded locations averaged 3,569 ± 3,418 and ranged from 394 to 10,428 per elephant (Table 2-1). The total dataset consisted of 53,538 locations with 41,932 for females and 11,606 for males (Table 2-1). There was no difference between sex for the number of days tracked or number of locations recorded (Table A2-3). However, there was a marginal statistical difference (P = 0.08; Table A2-3) between sex and fix success, with female fix success being greater than males (Table A2-3; 74 ± 25 and 53 ± 16).

Table 2-1. Summary table of elephant movement metrics. ‘M’ = Male, ‘F’ = Female, ‘N.day’ = Number of days tracked, ‘F.Succ’ = Fix success, ‘MCP95’ = Minimum Convex Polygon 95%, ‘AKDE’ = Autocorrelated kernel density estimator, ‘Daily Dist’ = Daily Distance, ‘HR Xing’ = Home range crossing time. ‘OUF’ = Ornstein Uhlenbeck with foraging. Values within parenthesis are the 95% confidence intervals.

id	id1	Sex	Landscape	Behaviour	N.day	F.Succ [%]	MCP95 [km^2]	Best Model	AKDE [km^2]	Daily Dist [km]	HR Xing [months]	Path Tortuosity [hours]
1	Awang Banun	M	Belum	Resident	484	72	NA	OUF	106 (69-150)	4.6 (4.5-4.7)	19 (11.6-31.1)	40.4 (37.1-44)
2	Awang Mendelum	M	Belum	Resident	355	42	NA	OUF	615 (258-1124)	5.8 (5.6-5.9)	1.7 (0.5-5.8)	1 (0.9-1.1)
3	Awang S Kedah	M	Belum	Non-Resident	875	44	701	OUF	NA	6.1 (6-6.2)	6.6 (0-13.3)	58.2 (54.8-61.9)
4	Castello	M	Gua Musang	Resident	86	38	NA	OUF	12 (6-20)	2.9 (2.6-3.2)	6.1 (2.6-14.7)	41.3 (28.8-59.4)
5	Dayang Siput	F	Siput-Lenggong	Non-Resident	353	87	211	OUF	NA	5.3 (5.2-5.5)	1.5 (0.5-4.2)	45.3 (41.8-49.2)
6	Mama Kay	F	Belum	Resident	168	96	NA	OUF	114 (56-191)	4.7 (4.6-4.9)	18 (7.2-45)	41.3 (36.5-46.8)
7	Mek Banun	F	Belum	Resident	102	94	NA	OUF	164 (65-310)	4.5 (4.3-4.6)	21.4 (5.2-88.8)	47.7 (41.2-55.2)
8	Mek Fish	F	Belum	Resident	581	58	NA	OUF	54 (39-72)	4.4 (4.3-4.5)	13.1 (9.1-18.7)	40.7 (37.3-44.3)
9	Mek Kamasul	F	Temerloh	Resident	1016	86	NA	OUF	268 (198-350)	5.6 (5.6-5.7)	21.7 (15.5-30.4)	1.1 (1.1-1.2)
10	Mek Pergau	F	Belum	Resident	931	69	NA	OUF	467 (236-775)	6.9 (6.5-7.3)	2.6 (1.1-6.2)	19.5 (16.9-22.4)
11	Puteri Rafflesia	F	Belum	Resident	889	96	NA	OUF	131 (74-203)	2.8 (2.7-2.8)	2.2 (1.1-4.4)	43.1 (41-45.3)
12	Rafflesia	F	Belum	Resident	77	95	NA	OUF	179 (64-352)	4.8 (4.6-5)	18.9 (3.4-104.5)	49.5 (42-58.3)
13	Yeob Bendang	M	Siput-Lenggong	Non-Resident	73	66	58	OUF	NA	5.5 (5.2-5.9)	29 (0-58.9)	47.7 (38.4-59.4)
14	Yeong Chepor	F	Siput-Lenggong	Non-Resident	290	27	228	OUF	NA	5.3 (5-5.6)	3.5 (0.1-228.2)	56.5 (47.1-67.8)
15	Yeong Jalong	F	Siput-Lenggong	Non-Resident	190	37	196	OUF	NA	6.7 (6.1-7.2)	1.3 (0.2-8.3)	36.8 (28.2-48)

2.4.2 Home range and movement patterns

We found the average home range size (combining estimates from two estimators: 1) AKDE and MCP) for all elephants (n = 15 elephants) to be variable at 228 ± 203 km^2 with a range of 12 – 701 km^2 (Table 2-1). Home range overlap was also variable with an average of 45 ± 34 % and a range of 1 – 100 %, while for daily distance travelled (track length), there was more consistency with an average of 5.0 ± 1.1 km per day and a range of 2.8 – 6.9 km per day (Table 2-1). We found the average home range crossing time to be almost one year, however, it was highly variable at 11.1 ± 9.4 months and ranged from 1.3 to 29.0 months (Table 2-1). For path tortuosity, elephants tended to move more directionally (in straighter lines) with an average of 38.0 ± 17.4 hours and a range of 1.0 ± 58.2 hours (Table 2-1). The distribution of turning angles was evenly spread among elephants, however, there were some increases in turning angles that were close to zero degrees, indicating more straight-line movements (Table A2-4). In addition, for more appropriate comparisons between individual home range estimates and track lengths We also calculated annual home range size (at 12-month track lengths and 2-hour fixes) and using one home range estimator (95% MCP) to be 191 ± 107 km^2 based on a sample size of eight elephants.

2.4.3 Sex response

Home range size varied between female (n = 10 elephants) and male (n = 5 elephants) elephants. The probability that home range size of males (average: 296 ± 329; and range: 12 – 701 km^2) was greater than females (average: 194 ± 112 km^2; and range: 54 – 467 km^2) was high at 0.97 (Figure 2-3; Table A2-5). We found male (n = 5 elephants) home ranges overlapped female (n = 10 elephants) home ranges on average by 64 ± 23 % and ranged 23 – 91 % (Prob = 0.93; Figure 2-3; Table A2-5). Males (n = 5 elephants) took longer to cross their home range then females (n = 5 elephants; Prob = 0.66; Figure 2-3; Table A2-5), which resulted in an average of 12.5 ± 11.3 months and 10 .4 ± 8.9 months respectively. We found little variation in the distance travelled per day, with males (n = 5 elephants) on average travelling 4.9 ± 1.2 km and females (n = 10 elephants) 5.1 ± 1.1 km (Figure 2-3; Table A2-5), which resulted in a low probability of difference between sex (Prob = 0.56; Figure 2-3).

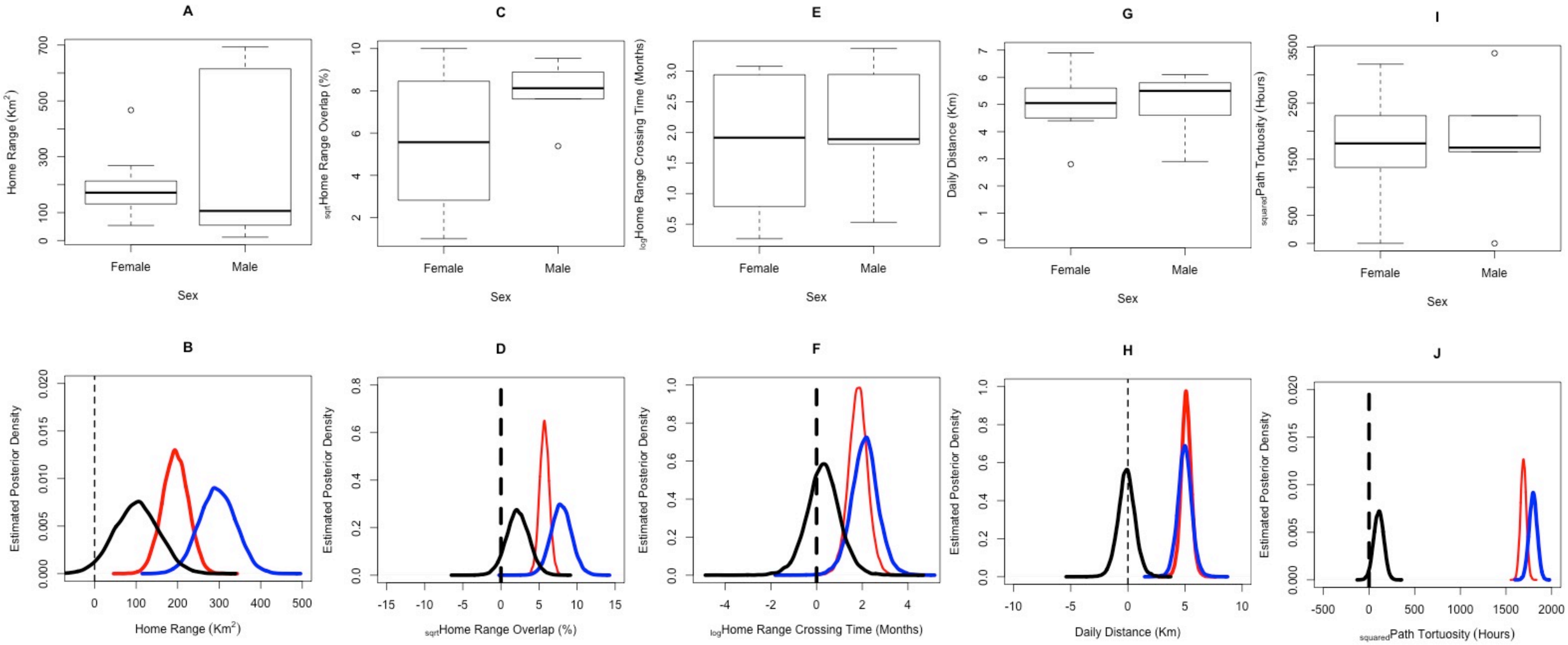


Figure 2-3. Boxplot and Posterior Density Estimates for female and male home range (km^2) [A and B], home range overlap ($_{sqrt}$%) [C and D], home range crossing time ($_{log}$Months)[E and F], daily distance travelled (km/day) [G and H], and Path Tortuosity ($_{squared}$Hours)[I and J]. Black line represents the difference between the posterior distribution of female and male, red line represents the posterior distribution of females and blue represents the posterior distribution of males.

Path tortuosity, represented by velocity autocorrelation timescale, were proportionally more directional (movement in a straight line) for males (n = 5 elephants) than females (n = 10 elephants; Prob = 0.97; Figure 2-3; Table A2-5). We found little overlap in the 95% credible intervals in regard to path tortuosity, with males producing larger values than females (Table A2-5). There was high similarity in turning angle distributions with 96% overlap between sexes (Figure 2-3). The minor differences in overlap were related to males (n = 5 elephants) displaying a tendency to move more acutely to the left (TAs closer to -180) and right (TAs closer to 180), while females (n = 10 elephants) produced more steps with straighter turning angles (TA closer to zero; Figure 2-4). The distributions of individual turning angles per elephant can be found in the Table A2-4.

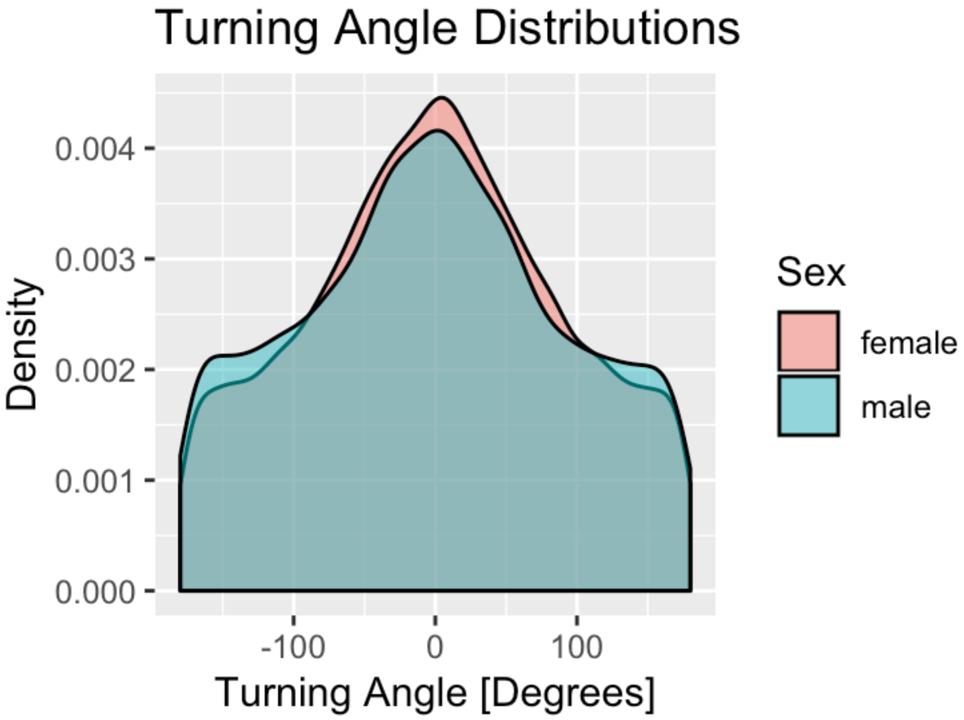


Figure 2-4. Density distributions of turning angles between females and males. We found a 96% overlap between sexes. Turning angles are in degrees and calculated from the *von Mises distribution* (Pastore, 2018). Positive turning angles represent turns to the right, while

negative turning angles represent turns to the left. The greater the turning angle value the more acute the turn.

2.4.4 Human pressure

Elephant home ranges (n = 15 elephants) decreased in size with increasing human footprint and human density (Figure 2-5); with Bayesian p-values of 0.512 and 0.521, indicating an adequate fit of the regression model to the data (the closer the value is to 0.5 the better the fit, bounded by 0-1). The relationship between human footprint and home range size was stronger than that with human density, displaying tighter 95% confidence intervals around the regression line. Males (n = 5 elephants) and females (n = 10 elephants) were equally affected by human footprint (Figure 2-5) and their home ranges were exclusively within areas that are considered to be at high risk for species extinction (i.e., when human footprint values are ≥ 3 (Di Marco et al., 2018). This resulted in a mean human footprint of 8.7 ± 4.2 with a range of 0.0 to 35.0 (Figure 2-5; Table A2-1). We found males (n = 5 elephants) on average to persist in areas that were more disturbed (greater human footprint values) than females (n = 10 elephants) with human footprint values of 9.4 ± 5.8 (males) and 8.4 ± 3.6 (females). In regard to human density, the majority of home ranges (73%, 11 elephants) persisted in densities lower than 36 humans per square kilometre (lowest density = 1.47 km^2) and the remaining four elephants resided in densities of 95, 277, 293 and 540 humans per square kilometre (Figure 2-5; Table A2-2).

Home range overlap (n = 15 elephants) was not affected by human footprint or human density as indicated by the horizontal regression lines and wide 95% confidence intervals (Figure A2-1; Figure A2-2. Bayesian p-values of 0.498 and 0.513). We found that home range crossing time increased slightly with increasing human footprint and human density values, however, the 95% confidence intervals were far from the regression line, implying the relationship needs to be taken with caution (Figure A2-1; Figure A2-2, Bayesian p-values of 0.492 and 0.516). Daily distance was not affected by human footprint, however, daily distance was found to increase in size with increases in human density (Figure A2-1; Figure A2-2; Bayesian p-values of 0.504 and 0.502). Daily distance for both human footprint and human density produced 95% confidence intervals that were tight around the regression line, indicating the trends to be valid (Figure A2-1; Figure A2-2).

Path tortuosity (n = 15 elephants) increased with increasing human footprint (i.e., more straight-line movements in areas of higher human footprint), while for human density there was little to no effect with a horizontal regression line and wide 95% confidence intervals (Figure A2-1; Figure A2-2; Bayesian p-values of 0.507 and 0.501).

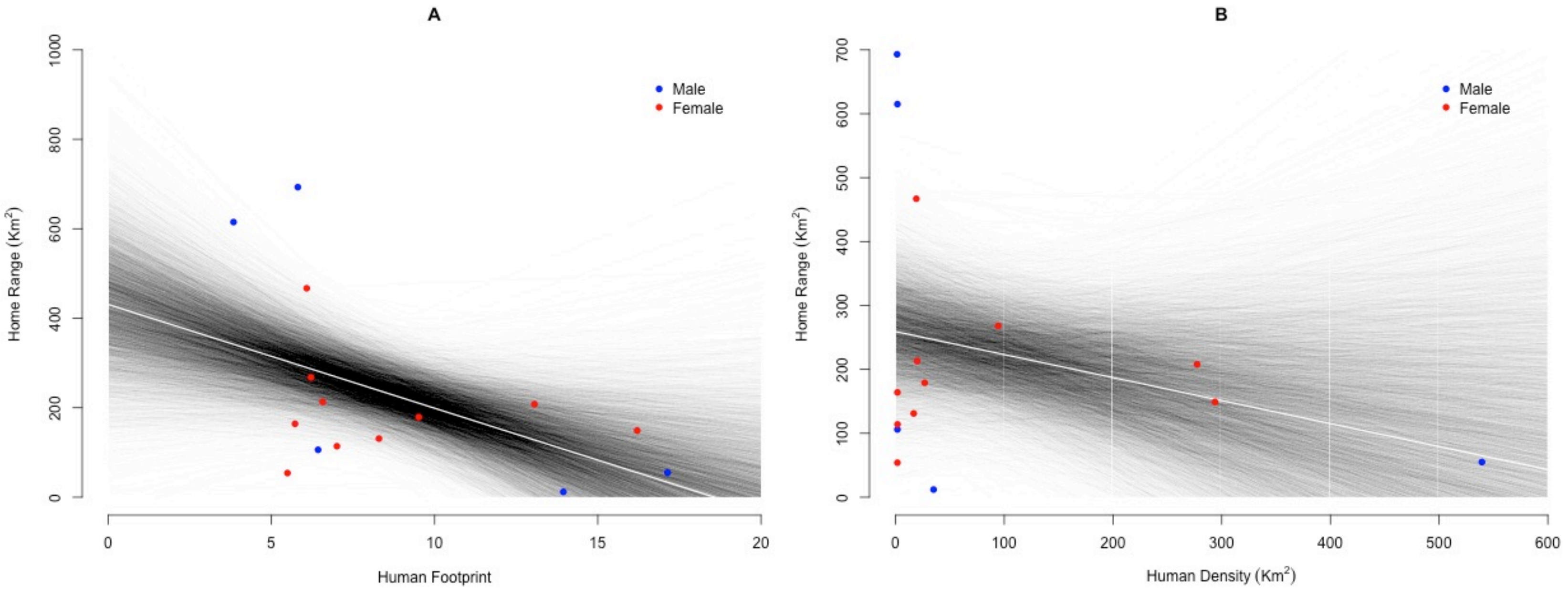


Figure 2-5. Elephants' home range (km^2) estimates in relation to human footprint [A] and human density (km^2) [B]. Regression line is the species estimate from a linear regression model formulated in a Bayesian framework. Error lines are 95% CI. Bayesian p-value = 0.512 [A] and 0.521 [B].

2.5 Discussion

This study has shown how elephants move throughout Peninsular Malaysia. We have increased our understanding of elephant movement by estimating home range size, movement patterns, and effects of human pressure. This study has found Asian elephants to require large areas (up to 600km^2). We also found increased human pressure led to decreased home range size and modified behaviour by increasing straight-line movements. Of concern, we found the majority of home ranges contained high levels of human pressure, which have been previously linked to high extinction risk (Di Marco et al., 2018). Of interest, a supplementary analysis (see Appendices 2.10.3) investigated the habitat selection and found elephants to avoid steep slopes and high elevation areas. Furthermore, elephants were found to be attracted to disturbed habitat (regrowth forest) and chose not to venture far from roads or forest, whilst showing no preference to proximity to water.

We found evidence to support our optimal foraging prediction that male elephants would increase their home range and movement rates to balance their larger energetic requirements with reproductive opportunities. For example, males increased their reproductive opportunities by having larger home ranges (on average 296 km^2 vs 194 km^2) and greater home range overlap (64 %) than females. To minimise the energetic cost of a larger home range male minimized their travel distance (more straight-line movements) between resources than females. Interestingly males and females on average travelled similar distances within a day (4.9 km and 5.1 km), suggesting that the straight-line movements alone are effective at reducing the trade-off of a larger home range. We also found evidence that elephants are changing foraging strategies in disturbed areas by decreasing home range size with increases in human density and human footprint. As elephants require large quantities of food daily; the decrease in home range size suggests elephants are able to meet the same energy requirements at smaller scales because of increases in food abundance.

Our home range estimates (on average 228 ± 203 km^2) were similar to other Asian elephant studies (Alfred, Ahmad, Payne, Williams, & Ambu, 2010; Fernando et al., 2008; Williams et al., 2008), although we did not record any individual differences of large magnitude – as was the case in India with one elephant home range estimated to be 3,000-4,000 km^2 (Datye & Bhagwat, 1995). Furthermore, a previous study in Peninsular Malaysia found one elephant's home range to be extremely large at 6,804 km^2 (Stüwe et al., 1998) - we suggest this home range size is not natural and likely the result of being translocated. A caveat of our home range analysis is the higher proportion of female elephants. Future home range studies should focus on collaring non translocated male elephants to cement home range estimates. Another caveat in our home range estimates for non-resident elephants is the use of the MCP estimator, which is known to underestimate home range size, although it underestimates the least when compared to other estimators (Fleming & Calabrese, 2017; Noonan, Tucker, et al., 2019b). Our results from the MCP estimator were very consistent, and on average were not smaller than AKDE estimates (Table 2-1), therefore, we suggest the underestimation effect of the MCP estimator was minimal.

Elephants have huge daily demands of food and water (Vancuylenberg, 1977). Therefore, food and water are expected to be the main drivers behind elephant home range size. When food and water are abundant all year round, elephant home ranges are usually smaller and stable e.g. 115 ± 64 km^2 (Fernando et al., 2008). We suspect that the low variation in our home range estimates in Peninsular Malaysia are due to the abundance of grasses and early successional plants in disturbed habitat and at forest edges which are common throughout the landscape. This means the elephants do not need to travel far between food sources. They also do not need to travel far for water given it rains year-round in Peninsular Malaysia and much of their preferred fodder contains a high water content (Chen, Deng, Zhang, & Bai, 2006; Sukumar, 1990).

Understanding movement patterns can reveal important decision-making processes for managers of land and wildlife. This study has found a high percentage of home range overlap, which is not surprising as elephants are known to be non-territorial (Fernando et al., 2008). The lack of territoriality is believed to be due to the trade-off of spending time defending a territory versus eating large quantities of food (Belcher & Darrant, 1999; Sandell, 1989), as elephants devote a large part of their day to feeding (17 hours per day) and traveling up to 64.7 km per day (Sukumar, 2003; Wall et al., 2013). Our daily distance estimates (track length) were consistent (5.0 ± 1.1 km per day), suggesting that food resources are distributed evenly across their home ranges, while other Asian elephant studies have reported greater variability in daily movements ranging from 1.0 – 15 km per day, which places our findings at the lower end of the literature results (Rowell, 2014).

Path tortuosity of elephants can be affected by natural and human influences (Jachowski et al., 2013; Wato et al., 2018). Our results for path tortuosity and turning angles suggest elephants are moving between resources in bouts of straight-line movements. We infer these straight-line movements as individuals using their spatial memory to move onto the next food resource when local food is exhausted, which is likely to be aided by existing forest trails from logging activities or ancestral routes. Previous studies in Africa have concluded that spatial memory is the mechanism driving straight-line movements to water sources (Polansky et al., 2015; Wato et al., 2018). It may also be possible that elephants are choosing the most direct and shortest path between food (and therefore cover) to avoid interaction with humans. Additionally, fruiting trees might also influence movements sporadically and for shorter periods of time, however, there is little data to support this (Kromann-Clausen, 2015).

Our study found elephants took around 11 months to cross their home range; this is in line with a previous study in Sri Lanka which found elephant home range size to become stable after 12 months (Fernando et al., 2008). It is possible the time taken to cross their home range could be an indicator of how much time is needed for food resources to recover in Peninsular Malaysia. This is further supported by a previous study in Malaysia that found elephants were taking between 5 to 8 months to revisit a single foraging site after it was initially exhausted of food (English et al., 2014). The consequences of vegetation communities not having enough time to recover (when elephants have been restricted to a small area) is well-documented, where vegetation abundance and community structure are significantly altered through overconsumption by elephants (Asner, Vaughn, Smit, & Levick, 2016; Law, 1970).

Asian elephant are sexual dimorphic species, with adult males weighing around 5000 kg compared to 3000 kg for females. The increase in size and weight of males, and in turn their metabolic demands, is expected to be reflected by a larger home range (Dahle & Swenson, 2003; Harestad & Bunnell, 1979). Previous studies on Asian elephant home ranges have not found consistent differences between sexes, however, one study in Sri Lanka found some differences between sexes when males were in musth (Fernando et al., 2008). Future research in Peninsular Malaysia could explore the influence of musth on male home range size. This study has provided the first consistent piece of evidence on Asian elephants to support the morphometric and energetic predictions (Dahle & Swenson, 2003; Harestad & Bunnell, 1979); as we found males displaying home ranges that were on average 1.5 times larger, which coincided with greater home range overlap (65%) when compared to females.

Human pressure is known to negatively impact the movement of many animal species (Tucker et al., 2018). Our human pressure results indicate that home range size decreases with increases in human footprint and human density. These results are somewhat surprising as other large mammal studies including elephants have found increases in home range size with increases in density of roads, habitat fragmentation and human density (Alfred et al., 2010; Morato et al., 2016; Poessel et al., 2014). We suggest our decrease in home range size is likely due to an increase in the abundance of preferred grasses and early successional plants that are common in disturbed areas, which result in smaller distances needed to travel to meet metabolic demands (Terborgh, Davenport, Ong, & Campos-Arceiz, 2018; Yamamoto-Ebina et al., 2016). Foraging in disturbed areas can also be a double-edged sword for elephants – on the one hand there is higher abundance of preferred food in disturbed areas, but on the other hand disturbed areas can mean higher risks of conflict (and consequent injury or mortality) due to the increased contact with humans. We did find some evidence that certain elephants are able to exist in high human densities (five elephants at 95, 277, 293 and 540 humans per km^2). This could be due to site-specific factors such as increased tolerance levels or ability to avoid detection by humans through low elephant density.

2.6 Policy implications

This study found: (i) elephants require large areas (up to 600 km^2); (ii) avoid steep slopes and highly elevated areas; (iii) home range and movement patterns to be negatively affected by human pressure; (iv) differences between sexes; (v) preference for disturbed habitat; (vi) ranging in areas with high extinction risk. The information generated from our study can be used to assist policy and management of elephants in Peninsular Malaysia and potentially in other elephant range states. For Peninsular Malaysia's CFS land-use masterplan, our results, such as slope and elevation limits, can assist in evaluating the efficacy of areas nominated for protection and connectivity (DTCP, 2014). This study will also inform the National Elephant Conservation Action Plan, which will assist in achieving a well understood biology to inform conservation decisions (DWNP, 2013). Consequently, understanding basic movement ecology and spatial requirements of elephants is important when making management and conservation decisions. Accordingly, we recommend: 1) conservation actions should consider terrain with shallow slopes and low elevation; 2) conservation resources and protection should place importance on areas of disturbed habitat and high human pressure; 3) habitat management (e.g. long-term reforestation) is considered in areas of disturbed habitat and high human density to decrease conflict by reducing the abundance of successional plants through promoting large tree species; and 4) maintaining large areas for elephants to fulfil their spatial requirements.

Overall, our results emphasize the value in generating movement data for conserving wide ranging megafauna and other wildlife species. This is particularly so as Asian elephants and other South-east Asian megafauna persist in a region where they face the largest number of threats to their survival (Allan et al., 2019). The conservation of these endangered megafauna will require, among other things, the generation of baseline knowledge, protection of suitable habitat, landscape connectivity, increasing people's tolerance, and protection from poaching.

2.7 *Authors' contributions*

JW and ACA conceived the idea; JW, ACA, NO, and SS collected the data; JW, HB, JS, CF, PL contributed to the methodical design and modelling approach; JW analysed the data; JW and ACA led the writing of the manuscript; all authors contributed critically to the writing.

2.8 *Acknowledgements*

This study is part of the Management & Ecology of Malaysian Elephants (MEME), a joint research project between the Department of Wildlife and National Parks (DWNP) Peninsular Malaysia and the University of Nottingham Malaysia Campus. We are very grateful to DWNP, and especially to Dato' Abdul Rasid Samsudin and Abdul Kadir bin Abu Hashim, DWNP's former and current Director Generals, for the permits to conduct this research and for the continuous support in the field. Field activities were generously financed by grants from Yayasan Sime Darby (grant M0005.54.04), Wildlife Reserves Singapore (grant S0002.54.02), and Marinescape (grant M0004.54.04). DWNP's elephant translocation team and Perak's elephant unit conducted the elephant capturing and sedation; Mohammad Rizal Bin Paimin, Steven Lim, Mei Mei Chu, Aris Mohamad Oziar, Alicia Solana Mena, Param bin Pura, Muhammad Tauhid bin Tunil, Sudin Anak lelaki Din, Rizuan Bin Angah, and many other individuals provided key assistance during elephant collaring and tracking activities. We are thankful to Antino de la Torre for providing useful feedback on the manuscript and the Smithsonian Conservation Biology Institute provided technical support and training to JW. We are grateful to all.

2.9 *Data Accessibility*

The elephant movement data presented in this manuscript are already archived at movebank.org.

2.10 Appendices

2.10.1 Tables

Table A2-1. Individual summary of human footprint values. 'SD' = standard deviation.

id	Mean	SD	Median	Min	Max
1	6.43	4.11	8.00	0.26	15.00
2	3.84	3.85	1.63	0.00	15.00
3	5.81	4.21	7.00	0.00	15.02
4	13.94	3.24	12.27	12.25	20.26
5	13.06	5.68	13.25	5.00	35.00
6	7.01	3.88	8.00	0.25	15.02
7	5.72	4.20	4.01	0.26	15.00
8	5.49	3.73	4.01	0.26	15.00
9	6.21	2.61	5.25	4.25	15.26
10	6.08	3.26	4.53	1.42	19.00
11	8.29	2.58	8.00	1.79	20.13
12	9.52	3.19	9.04	2.43	21.41
13	17.14	5.32	16.00	9.63	35.00
14	6.57	3.59	4.62	3.26	13.11
15	16.21	7.94	14.25	5.00	35.00

Table A2-2. Individual summary of human density. 'Area (km^2)' = total area in square kilometres, which is bounded by the furthest GPS points, 'Total' = total number of humans within an area.

id	Area (km^2)	Total	Density (km^2)
1	153	267	1.75
2	382	675	1.77
3	951	1394	1.47
4	9	309	35.00
5	240	66458	277.34
6	87	160	1.84
7	93	161	1.74
8	95	163	1.73
9	297	28002	94.41
10	388	7433	19.14
11	115	1916	16.72
12	121	3241	26.84
13	62	33451	539.33
14	233	4637	19.90
15	230	67700	293.81

Table A2-3. Results of t-test comparing the number of GPS tracking days, number of locations, and the fix success rate of the GPS telemetry and by elephant sex (male vs. female).

Test	**Sex**	**Mean ± SD**	***t***	**df**	**P**	**Cohen's d [95% CI]**
Tracking days	Male	369 ± 329	0.46	8.89	0.65	-0.25 [-1.44, 0.93]
	Female	457 ± 364				
No. Locations	Male	2,321 ± 1,993	1.23	12.91	0.23	-1.44 [-2.28-0.60]
	Female	4,193 ± 3,887				
Fix Success (%)	Male	53 ± 16	1.89	11.94	0.08	-1.05 [-2.30, 0.20]
	Female	74 ± 25				

Table A2-4. Individual proportions of turning angles (in degrees) as percentage [%] in 30-degree bins. Turning angles ranged from -180 to 180 degrees. Negative turning angle values equated to left sided movements and positive values were right sided movements. The closer the turning angle was to -180 and 180 the more acute the turning angle. ‘M’ = Male, ‘F’ = Female, ‘No. TAs’ = Total number of turning angles.

id	**Sex**	**Landscape**	**No. TAs**	**Degree [-180,-137]**	**Degree [-136,-95]**	**Degree [-94,-60]**	**Degree [-59,-33]**	**Degree [-32,-10]**	**Degree [-9,11]**	**Degree [12, 34]**	**Degree [35,61]**	**Degree [62,96]**	**Degree [97,137]**	**Degree [138,180]**
1	M	Belum	3953	9.6%	10%	9.5%	8.4%	9.1%	9.3%	8.6%	8.8%	9%	8.9%	8.8%
2	M	Belum	1687	10%	9.8%	9.9%	8.6%	9.4%	9%	8.4%	9.2%	8.2%	9.4%	8.1%
3	M	Belum	4303	9.4%	9.2%	8.4%	9.3%	9.2%	9.8%	9.5%	9.3%	7.6%	8.3%	9.9%
4	M	Gua Musang	312	9.3%	9%	8.3%	5.4%	9.3%	8.3%	13.5%	12.2%	8.7%	9%	7.1%
5	F	Siput-Lenggong	3509	8.8%	8.2%	9.3%	9%	9.8%	9.4%	10.4%	8.2%	9.2%	8%	9.6%
6	F	Belum	1904	10.5%	9.1%	9.1%	6.9%	7.6%	10.3%	7.3%	7.9%	10.3%	10.1%	10.9%
7	F	Belum	1123	9.5%	9%	10.5%	10.4%	8.5%	9.7%	8.6%	7.9%	9%	9.8%	6.9%
8	F	Belum	3867	8.9%	9.9%	9.3%	9.5%	9%	8.2%	8.2%	9%	9.1%	9.6%	9.3%
9	F	Temerloh	10189	5.5%	7.2%	9.9%	11.30%	11.1%	11.4%	11.3%	10.9%	9%	6.9%	5.4%
10	F	Belum	7547	9%	9.8%	9.2%	8.9%	8.3%	8.6%	8.7%	9.2%	10.3%	9.2%	8.7%
11	F	Belum	10110	7.9%	8.7%	9.3%	8.9%	9.8%	9.9%	9.5%	9.6%	9.2%	9.1%	8.1%
12	F	Belum	847	7.4%	10.6%	9.8%	9.6%	9.3%	7.2%	11%	8.1%	10.6%	7.9%	8.4%
13	M	Siput-Lenggong	505	8.5%	9.3%	7.3%	11.7%	9.1%	9.1%	8.1%	9.7%	11.9%	7.5%	7.7%
14	F	Siput-Lenggong	731	7.9%	10.5%	10.1%	10.1%	8.5%	9.2%	10.7%	8.3%	8.3%	8.2%	8.1%
15	F	Siput-Lenggong	682	10.4%	8.2%	7.9%	8.8%	9.8%	8.1%	7%	10.3%	10.9%	9.2%	9.4%

Table A2-5. Results of the hierarchical Bayesian fixed-effect one-way ANOVAs for home range and movements by sex. ‘Normality’ = normality of residuals (Shapiro-Wilk test, <0.05 = non-normally distributed). ‘Transform’ is the data transform technique used on non-normally distributed variables. ‘Normailty1’ = normality of residuals after data transformation. ‘Probability’ = probability that males were greater than females (bounded from 0 to 1), values closer to one denote higher probability. ‘Mod.Fit’ refers to how well the Bayesian simulated dataset is greater than the actual data. Values close to 0.50 indicate a good fit (i.e., no difference between the simulated and actual datasets). ‘Mn.Cr’, ‘Lw.Cr’, ‘Up.Cr’ refers to the mean, lower and upper credible intervals for the estimated posterior density (2.5 – 97.5% quantiles).

Variable	Sex	Normality	Transform	Normailty1	Probability	Mod.Fit	Mn.Cr	Lw.Cr	Up.Cr
Home Range	male	0.25	NA	NA	0.97	0.512	295	209	381
	female						194	133	254
HR.Overlap	male	0.01	sqrt	0.32	0.93	0.500	7.91	5.26	10.60
	female						5.70	4.44	6.96
HR.Xing	male	0.02	log	0.05	0.66	0.491	2.11	0.91	3.29
	female						1.82	0.97	2.66
Daily Distance	male	0.54	NA	NA	0.43	0.502	4.97	3.76	6.21
	female						5.10	4.21	5.98
Path Tortuosity	male	0.005	square	0.33	0.97	0.523	1797	1710	1883
	female						1690	1629	1752

2.10.2 Figures

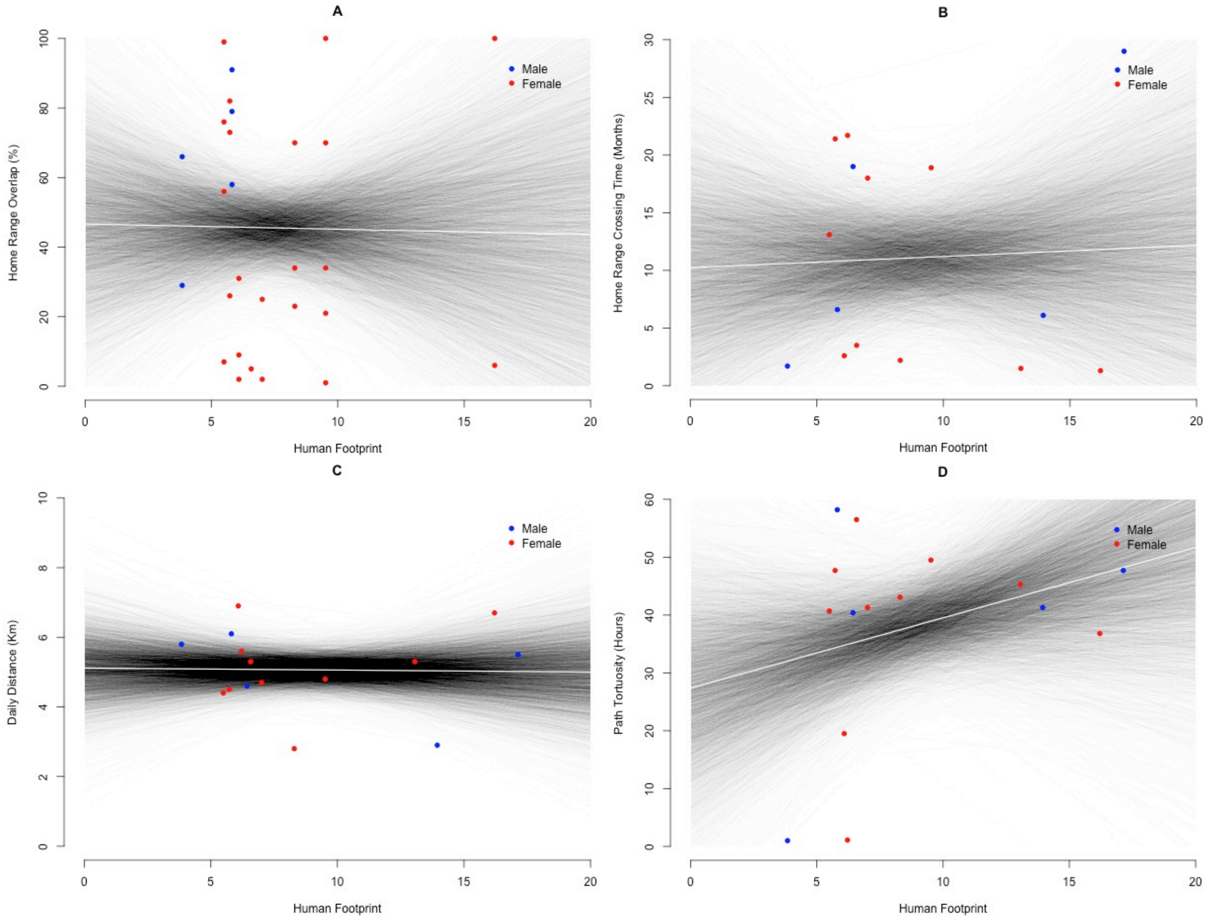


Figure A2-1. Elephants' home range overlap (%) [A], home range crossing time (months) [B], daily distance (km) [C], Path Tortuosity (hours) [D] estimates in relation to human footprint. Regression line is the species estimate from a linear regression model formulated in a Bayesian framework. Error lines are 95% CI. Bayesian p-value = 0.498 [A], 0.492 [B], 0.504 [C], and 0.507 [D], closer the value is to 0.5 the better the fit (bounded by 0-1).

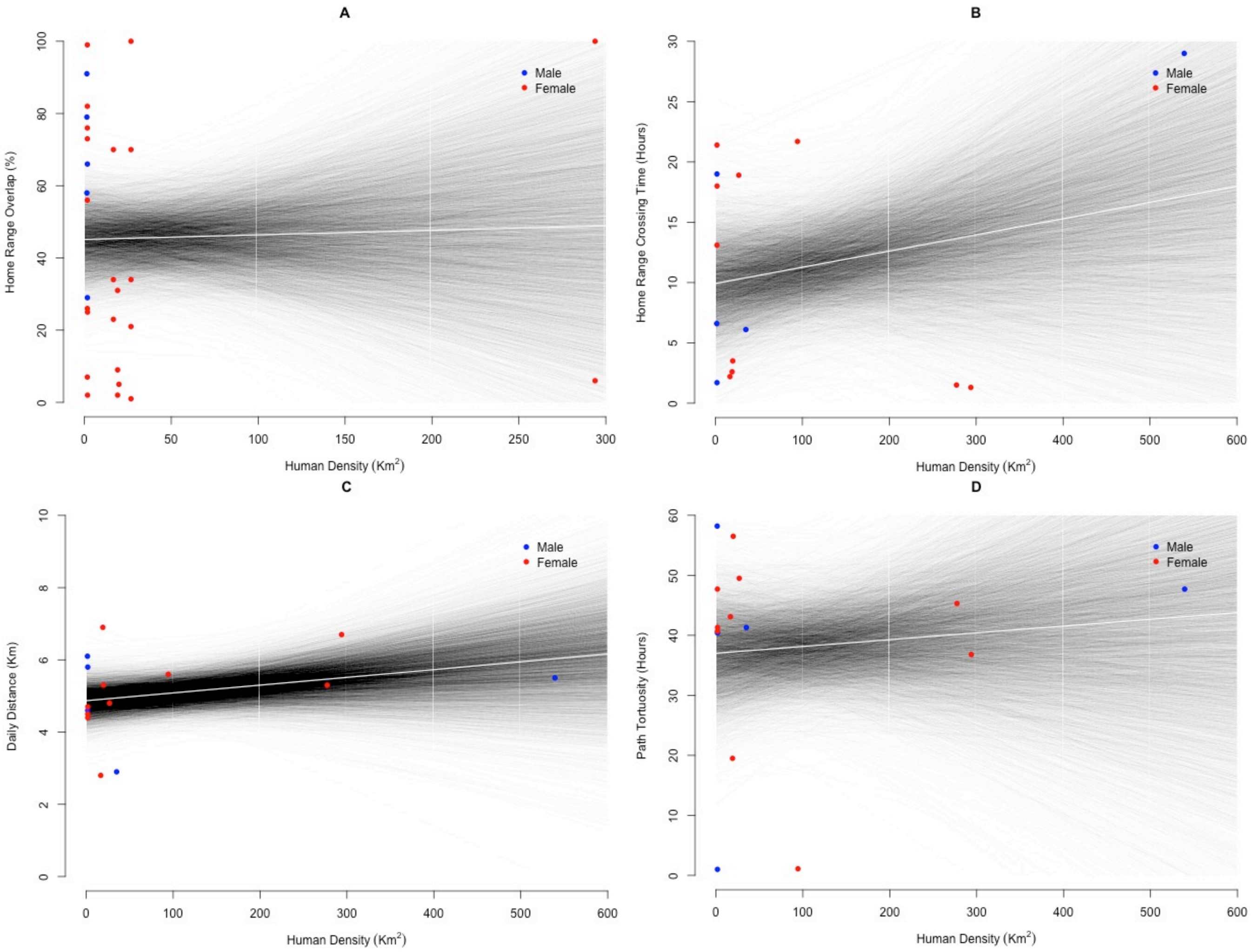


Figure A2-2. Elephants' home range overlap (%) [A], home range crossing time (months) [B], daily distance (km) [C], Path Tortuosity (hours) [D] estimates in relation to human density (km^2). Regression line is the species estimate from a linear regression model formulated in a Bayesian framework. Error lines are 95% CI. Bayesian p-value = 0.513 [A], 0.516 [B], 0.502 [C], and 0.501 [D], closer the value is to 0.5 the better the fit (bounded by 0-1).

2.10.3 Habitat selection analysis

2.10.3.1 Abstract

Understanding how environmental variables impact fine scale choices can provide valuable insights into a species movement ecology. We used GPS telemetry to study the movements of 15 wild Asian elephants (*Elephas maximus*) and a mechanistic modelling framework to estimate fine scale habitat selection throughout tropical rainforests in Peninsular Malaysia. Our objective were to quantify the effects of environmental variables on forest elephant movement behaviour using a mechanistic modelling framework that includes both habitat preference and movement rates. We found elephants avoided steep slopes and high elevation areas. Furthermore, elephants were found to be attracted to disturbed habitat (regrowth forest) and chose not to venture far from roads or forest, whilst showing no preference to proximity to water. Given the rates of deforestation, human population growth and poaching throughout all elephant range states, understanding fine scale movement decisions can play an important role in future conservation decisions. Our results are relevant for landscapes throughout Asian and Africa, where researchers want to inform conservation and policy by increasing their knowledge about elephant movement ecology.

2.10.3.2 Introduction

Animals are consistently making trade-offs in time and space as the distributions of food, water, mates, predators are in a consistent state of change. Estimating habitat selection can reveal how animals are balancing these trade-offs throughout their home range. For example, elephants are known to avoid steep slopes and mountainous areas due to the exponential increase in energy expenditure required for heavy animals (Wall, Douglas-Hamilton, & Vollrath, 2006). Additionally, elephants in tropical Asia have displayed habitat preference towards disturbed or human-made habitats, which support consistent and high abundances of food over relatively small areas (Terborgh et al., 2018; Wadey et al., 2018; Williams et al., 2008; Yamamoto-Ebina et al., 2016). Human presence has modified elephant behaviour and in turn the habitat selected, where elephants have been reported to occupy forested areas during the day as refuges when preferred feeding areas (e.g. agricultural crops) have high human presence, and foraging at night in such areas when human presence is low (Sukumar & Gadgil, 1988). In Borneo, permanent water sources have been suggested to influence habitat selection of elephants due to the limited suitable forest habitat and availability of water, which has resulted in a disproportionate use of habitat and movement throughout the landscape (Alfred et al., 2012).

Little is understood about the impacts of environmental variables on elephant movements in Peninsular Malaysia. Here, we investigate and quantify how wild Asian elephants make fine scale decisions throughout tropical rainforests. We used GPS telemetry data from forest elephants to quantify the effects of environmental variables on forest elephant movement behaviour using a mechanistic modelling framework that accounts for habitat preference and movement rates. Our research is aligned with the objectives of

Malaysia's CFS and NECAP policies, which can inform management recommendations to reduce the impacts on elephants and other large mammals in Asia and Africa.

2.10.3.3 Methods

Habitat selection was modelled individually for each elephant (Beyer et al., 2014), which defines a probability of a "step" between sequential telemetry locations a to location b, and which is conditional on habitat covariates, *X*, at location *b*, to be:

$$f(b|a,X) = \frac{\phi(a,b;\theta)\omega(X_b;\beta)}{\int_{c\in D}\phi(a,b;\theta)\omega(X_c;\beta)dc}\,(equation\ 1)$$

where ϕ (a, b; θ) is a probability density function describing the probability of displacement to location b from location a, $\omega(X)$ is the resource selection probability function, and *X* is a matrix of habitat covariates (sometimes referred to as the displacement kernel or habitat independent movement kernel). Here, ϕ (a, b; θ) is a bivariate normal distribution with equal variance in the x and y dimensions determined by the parametre θ, and ω is a logistic model with coefficients β representing the habitat preferences (Beyer et al., 2014; Raynor, Beyer, Briggs, & Joern, 2016).

Habitat covariates included: slope (degrees); elevation (metres); human footprint (km^2); human density ($number/km^2$); distance to natural and man-made features – forest (primary and secondary), mosaic (mixture of natural and planted vegetation), open areas (clearances and other open areas), plantation, regrowth (areas that have been recently logged or used for agricultural purposes and forest that has regenerated naturally), roads (km), roads squared (km^2; size of roadless area, e.g. smaller values indicate a smaller total area without roads, while larger values denote larger areas without roads), and water (km). We included slope and elevation because elephants are known to avoid steep slopes and alter movements along different elevation gradients (Bohrer, Beck, Ngene, Skidmore, & Douglas-Hamilton, 2014; Wall et al., 2006). Human density and human footprint were included because they are known to decrease habitat quality and increase extinction risk and may therefore influence habitat selection (Di Marco et al., 2018; Liu et al., 1999). We used distance to natural and man-made features because these covariates reflect different types of habitat fragmentation, which are known to affect home range and movement rates (Alfred et al., 2010). We included distance to roads because a previous study in Peninsular Malaysia found roads to simultaneously act as both a barrier and an attractant to elephants (Wadey et al., 2018). We included distance to roads squared because roadless areas were found to be a strong determinant of home range size in Congo forest elephants (Blake et al., 2008). Distance to water was included as it is a key covariate that is known to restrict elephant movement and influence ranging behaviour (Alfred et al., 2010; Polansky et al., 2015). All covariates were raster format data sets with a spatial resolution of 100 × 100 m (see Data Source A2-1; Data Source A2-2; Data Source A2-3). The land use covariates (e.g. distance to water) spatial resolution was originally at 250 meters, we rescaled all land use covariates to 100 meters. All covariates were evaluated for each individual elephant but excluded if they were either highly correlated with the previous covariates, or were not present in the landscape, and/or because there was no variability within the covariate for an animal. For example, if an elephant remained in the forest then the distance to forest covariate would only consist of zero values and thus be meaningless to model.

The habitat selection model was as follows:

$$logit\big(\omega(Xb;\beta)\big) = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \beta_4 X_4 + \beta_5 X_5 + \beta_6 X_6 + \beta_7 X_7 + \beta_8 X_8 + \beta_9 X_9 + \beta_{10} X_{10} + \beta_{11} X_{11} + \beta_{12} X_{12} \ (equation\ 2)$$

Each step was paired with 100 random steps in a case-controlled “step selection function” design (Fortin et al., 2005). We modelled habitat preference by fitting equation 1 to the location data (Beyer et al., 2014). Habitat reference models were fitted using the maximum likelihood algorithm and confidence intervals for the parametre estimates were calculated from the Hessian matrix (±1.96 times the square roots of the diagonal elements of the covariance matrix).

2.10.3.4 Results

Most elephants showed a preference for gentle slopes with 11 of 15 elephants exhibiting negative coefficients and confidence intervals that did not overlap zero, while another three showed no significant preference for slope (confidence intervals were overlapping; Figure A2-3; Table A2-6; Table A2-7). One elephant (id = 2) had a positive selection for slope, despite roaming in an area with shallow slopes (median = 11.2° and interquartile range (IQR) = 6.5 – 15.9°; Table A2-8). Elephant slope selection ranged from 0 – 43°, with an average of 11° ± 3° and an IQR of 6 - 15° (Table A2-8; Table A2-9; Table A2-10).

We found the majority of elephants selected for lower elevation with 7 of 15 elephants producing negative confidence intervals that did not overlap zero, while five showed no significant preference (Figure A2-3; Table A2-6). Three elephants (id = 2, 10, 14) showed positive selection for elevation, and two of these elephants (id = 2, 14) selected greater elevation despite roaming in areas of low elevation (median = 323 m and 167 m and IQR = 277 – 383 m and 125 – 267 m; Table A2-8; Table A2-9; Table A2-10), while the third positive selection (id = 10) is an artefact of residing in an higher elevation area (median = 737 m and IQR = 657 – 848 m; Table A2-9). The minimum and maximum elevation for all elephants was 48 and 1,324 m respectively, with an average of 377 ± 166 m and IQR of 267 – 461 m (Table A2-8; Table A2-9; Table A2-10).

Sample sizes for human density (n = 5) were reduced because there was no variability in human density for 10 elephants (see methods section for more details of covariate exclusion) and therefore limited deeper inferences about selection. For the five elephants that were included, three displayed preference for lower human densities (negative selection), one elephant showed no preference and one showed a preference for greater human density (positive selection; Figure A2-3; Table A2-6). The average human density for elephants was 93 ± 166 humans per km^2 with an IQR of 16 – 320 humans per km^2 and range of 1 – 900 humans per km^2 (Table A2-8; Table A2-9; Table A2-10). Selection for human footprint was not conclusive, with three elephants displaying negative selection and another three with no selection, while two elephants displayed positive selection (Figure A2-3; Table A2-6). The average human footprint (as an index of human pressure, see methods for more details) was 8 ± 4 with an IQR of 6 – 10 (Table A2-8; Table A2-9; Table A2-10) and ranged 0 – 33. Seven elephants were removed from using human footprint as a variable for habitat selection due to being highly correlated with human density (see methods section for details).

Regardless of selection preference, we found that all elephants remained close to the forest edge with an average distance from forest of 1 ± 2 km, an IQR of 0.5 – 3 km and range of 0 – 14 km (Table A2-8; Table A2-9; Table A2-10). Elephants which produced a positive selection (5 out of 11 elephants) took more steps away from the forest edge before returning with fewer steps, while elephants that produced negative selection (3 out of 11 elephants) took fewer steps away from the forest edge but more steps when returning back to the forest (Figure A2-3). We excluded elephants (3 out of 11) due to individuals not leaving forested areas. Again, irrespective of selection, elephants remained relatively close to areas with a mosaic of vegetation, with an average distance of 3 ± 2 km, an IQR of 1 – 4 km and a range of 0 – 24 km (Figure A2-3; Table A2-8; Table A2-9; Table A2-10). We found four elephants with negative selection, three with positive selection and one with no selection from a total of eight elephants with regard to distance to mosaic (only eight elephants contained mosaic vegetation in their home range). The majority of elephants (6 out of 10; only ten elephants contained open vegetation in their home range) showed no preference for open vegetation (no selection). However, there were some elephants (3 out of 10) that were attracted towards open areas, while 2 out of 10 preferred areas away from open vegetation (positive selection; Figure A2-3). We found elephants to be on average 3 ± 2 km from open vegetation with an IQR of 1 – 4 km and a range of 0 – 26 km (Figure A2-3; Table A2-8; Table A2-9; Table A2-10).

Elephants either moved towards or away from plantations, with 5 out of 10 producing negative selection and 4 out of 10 showing positive selection (only ten elephants contained plantations in their home range). On average, elephants tended to avoid plantations which was evident by an average distance of 10 ± 8 km (IQR of 8 – 12 km; ranged 0 – 46 km; Figure A2-3; Table A2-8; Table A2-9; Table A2-10). We found elephants displaying a clear preference for regrowth vegetation, with 10 out of 14 displaying negative coefficients, while the other four elephants (two displaying positive selection and the other two showing no selection) were always in close proximity to regrowth vegetation with median distance values of 500, 180, 980 and 210 metres (Figure A2-3; Table A2-6; Table A2-7; Table A2-8; Table A2-9; Table A2-10). The average distance from regrowth for all elephants was 1 ± 2 km with an IQR of 0.5 – 3 km and a range of 0 – 14 km (Table A2-8; Table A2-9; Table A2-10).

We found elephants interacting with roads in a complex way. On the one hand, the majority of elephants showed no preference for roads (9 out of 15 elephants). On the other hand, all elephants were found to be in close proximity to a road (average of 2 ± 1 km; IQR of 0.5 – 3 km; range 0 – 23 km; Table A2-8; Table A2-9; Table A2-10). The two elephants (id = 8 and 10) that did display a positive preference (selection to move away from road), were also found in close proximity to a road, with median distance values of 220 m and 1.7 km (Figure A2-3; Table A2-6). Selection for roadless areas (distance to roads in squared kilometres) was not conclusive, with equal numbers of elephants selecting for smaller roadless areas (negative selection; 4 out of 14) and larger roadless areas (positive selection; 4 out of 14; Figure A2-3; reduction of one elephant was due to low variability in distance to roads squared values). Despite differences in selection, there was high variability within each type, with the average roadless area for negative selection being 15 ± 16 km^2 (IQR = 1 – 15 km^2) and for positive selection being 17 ± 25 km^2 (IQR = 0 – 18 km^2). Overall, we found the average size of a roadless area to be 13 ± 6 km^2, IQR of 2 – 15 km^2 with a range of 0 – 513 km^2 (Table A2-8; Table A2-9; Table A2-10).

Elephants were not attracted to large bodies of water (e.g. lakes and rivers), with eight out of nine elephants either showing no preference or lacking movements towards water (selection either being none or positive; Figure A2-3; Table A2-6), while only one elephant showed a preference to be close to water (negative selection). The minimum and maximum distance to water for all elephants was 0 – 24 km, with an average of 4 ± 2 km and IQR of 2 – 5 km (Table A2-8; Table A2-9; Table A2-10). Six elephants were removed from using distance to water as a variable for habitat selection due to the lack of large bodies of water within their home ranges.

2.10.3.5 Discussion

Our habitat selection results show that elephants avoided areas with steep slopes and high elevation. They also showed a preference for disturbed habitat (regrowth forest) and did not venture far from roads and forests, whilst showing no preference for proximity to water. Our slope preferences are in line with a previous study which found elephants to avoid steep slopes due to the exponential increase in energy cost (Wall et al., 2006). Energetic costs are likely to be the main reason our elephants avoid steep areas; other factors may be risk of injury, overheating, and the lack of water and food that is commonly associated with steep slopes.

Elevation does not always deter elephants - a study in Kenya found elephants to move between elevations of 650 and 1,100 m in search of new vegetation after rainfall (Bohrer et al., 2014). Asian elephants in the eastern Himalayas are known to reach elevations of 3,000 metres during the summer to visit important mineral licks (Choudhury, 1999). In Peninsular Malaysia, we suspect food to be less abundant in high elevation areas, which is probably the result of a more intact canopy cover preventing light penetration for preferred foods to grow, i.e., grasses and early successional plants. Therefore, in our study, we suggest elephants are likely to be choosing shallower slopes and lower elevation areas because of the energetic cost associated with steep slopes and the small abundance of food found in higher elevation areas.

We disregarded water as an influencing factor because water is available all year round and in water-rich plants, which is supported by our habitat selection results showing only 1 out of 15 elephants having a preference to proximity to water. The lack of preference to proximity to water for elephants is uncommon in the literature as majority of studies have found elephant movement decisions to be largely influenced by water (Garstang et al., 2014;

Loarie et al., 2009; Ndaimani, Murwira, Masocha, & Zengeya, 2018; Polansky et al., 2015; Wato et al., 2018). However, majority of these studies are from Africa where water is seasonal and not plentiful across the landscape as it is in Peninsular Malaysia. A caveat in our habitat selection analyses is that we used one single land use image from 2010 to describe our distance rasters, which means that our model are missing some details about the effect of logging or deforestation during our study period.

Based on previous forest elephant studies in Africa (Blake et al., 2008; Granados et al., 2012), we expected elephants to generally avoid roads. However, our habitat preference results suggest elephants were attracted to areas adjacent to roads. Two recent studies in Peninsular Malaysia found elephants were attracted to the roadside because of the availability of grasses and other early successional plants that are commonly associated with roadside vegetation (Wadey et al., 2018; Yamamoto-Ebina et al., 2016). It is likely that the elephants in our study were attracted to roadside areas for this preferred food. Interestingly, one elephant (id = 3; Table 2-1) did leave the roadside and settled in Thailand, only after being involved in a vehicle collision. These recent results complement our findings of elephants showing a preference for disturbed habitats while not venturing far from forest edges. Elephants are likely employing risk avoidance strategies by using forest edges as refuges when human activity is high and then venturing into disturbed habitat where food is abundant and to forage when human activity is low. Risk avoidance in African elephants has been suggested as a strategy to avoid areas of higher poaching pressure (Blake et al., 2008; Granados et al., 2012), while in Asia risk avoidance is the suggested reason as to why crop-raiding and road-crossings are preferentially done at night when human activity is low (Sukumar & Gadgil, 1988; Vidya & Thuppil, 2010; Wadey et al., 2018). We expected elephants to be attracted to open areas as they contain grasses and successional plants, however, we did not find any evidence to support this. This may be due to the lack of larger vegetation cover, e.g., trees and bushes to conceal elephants when they forage in high risk areas.

2.10.3.6 Data sources

Data Source A2-1. Elevation and slope.

Downloaded from Earth-Explorer (https://earthexplorer.usgs.gov):

Landsat 8 program 2013, Level 1 Operational Land Imager (OLI) and Thermal Infrared Sensor (TIRS). NASA EOSDIS Land Processes DAAC, USGS Earth Resources Observation and Science (EROS) Center, Sioux Falls, South Dakota (https://lpdaac.usgs.gov), accessed July 1, 2015. Pixel size at 100 meters.

Data Source A2-2. Land use.

Distance to: forest, mosaic, open, plantation, regrowth, water were created from the open source map (Miettinen, Shi, & Liew, 2016) and downloaded from Online Research Mapping Tool (ORMT; https://ormt-crisp.nus.edu.sg/ormt/Home/Disclaimer), accessed December 28, 2016. Pixel size at 250 meters and rescaled to 100 meters

Data Source A2-3. Roads.

Distance to roads layer was created from the OpenStreetMaps database: K. Curran, J. Crumlish, and G. Fisher. OpenStreetMap. *International Journal of Interactive Communication Systems and Technologies*, 2(1):69–78, 2012. ISSN 2155-4218. Downloaded from: https://www.openstreetmap.org/search?query=peninsular%20malaysia, accessed December 15, 2016. Pixel size is less than 10 meters.

2.10.3.7 Figures

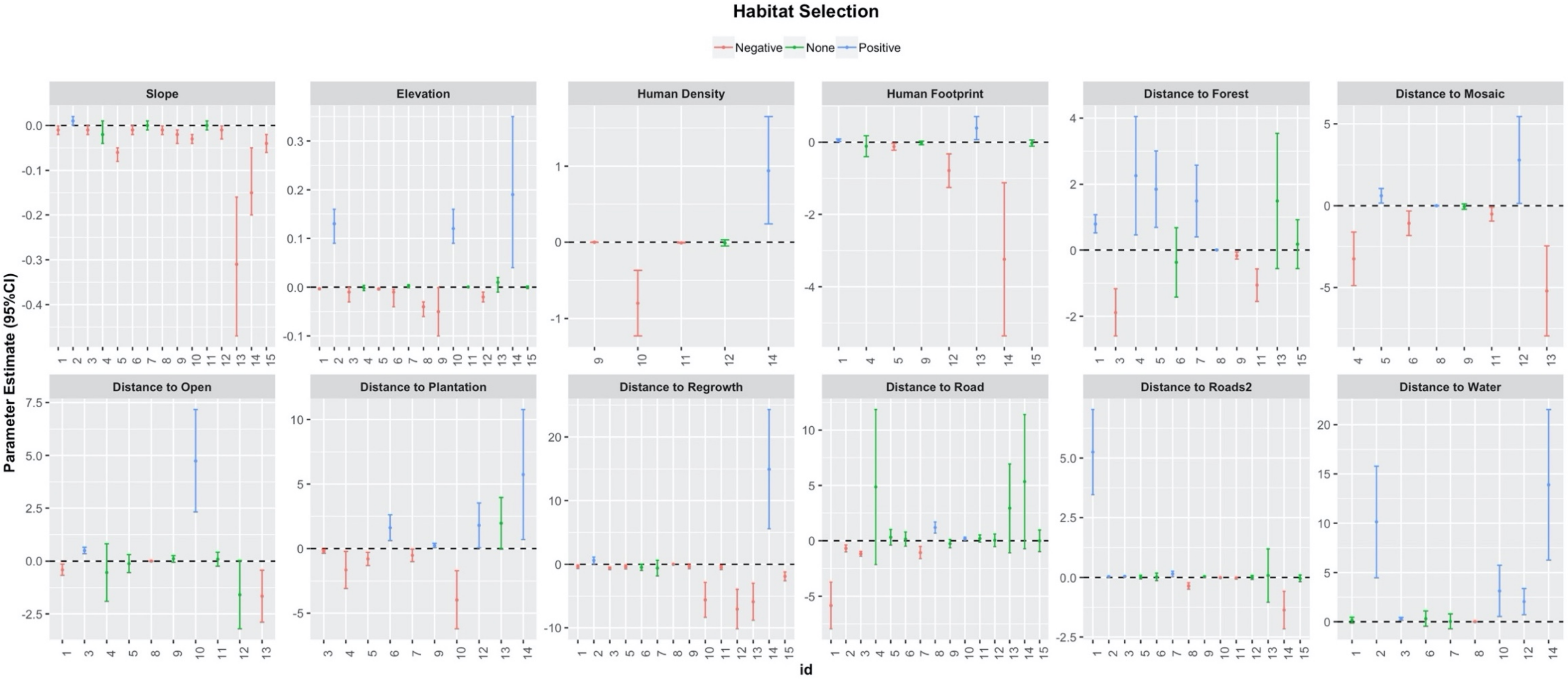


Figure A2-3. Habitat selection estimates among all elephants with mean (circle), 95% confident intervals (lines). No selection occurs when confident intervals overlap zero (dashed line). Points that are red indicates a negative selection with the variable, blue are positive with the variable, and green are not different from random.

2.10.3.8 Tables

Table A2-6. Maximum likelihood parametre estimates and 95% confidence intervals for 15 individual radio-collared Asian elephants (*Elephas maximus*). The parametres represent the habitat preference for slope (β1), elevation (β2), human density (β3), human footprint (β4), distance to forest (β5), and distance to mosaic (β6).

id	β1	β2	β3	β4	β5	β6
1	-0.01 (-0.02,-0.00)	-0.00 (-0.00, -0.00)	NA (NA, NA)	0.05 (0.02, 0.09)	0.79 (0.52, 1.07)	NA (NA, NA)
2	0.01 (0.00, 0.02)	0.13 (0.09, 0.16)	NA (NA, NA)	NA (NA, NA)	NA (NA, NA)	NA (NA, NA)
3	-0.01 (-0.02, -0.00)	-0.01 (-0.03, -0.00)	NA (NA, NA)	NA (NA, NA)	-1.89 (-2.60, -1.17)	NA (NA, NA)
4	-0.02 (-0.04, 0.01)	0.00 (-0.01, 0.00)	NA (NA, NA)	-0.11 (-0.40, 0.18)	2.26 (0.46, 4.05)	-3.25 (-4.88, -1.62)
5	-0.06 (-0.08, -0.05)	-0.00 (-0.01, -0.00)	NA (NA, NA)	-0.12 (-0.22, -0.03)	1.85 (0.69, 3.01)	0.61 (0.16, 1.06)
6	-0.01 (-0.02, -0.00)	-0.01 (-0.04, -0.00)	NA (NA, NA)	NA (NA, NA)	-0.37 (-1.42, 0.68)	-1.08 (-1.83, -0.32)
7	0.00 (-0.01, 0.01)	0.00 (-0.00, 0.01)	NA (NA, NA)	NA (NA, NA)	1.49 (0.40, 2.58)	NA (NA, NA)
8	-0.01 (-0.02, -0.00)	-0.04 (-0.06, -0.03)	NA (NA, NA)	NA (NA, NA)	0.00 (0.00, 0.00)	0.00 (0.00, 0.00)
9	-0.02 (-0.04, -0.01)	-0.05 (-0.10, -0.00)	-0.00 (-0.00, -0.00)	-0.02 (-0.07, 0.03)	-0.17 (-0.27, -0.06)	-0.05 (-0.21, 0.11)
10	-0.03 (-0.04, -0.02)	0.12 (0.09, 0.16)	-0.80 (-1.23, -0.37)	NA (NA, NA)	NA (NA, NA)	NA (NA, NA)
11	0.00 (-0.01, 0.01)	0.00 (-0.00, 0.01)	-0.01 (-0.01, -0.00)	NA (NA, NA)	-1.06 (-1.55, -0.57)	-0.52 (-0.95, -0.09)
12	-0.01 (-0.03, -0.00)	-0.02 (-0.03, -0.01)	-0.01 (-0.05, 0.03)	-0.78 (-1.25, -0.32)	NA (NA, NA)	2.79 (0.14, 5.45)
13	-0.31 (-0.47, -0.16)	0.01 (-0.01, 0.02)	NA (NA, NA)	0.39 (0.07, 0.71)	1.49 (-0.56, 3.54)	-5.21 (-7.96, -2.46)
14	-0.15 (-0.05, -0.20)	0.19 (0.04, 0.35)	0.94 (0.24, 1.65)	-3.24 (-5.36, -1.12)	NA (NA, NA)	NA (NA, NA)
15	-0.04 (-0.06, -0.02)	0.00 (-0.01, 0.02)	NA (NA, NA)	-0.03 (-0.11, 0.06)	0.18 (-0.56, 0.92)	NA (NA, NA)

Table A2-7. Maximum likelihood parametre estimates and 95% confidence intervals for 15 individual radio-collared Asian elephants (*Elephas maximus*). The parametres represent the habitat preference for distance to open (β7), distance to plantation (β8), distance to regrowth (β9), distance to road (β10; β11 quadratic), and distance to water (β12).

id	**β7**	**β8**	**β9**	**β10**	**β11**	**β12**
1	-0.41 (-0.67, -0.14)	NA (NA, NA)	-0.39 (-0.66, -0.11)	-5.84 (-7.96, -3.73)	5.25 (3.46, 7.03)	0.16 (-0.14, 0.46)
2	NA (NA, NA)	NA (NA, NA)	0.61 (0.08, 1.13)	-0.69 (-1.00, -0.38)	0.03 (0.01, 0.05)	10.13 (4.47, 15.80)
3	0.50 (0.35, 0.65)	-0.22 (-0.36, -0.08)	-0.65 (-0.84, -0.46)	-1.18 (-1.39, -0.97)	0.04 (0.03, 0.05)	0.29 (0.14, 0.44)
4	-0.54 (-1.90, 0.82)	-1.65 (-3.08, -0.22)	NA (NA, NA)	4.86 (-2.14, 11.85)	NA (NA, NA)	NA (NA, NA)
5	-0.12 (-0.54, 0.31)	-0.80 (-1.31, -0.29)	-0.42 (-0.73, -0.11)	0.31 (-0.39, 1.01)	0.01 (-0.06, 0.09)	NA (NA, NA)
6	NA (NA, NA)	1.61 (0.62, 2.61)	-0.48 (-0.95, 0.00)	0.15 (-0.49, 0.79)	0.02 (-0.13, 0.18)	0.31 (-0.47, 1.09)
7	NA (NA, NA)	-0.52 (-1.00, -0.04)	-0.60 (-1.82, 0.63)	-1.07 (-1.61, -0.52)	0.15 (0.03, 0.26)	0.03 (-0.73, 0.79)
8	-0.00 (-0.00, -0.00)	NA (NA, NA)	-0.00 (-0.00, -0.00)	1.19 (0.69, 1.69)	-0.36 (-0.49, -0.22)	-0.00 (-0.00, -0.00)
9	0.11 (-0.05, 0.26)	0.24 (0.07, 0.41)	-0.39 (-0.69, -0.09)	-0.26 (-0.63, 0.11)	0.03 (-0.00, 0.06)	NA (NA, NA)
10	4.74 (2.32, 7.17)	-3.97 (-6.22, -1.71)	-5.58 (-8.32, -2.84)	0.19 (0.05, 0.32)	-0.01 (-0.02,-0.00)	3.13 (0.53, 5.74)
11	0.09 (-0.24, 0.42)	NA (NA, NA)	-0.53 (-0.83, -0.22)	0.20 (-0.12, 0.52)	-0.03 (-0.07, -0.01)	NA (NA, NA)
12	-1.59 (-3.21, 0.03)	1.80 (0.06, 3.53)	-7.05 (-10.16, -3.93)	0.04 (-0.53, 0.61)	0.00 (-0.08, 0.08)	2.05 (0.71, 3.38)
13	-1.66 (-2.89, -0.43)	1.96 (-0.04, 3.95)	-5.88 (-8.79, -2.97)	2.93 (-1.08, 6.94)	0.08 (-1.04, 1.19)	NA (NA, NA)
14	NA (NA, NA)	5.73 (0.70, 10.77)	14.93 (5.56, 24.31)	5.34 (-0.72, 11.40)	-1.37 (-2.16, -0.58)	13.90 (6.26, 21.54)
15	NA (NA, NA)	NA (NA, NA)	-1.89 (-2.57, -1.20)	-0.01 (-0.98, 0.96)	-0.04 (-0.17, 0.10)	NA (NA, NA)

Table A2-8. Summary of the covariate habitat use. ‘min’ = minimum, ‘q1’ = first quantile, ‘med’ = median, ‘q3’ = third quantile, Slope is in degrees, ‘Elev’ = elevation [m], ‘HD’ = human density [km^2], ‘HFP’ = human footprint, ‘DF’ = distance to forest [km], ‘DM’ = distance to mosaic [km], ‘DO’ = distance to open [km], ‘DP’ = distance to plantation [km], ‘DR’ = distance to regrowth [km], ‘DRD’ = distance to roads [km], ‘DRD2’ = distance to roads [km^2], ‘DW’ = distance to water [km].

id	**Summary**	**Slope**	**Elev**	**HD**	**HFP**	**DF**	**DM**	**DO**	**DP**	**DR**	**DRD**	**DRD2**	**DW**
1	min	0.00	237.00	1.75	0.26	0.00	0.00	0.00	15.39	0.00	0.00	0.00	0.00
1	q1	6.57	281.00	1.75	5.24	0.08	0.83	0.26	21.37	0.08	0.10	0.01	0.22
1	med	11.12	316.00	1.75	6.95	0.30	1.53	0.96	22.52	0.36	0.22	0.05	0.73
1	mean	11.78	350.17	1.75	6.70	0.32	2.27	1.64	22.81	0.56	0.55	0.95	1.34
1	q3	15.99	371.00	1.75	8.11	0.51	3.36	2.78	24.08	0.70	0.70	0.49	1.81
1	max	37.05	922.00	1.75	14.78	1.23	7.63	6.74	31.13	5.33	5.66	32.08	7.42
2	min	0.00	231.00	1.75	0.00	0.00	0.00	0.00	16.07	0.00	0.00	0.00	0.00
2	q1	6.94	278.00	1.75	0.83	0.00	1.06	0.52	19.94	0.22	0.14	0.02	0.18
2	med	11.20	313.00	1.75	3.71	0.18	2.64	1.92	22.03	0.50	0.54	0.29	0.54
2	mean	11.75	350.43	1.75	3.99	0.26	3.75	2.94	21.77	2.11	2.19	13.34	1.02
2	q3	15.74	377.75	1.75	6.81	0.45	6.40	5.30	22.69	4.17	3.76	14.17	1.09
2	max	36.60	1053.00	1.75	13.45	1.23	11.58	11.04	36.98	10.67	13.45	181.00	11.53
3	min	0.23	186.00	1.04	0.00	0.00	0.00	0.02	2.36	0.00	0.00	0.00	0.00
3	q1	8.62	347.00	1.75	1.40	0.00	4.26	5.46	8.74	0.38	0.10	0.01	0.97
3	med	13.72	436.00	1.75	5.41	0.00	7.84	8.20	12.16	2.36	0.81	0.65	3.50
3	mean	13.97	457.18	1.90	5.19	0.07	7.79	8.66	15.08	4.35	4.25	54.02	4.60
3	q3	18.48	549.00	1.75	7.81	0.06	10.58	10.80	16.28	7.47	7.38	54.44	6.94
3	max	38.63	1041.00	73.33	13.67	0.89	23.62	26.14	46.19	19.70	22.66	513.46	23.75
4	min	0.52	74.00	NA	12.25	5.14	0.00	0.14	2.42	0.00	1.75	3.06	NA
4	q1	4.51	109.00	NA	12.27	6.26	0.02	0.54	3.63	0.00	2.34	5.48	NA
4	med	8.31	131.00	NA	12.28	6.96	0.24	0.82	4.39	0.03	2.77	7.65	NA
4	mean	9.48	157.24	NA	13.42	6.79	0.32	1.01	4.28	0.12	2.77	7.95	NA
4	q3	13.09	153.00	NA	13.79	7.29	0.53	1.48	4.85	0.23	3.20	10.24	NA
4	max	30.95	451.00	NA	20.26	7.92	1.22	2.43	5.74	0.43	3.79	14.40	NA
5	min	0.10	84.00	50.70	5.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	NA
5	q1	5.89	157.00	50.70	8.25	0.00	1.33	2.75	1.76	0.00	1.14	1.30	NA
5	med	9.64	296.00	50.70	12.38	0.17	2.61	4.03	2.77	0.12	2.02	4.10	NA
5	mean	11.00	417.35	233.66	12.10	0.41	4.26	5.01	4.75	0.80	2.65	11.04	NA
5	q3	15.08	647.50	50.70	15.03	0.58	7.62	7.66	7.50	1.07	3.48	12.12	NA
5	max	36.43	1260.00	899.72	32.98	2.96	10.25	10.39	13.99	4.64	8.32	69.21	NA

Table A2-9. Summary of the covariate habitat use. ‘min’ = minimum, ‘q1’ = first quantile, ‘med’ = median, ‘q3’ = third quantile, Slope is in degrees, ‘Elev’ = elevation [m], ‘HD’ = human density [km^2], ‘HFP’ = human footprint, ‘DF’ = distance to forest [km], ‘DM’ = distance to mosaic [km], ‘DO’ = distance to open [km], ‘DP’ = distance to plantation [km], ‘DR’ = distance to regrowth [km], ‘DRD’ = distance to roads [km], ‘DRD2’ = distance to roads [km^2], ‘DW’ = distance to water [km].

id	**Summary**	**Slope**	**Elev**	**HD**	**HFP**	**DF**	**DM**	**DO**	**DP**	**DR**	**DRD**	**DRD2**	**DW**
6	min	0.37	224.00	1.75	0.25	0.00	0.00	0.02	2.62	0.00	0.00	0.00	0.03
6	q1	8.95	420.00	1.75	2.85	0.00	0.82	1.73	5.03	0.13	0.28	0.08	4.05
6	med	13.54	480.00	1.75	6.74	0.00	2.97	4.50	7.13	0.98	1.00	1.01	5.55
6	mean	13.48	494.55	1.82	5.94	0.10	3.34	4.59	7.45	1.47	1.39	4.01	5.25
6	q3	17.45	576.00	1.75	8.41	0.17	5.03	6.49	9.20	2.33	2.00	4.00	6.71
6	max	35.25	796.00	58.91	12.81	0.83	11.20	12.62	14.91	7.77	7.08	50.18	9.11
7	min	0.23	237.00	1.75	0.27	0.00	0.00	0.00	16.97	0.00	0.00	0.00	0.00
7	q1	8.39	347.00	1.75	4.82	0.13	1.39	0.98	24.17	0.00	0.14	0.02	1.18
7	med	13.32	498.00	1.75	7.25	0.35	3.35	3.51	26.79	0.00	0.42	0.18	3.87
7	mean	13.92	536.12	1.75	6.69	0.38	3.01	2.88	26.65	0.21	0.72	0.94	3.72
7	q3	19.03	672.00	1.75	8.77	0.62	4.29	4.47	28.09	0.28	1.32	1.73	4.94
7	max	37.78	1216.00	1.75	14.61	1.02	6.47	5.32	37.03	2.28	2.40	5.77	11.21
8	min	0.00	242.00	1.75	0.26	0.00	0.00	0.00	NA	0.00	0.00	0.00	NA
8	q1	6.97	280.00	1.75	3.82	0.03	0.49	0.34	NA	0.06	0.10	1.00	NA
8	med	11.16	316.00	1.75	6.55	0.22	1.08	0.89	NA	0.33	0.22	5.00	NA
8	mean	11.15	327.31	1.75	5.95	0.25	1.68	1.29	NA	0.45	0.40	37.82	NA
8	q3	14.87	358.00	1.75	7.81	0.40	2.36	1.81	NA	0.57	0.51	26.00	NA
8	max	29.67	774.00	1.75	14.78	1.00	6.98	6.16	NA	4.01	4.33	187.30	NA
9	min	0.00	48.00	22.41	4.25	0.00	0.00	0.00	0.18	0.00	0.00	0.00	NA
9	q1	1.72	76.00	24.54	4.74	1.17	0.32	0.50	4.15	0.00	4.46	19.89	NA
9	med	2.90	89.00	24.54	5.48	4.38	0.74	1.20	5.62	0.00	5.93	35.17	NA
9	mean	3.58	92.00	85.41	6.20	4.84	0.88	1.50	5.45	0.15	5.71	35.73	NA
9	q3	4.52	103.00	219.57	7.25	7.64	1.36	2.28	6.89	0.13	7.08	50.18	NA
9	max	31.02	291.00	492.63	15.27	13.63	3.08	4.51	8.53	2.19	9.55	91.24	NA
10	min	0.20	126.00	1.75	1.72	0.00	0.00	0.00	2.74	0.00	0.00	0.00	0.07
10	q1	8.06	663.00	14.59	4.26	0.00	2.26	1.87	11.61	0.24	0.82	0.68	2.81
10	med	12.27	756.00	25.68	4.76	0.00	3.89	2.92	15.58	0.68	1.70	2.90	4.43
10	mean	12.87	738.25	22.19	6.30	0.08	3.82	3.17	15.43	1.11	1.89	5.31	6.02
10	q3	17.12	847.00	25.68	8.14	0.03	5.11	4.06	18.88	1.57	2.70	7.29	8.27
10	max	43.26	1324.00	65.55	18.98	1.43	11.54	10.75	27.69	7.54	5.77	33.29	20.50

Table A2-10. Summary of the covariate habitat use. ‘min’ = minimum, ‘q1’ = first quantile, ‘med’ = median, ‘q3’ = third quantile, Slope is in degrees, ‘Elev’ = elevation [m], ‘HD’ = human density [km^2], ‘HFP’ = human footprint, ‘DF’ = distance to forest [km], ‘DM’ = distance to mosaic [km], ‘DO’ = distance to open [km], ‘DP’ = distance to plantation [km], ‘DR’ = distance to regrowth [km], ‘DRD’ = distance to roads [km], ‘DRD2’ = distance to roads [km^2], ‘DW’ = distance to water [km].

id	**Summary**	**Slope**	**Elev**	**HD**	**HFP**	**DF**	**DM**	**DO**	**DP**	**DR**	**DRD**	**DRD2**	**DW**
11	min	0.10	145.00	1.75	2.45	0.00	0.00	0.00	1.24	0.00	0.00	0.00	0.04
11	q1	9.34	395.00	1.75	6.72	0.00	0.55	1.03	4.12	0.08	0.67	0.45	5.36
11	med	14.77	536.00	1.75	8.24	0.03	0.99	1.51	5.21	0.26	1.10	1.22	6.51
11	mean	15.15	527.95	6.68	8.17	0.13	1.20	1.63	5.63	0.41	1.23	2.24	6.07
11	q3	20.62	680.25	1.75	9.79	0.23	1.62	2.15	6.07	0.45	1.57	2.45	7.11
11	max	38.52	850.00	73.33	14.15	1.03	5.46	5.87	13.62	3.83	5.23	27.38	9.60
12	min	0.64	163.00	1.75	1.94	0.00	0.00	0.07	0.83	0.00	0.00	0.00	0.30
12	q1	8.72	282.25	1.75	7.09	0.00	0.41	0.86	3.86	0.02	0.20	0.04	4.05
12	med	13.13	359.50	1.75	9.20	0.17	0.92	1.28	4.49	0.17	0.64	0.41	6.32
12	mean	13.98	388.77	19.14	8.89	0.21	1.32	1.76	5.22	0.38	0.91	1.86	5.75
12	q3	18.38	479.00	40.89	10.80	0.32	1.85	2.18	5.68	0.37	1.22	1.49	7.21
12	max	36.94	796.00	73.33	15.40	0.96	5.15	6.04	12.15	3.70	5.19	26.92	10.72
13	min	0.20	88.00	50.70	9.65	0.00	0.00	0.09	0.25	0.00	0.00	0.00	NA
13	q1	2.58	109.00	50.70	13.24	0.03	0.48	1.23	0.96	0.00	0.41	0.17	NA
13	med	6.05	159.00	50.70	15.11	0.44	1.05	2.90	1.74	0.00	1.26	1.60	NA
13	mean	7.89	187.74	375.71	15.71	0.57	1.26	2.46	1.90	0.19	1.38	2.93	NA
13	q3	11.57	245.00	899.72	16.08	1.06	1.87	3.26	2.27	0.24	2.06	4.25	NA
13	max	27.50	432.00	899.72	32.98	2.44	3.54	4.30	6.14	2.06	4.88	23.85	NA
14	min	0.00	77.00	11.55	3.27	0.00	0.00	0.03	2.61	0.00	0.14	0.02	0.01
14	q1	5.15	131.00	16.52	4.30	0.00	1.20	1.89	4.25	0.00	1.17	1.37	1.50
14	med	9.48	172.00	29.05	4.95	0.13	2.20	2.59	5.61	0.18	3.47	12.05	2.19
14	mean	10.97	257.53	22.97	6.10	0.36	2.49	2.79	5.69	0.75	3.20	14.60	2.43
14	q3	15.44	238.75	31.61	7.45	0.70	3.82	3.66	7.16	1.34	4.91	24.06	3.15
14	max	37.78	859.00	32.16	13.19	1.98	5.81	6.75	9.42	4.39	8.50	72.25	6.63
15	min	0.10	96.00	50.70	5.00	0.00	0.00	0.02	0.29	0.00	0.00	0.00	NA
15	q1	2.79	123.00	50.70	8.26	0.00	0.90	1.17	1.70	0.00	0.73	0.53	NA
15	med	7.23	225.00	899.72	13.06	0.18	1.62	2.35	2.97	0.09	1.84	3.38	NA
15	mean	9.32	375.44	525.15	14.19	0.27	3.98	4.21	4.81	0.52	2.34	9.18	NA
15	q3	13.51	620.00	899.72	18.83	0.48	8.13	8.51	7.66	0.56	3.13	9.79	NA
15	max	36.66	1240.00	899.72	32.98	1.77	10.04	10.45	14.14	4.40	8.10	65.62	NA

Chapter 3: Why did the elephant cross the road? The complex response of wild elephants to a major road in Peninsular Malaysia

Authors:

Jamie Wadey[1]; Hawthorne L. Beyer[2]; Salman Saaban[3]; Nasharuddin Othman[3]; Peter Leimgruber[4]; Ahimsa Campos-Arceiz [1,5,*]

Affiliations:

[1] School of Environmental and Geographical Sciences, The University of Nottingham Malaysia Campus, Jalan Broga, Semenyih 43500, Selangor, Malaysia; [2] School of Biological Sciences, University of Queensland, Brisbane, Qld 4072, Australia; [3] Department of Wildlife and National Parks Peninsular Malaysia, Km. 10, Jalan Cheras, 56100 Kuala Lumpur, Malaysia; [4]Smithsonian Conservation Biology Institute, Front Royal, Virginia, United States of America; [5] Mindset Interdisciplinary Centre for Tropical Environmental Studies, The University of Nottingham Malaysia Campus, Jalan Broga, Semenyih 43500, Selangor, Malaysia.

[*]**Corresponding author.** Email: ahimsa@camposarceiz.com

Citation: Wadey, J., Beyer, H., Saaban, S., Othman, N., Leimgruber, P., & Campos-Arceiz, A. (2018). Biological Conservation. *Biological Conservation*, *218*, 91–98. http://doi.org/10.1016/j.biocon.2017.11.036

3.1 Abstract

Roads cause negative impacts on wildlife by directly and indirectly facilitating habitat destruction and wildlife mortality. We used GPS telemetry to study the movements of 17 wild Asian elephants (Elephas maximus) and a mechanistic modelling framework to analyse elephant response to a road bisecting their habitat in Belum-Temengor, northern Peninsular Malaysia. Our objectives were to (1) describe patterns of road crossing, (2) quantify road effects on movement patterns and habitat preference, and (3) quantify individual variation in elephant responses to the road. Elephants crossed the road on average 3.9 ± 0.6 times a month, mostly (81% of times) at night, and crossing was not evenly distributed in space. The road caused a strong and consistent barrier effect for elephants, reducing permeability an average of 79.5%. Elephants, however, were attracted to the proximity to the road, where secondary forest and open habitats are more abundant and contain more food resources for elephants. Although the road acts as a strong barrier to movement (a direct effect), local changes to vegetation communities near roads attract elephants (an indirect effect). Given that risk of mortality (from poaching and vehicle collisions) increases near roads, roads may, therefore, create attractive sinks for elephants. To mitigate the impact of this road we recommend avoiding further road expansion, reducing and enforcing speed limits, limiting traffic volume at night, managing habitat near the road and, importantly, enhancing patrolling and other anti-poaching efforts. Our results are relevant for landscapes throughout Asia and Africa, where existing or planned roads fragment elephant habitats.

Keywords: Elephas maximus, Habitat connectivity, Movement ecology, Permeability, Resource selection, Infrastructure

3.2 Introduction

The world's terrestrial megafauna are rapidly declining due to anthropogenic pressure (Ripple et al., 2016). In an increasingly human- dominated world (Venter et al., 2016), there are few places where large animals can live without coming into contact with people and the human footprint e.g. agriculture and infrastructure (Allan et al., 2017; Kareiva et al., 2007). Linear infrastructure, such as roads, are omnipresent features of human activity that are rapidly proliferating in the tropics (Ibisch et al., 2016; Laurance et al., 2009; 2014). Roads have negative impacts on wildlife by directly and indirectly facilitating habitat destruction and wildlife mortality (Clements, 2014; Laurance et al., 2009). The effect of roads is particularly concerning for megafauna, animals that require large home ranges (Harestad & Bunnell, 1979; Jetz, Carbone, Fulford, & Brown, 2004).

Animal behaviour, movement, and distribution can be affected by roads in several ways. Roads can affect habitat preference by modifying the environmental conditions near them e.g. through edge effects (Benítez-López et al., 2010; Fortin et al., 2013). Roads can also affect movement behaviour (Stephen Blake et al., 2008; Dussault et al., 2007; Eftestøl et al., 2013), altering wildlife's ability to move between neighbouring areas and utilise resources within the available habitat (Johnson et al., 1992). At larger scales, roads can reduce landscape permeability and connectivity by acting as barriers that impede the movement of animals from habitat on one side of the road to the other side (Beyer et al., 2014; van Strien & Grêt-Regamey, 2016), which can eventually result in the fragmentation of populations (Dunson & Travis, 1991; Laurance et al., 2009; Said et al., 2016).

There is mounting evidence that roads act as barriers to movement and alter the distribution of elephants in space. In the Congo basin, for example, roadless wilderness is a strong determinant of forest elephant (*Loxodonta cyclotis*) home range area (Stephen Blake et al., 2008). Analysing the movements of 28 elephants revealed only one road crossing occurred outside a protected area (Stephen Blake et al., 2008) and concluded that roads are a formidable barrier to forest elephant movements. Another study in central Africa found a similar response whereby two elephants exhibited no road crossings, while one individual never came within 11 km of the road and the second individual ranged 1–15 km away from the road (Granados et al., 2012). In India, however, Asian elephants (Elephas maximus) crossed a road in a wildlife sanctuary regularly, although elephants near the road showed high levels of agitation in response to large vehicles(Vidya & Thuppil, 2010). These variable effects of road crossing between central Africa and Asia suggest elephant responses to roads are complex and not well understood.

Southeast Asia is the region of the world with the largest number of threatened megafauna (Ripple et al., 2016; 2017). It is also a region of rapid economic growth, experiencing a massive and unprecedented expansion of road coverage (World Bank, 2016). The expected infrastructure development over coming decades (Dulac, 2013) will likely further threaten the region's megafauna, including Asian elephants – the largest terrestrial animal in the region. Asian elephants are endangered due to the rapid decline of their populations, mostly as a consequence of habitat loss and the resulting human-elephant conflict in the form of crop raiding (Choudhury et al., 2008; Fernando & Pastorini, 2011).

Within Southeast Asia, Peninsular Malaysia is an important stronghold for wildlife (Rostro-García et al., 2016), including Asian elephants (Saaban et al., 2011). In the past few decades Peninsular Malaysia has undergone a drastic transformation, passing from nearly 80% of forest cover in the 1940s (Aiken, 1994) to < 37% in 2010 (Miettinen et al., 2011).

Recognising the importance of the country's biodiversity (Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000), Malaysia's government has developed legislation and policies to protect it (Nagulendran et al., 2016). The Central Forest Spine (CFS) is a national land-use master plan to maintain habitat connectivity for wildlife across the major habitat patches in Peninsular Malaysia (DTCP, 2014). The implementation of the CFS plan involves the protection of key wildlife corridors and the construction of several viaducts under existing high- ways to facilitate movement by wildlife. The National Elephant Conservation Action Plan (NECAP) is the official policy for Asian elephant conservation in Peninsular Malaysia (DWNP, 2013).

Little is understood about the impact of roads on elephants in Peninsular Malaysia. Here, we investigate and quantify how Asian elephants respond to the presence of a major road bisecting a key wildlife corridor. We used GPS telemetry data from forest elephants to (1) describe the spatial and temporal patterns in road-crossing behaviour. We also (2) quantify the effects of the road on forest elephant movement behaviour and distribution using a mechanistic movement modelling framework that includes both habitat preference and movement rates (Avgar, Potts, Lewis, & Boyce, 2016; Beyer et al., 2014; Forester, Im, & Rathouz, 2009; Fortin et al., 2005; Raynor et al., 2016). Finally, we (3) explicitly evaluate individual variation in the response to roads in order to better understand the range of behavioural responses in the population of elephants. Our research, which is aligned with the objectives of Malaysia's CFS and NECAP policies, can inform management recommendations to reduce the impacts of roads on elephants and other large mammals.

3.3 Materials and methods

3.3.1 Study area

The study area (~ 4000 km^2) is located in northern Peninsular Malaysia (5°55′ N, 101°34′ E) and is known as the Belum-Temengor Landscape (BTL; Figure 3-1). BTL is a hilly and forested landscape dominated by dipterocarp and montane forests, with an altitudinal range of 260 to 2160 m above sea level. BTL consists of forest blocks under different management regimes: Royal Belum state park (Belum; 1246 km^2), a fully protected area that has never been commercially logged, and several forest reserves where some selective logging is permitted and ongoing (Figure 3-1). In the 1970s there were some important infrastructural developments in BTL, including the construction of a ~125 km^2 reservoir and of the East-West Highway, a 120-km long road that bisects the study area (Figure 3-1). The East-West Highway is fully asphalted, has a width of 2–3 lanes (~ 25 m), and often has additional structures such as steel and concrete barriers, and concrete drains on its sides (Figure 3-1). Between 1970 and 1995, the forest reserve that runs parallel to the road (Figure 3-1) was heavily logged. Between 2005 and 2014, traffic volume in the East- West Highway increased at an average annual rate of 4.1%; and in 2014, traffic was 2.3 times denser during day-time (227 vehicles per hour from 0600 to 2200 h) than during the night (97 vehicles per hour from 2200 to 0600 h; Table A3-1). BTL is a key priority landscape for CFS and NECAP (DTCP, 2014; DWNP, 2013). In 2015, a 200-m long and 11-m high viaduct was built to facilitate wildlife movement between the forests at both sides of the road (Figure 3-1; Figure A3-1)Human density in BTL is low, with small villages of indigenous orang asli people living either inside or along the fringes of the forest. The orang asli practice subsistence and small-scale cash-crop agriculture (Kasim & Baskaran, 2014); there are no large-scale plantations within the study area.

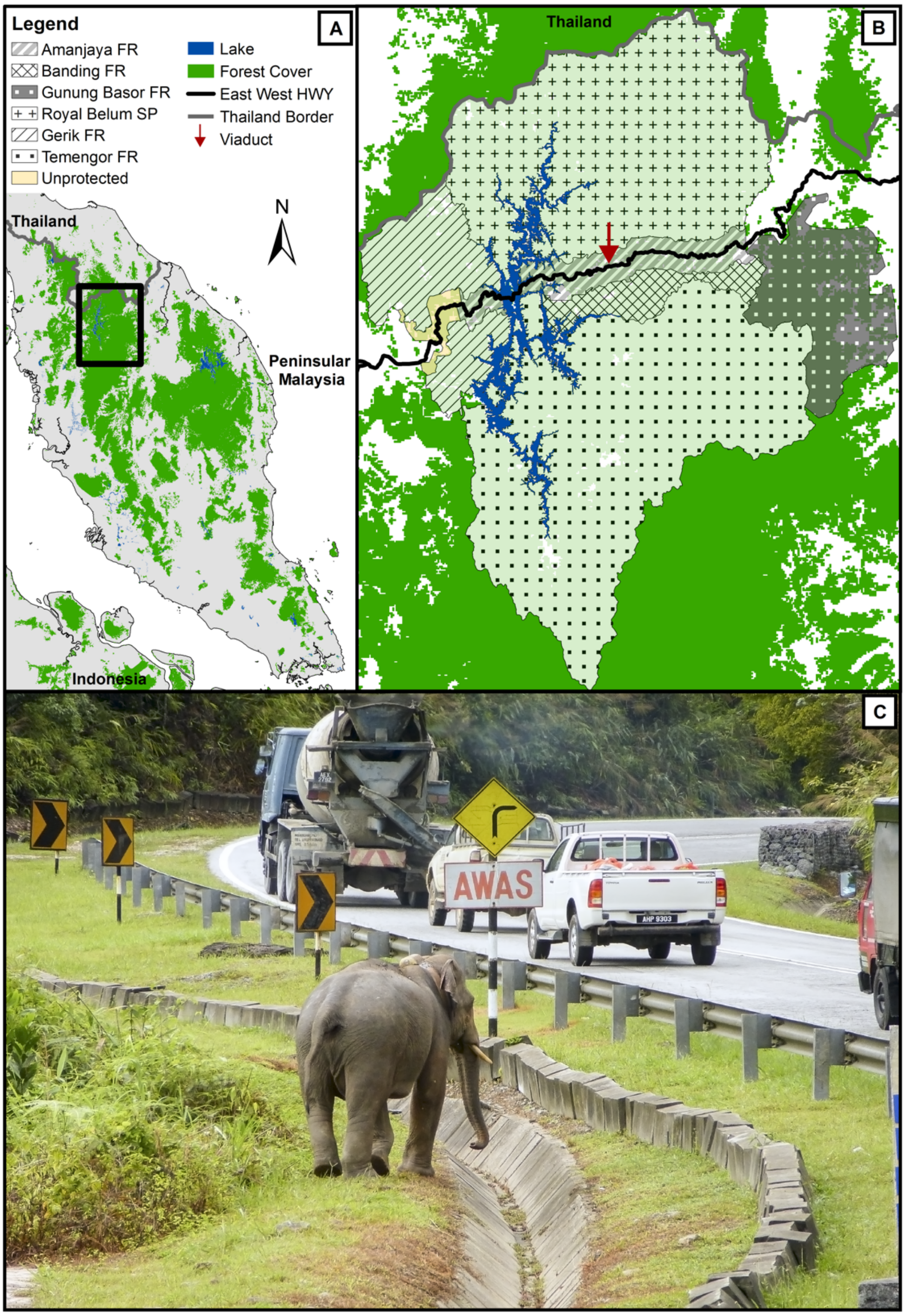


Figure 3-1. (A) Study area in northern Peninsular Malaysia, (B) different forest land use classifications of the study area, (C) sub-adult male Asian elephant beside East-West Highway fitted with GPS telemetry collar (photo credit: Alicia Solana Mena). FR = Forest Reserve; SP = State Park; HWY = Highway.

3.3.2 Elephant tracking

We tracked “translocated” and “local” wild elephants. Translocated elephants were animals relocated from human-elephant conflict areas to BTL by the Department of Wildlife and National Parks (DWNP) to mitigate conflict (Saaban et al., 2011). Local elephants were individuals found in BTL and collared within 200 m from the East-West Highway. We used Inmarsat satellite GPS collars for elephants (Africa Wildlife Tracking, Pretoria, South Africa), programmed to record one location every 2 h. All elephants were immobilised by the DWNP as described in Daim (1995). We complied with research and ethics requirements by the Malaysian government (permit #JPHL%TN(IP): 80–4/2) and the Smithsonian National Zoological Park Institutional Animal Care and Use Committee (NZP-IACUC #10–32).

Our GPS collars provided a metric to quantify the accuracy of each location, called horizontal dilution of precision (HDOP). We removed 1) locations that reported HDOP values > 25 m, 2) duplicate records, and 3) obvious GPS errors; i.e. locations that implied animals travelled > 10 km within 1 h. For details on analyses regarding elephant tracking and road crossing behaviour see appendices (Methods A3-2).

3.3.3 Describing patterns of road crossing

We tested whether there was an effect of the time of the day (daytime = 700 to 1900 and night-time = 1900 to 700) on the frequency of elephant road crossing by fitting a linear mixed effects model using the function lme (Pinheiro & Bates, 2000). The model included frequency of crossing events as the response variable, time of the day (day vs. night) as fixed factor, and the individual elephant as a random factor. Moreover, in order to understand the spatial patterns of road crossing, we divided the road into 90 1-km long segments and quantified the frequency of crossing in each of these segments.

3.3.4 Movement modelling

Habitat selection and animal movement were modelled based on the framework of Beyer et al. (2014), which defines a probability of a “step” between sequential telemetry location a to location b, and conditional on habitat covariates, X, at location b, to be:

$$Eq.(1)\ f(b|a,X) = \frac{\phi(a,b;\theta)\omega(X_b;\beta)}{\int_{c\in D}\phi(a,b;\theta)\omega(X_c;\beta)dc}$$

where $\varphi(a, b; \theta)$ is a probability density function describing the probability of displacement to location b from location a, and $\omega(X)$ is the resource selection probability function and X is a matrix of habitat covariates (sometimes referred to as the displacement kernel or habitat independent movement kernel). Here, $\varphi(a, b; \theta)$ is a bivariate normal distribution with equal variance in the x and y dimensions determined by the parametre θ, and ω is a logistic model with coefficients β re- presenting the habitat preferences (see Beyer et al., 2014, Raynor et al., 2017 for details).

Habitat covariates included slope (degrees), distance to roads (km), distance to roads squared (km^2), “wetness” (one component of a standard, principal-components transformation of multispectral remote sensing data), and permeability (binary covariate indicating whether the individual crossed the road in any particular step). We included slope because elephants are known to avoid steep slopes (Wall et al., 2006). We also included wetness as an indicator for soil and canopy moisture, which is a recommended method to classify forest maturity (Hansen, Franklin, Woudsma, & Peterson, 2014). We used wetness, rather than a categorical classification of forest types, because it allowed us to classify the forest in a continuous scale between open (grasslands and early succession habitats) and closed (mature and old growth forest) habitats (Hansen et al., 2014). Distance to roads and permeability represented the key covariates to quantify elephants' behavioural responses to roads. We included distance to roads squared because roadless area was a strong determinant of home range size in Congo forest elephants' (Stephen Blake et al., 2008) and we suspected the effect of the road on elephant movements could be non-linear (Yamamoto-Ebina et al., 2016). All covariates except permeability were raster format data sets with a spatial resolution of 30 × 30 m (see data sources in Methods A3-3). Other potential covariates were initially evaluated but excluded because they were highly correlated with the previous covariates (e.g. elevation) or because there was no evidence of them being relevant for the model (i.e. the confidence intervals of the selection parametres crossed zero; e.g. distance to water).

The habitat selection model was as follows:

$$Eq. (2)\ logit\big(\omega(Xb;\beta)\big) = \beta_1 + \beta_2 + \beta_3 + \beta_4 + \beta_5$$

Each observed step was paired with 100 random steps in a case- controlled "step selection function" design (Fortin et al., 2005). We simultaneously estimated the movement and habitat preference by fitting f(b|a, X) (Eq. (1)) to the location data (see Beyer et al., 2014 for details). Models were fit using maximum likelihood and confidence intervals for the parametre estimates were calculated from the Hessian matrix (± 1.96 times the square roots of the diagonal elements of the covariance matrix).

The permeability effect of the East-West Highway is represented by the parametre $\beta 5$. We define permeability as the degree in which the East-West Highway affects the capacity of elephants to move between two locations across the road (Beyer et al., 2014), where: (1)

negative permeability estimates with confidence intervals that do not overlap zero indicate that the road is a barrier to elephant movement, i.e. either the animals cannot cross from one side to the other or they still are able to cross but not as much compared to if the road was not there; (2) Positive permeability estimates with confidence intervals that do not overlap zero indicate that the road facilitates road-crossings, i.e. the road increases the number of crossings; and (3) permeability estimates with confidence intervals that overlap zero indicate that the road has a neutral effect on road permeability, i.e. the road has no effect on the animals ability to move from one side to the other.

3.4 Results

3.4.1 Elephant tracking

We collared a total of 17 wild Asian elephants between 2011 and 2015, including ten local (six female and four male) and seven trans- located (two female and five male) individuals. Elephants were tracked for an average (± SD) of 335 ± 296 days (range = 40–950 days; Table A3-2). Average fix success rate was 79 ± 19% (range = 36–97%; Table A3-2). There was no difference by sex or type of elephant (local vs. translocated) in the number of tracking days or their collar fix success (Table A3-3).

3.4.2 Road-crossing behaviour

We recorded a total of 750 road-crossing events and an overall average of 3.9 ± 0.6 crossings per elephant per month. Local elephants (N=10) crossed the road 14 times more frequently than translocated ones (N = 7; 7.0 ± 0.7 vs. 0.5 ± 0.1 crossings per month and elephant; t = 8.27, df = 117.35, P = 2.2e-13, Cohen's d = 1.04 [95% CI: 0.72, 1.36]; for interpretation of Cohen's d values see Lakens, 2013). There was no difference in crossing frequency by sex (males=4.0 ± 0.06, N=9; females=3.8 ± 0.09, N=10; t = −0.19, df = 172.37, P = 0.84, Cohen's d = 0.03 [95% CI: −0.26, 0.32]). Time of day influenced road crossing behaviour with elephants crossing the road predominantly at night (b (fixed effect estimate) =31.2, SE=11.2, df=14, t=2.7, P=0.018), with 81% of road crossings occurring at night (between 1900 and 0700; Figure 3-2).

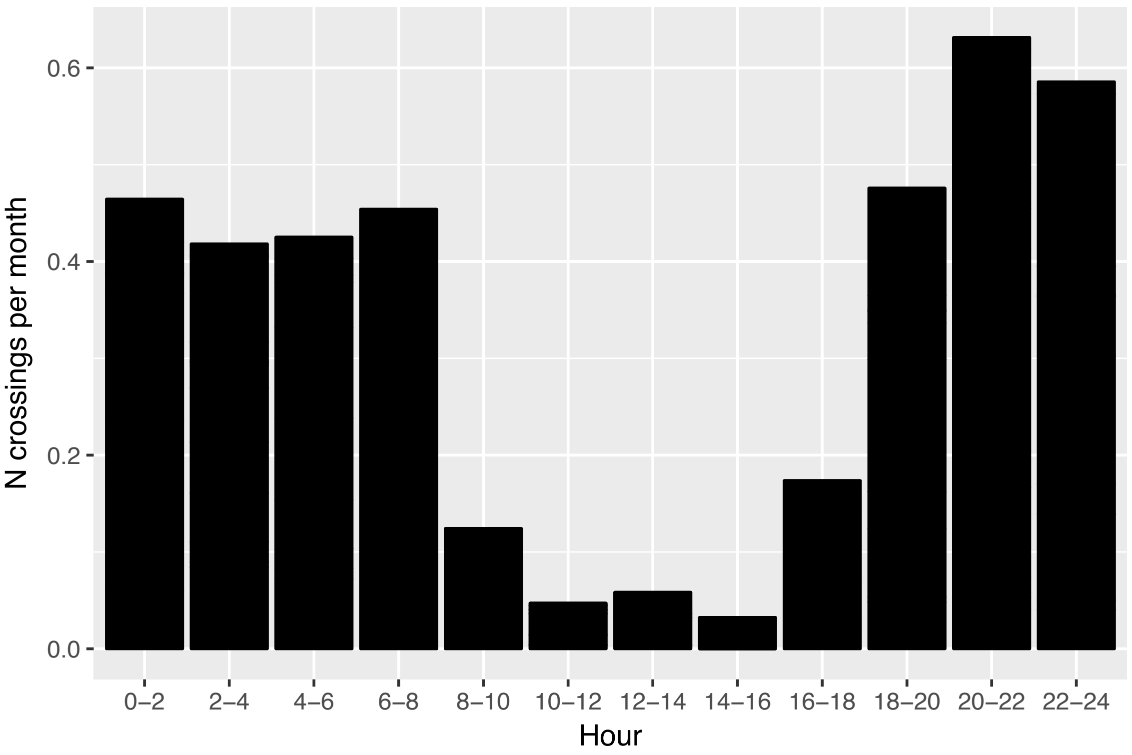


Figure 3-2. Time of day elephants crossed the road. Number of crossings per individual (N = 17 elephants) per month (i.e. 30 days).

Elephants crossed at least once in 56 (62%) of the 90 1-km segments in which we divided the road (Figure 3-3). The median number of crossing per km was nine, and the maximum number of crossing per km was 55 (Figure 3-3). The areas with high frequency of road-crossing events were concentrated in the western portion of the study area, on both sides of Temengor Lake (Figure 3-3). Only one road crossing event occurred in the segment where the viaduct is now located, which occurred before construction was completed in 2015 (Figure 3-3).

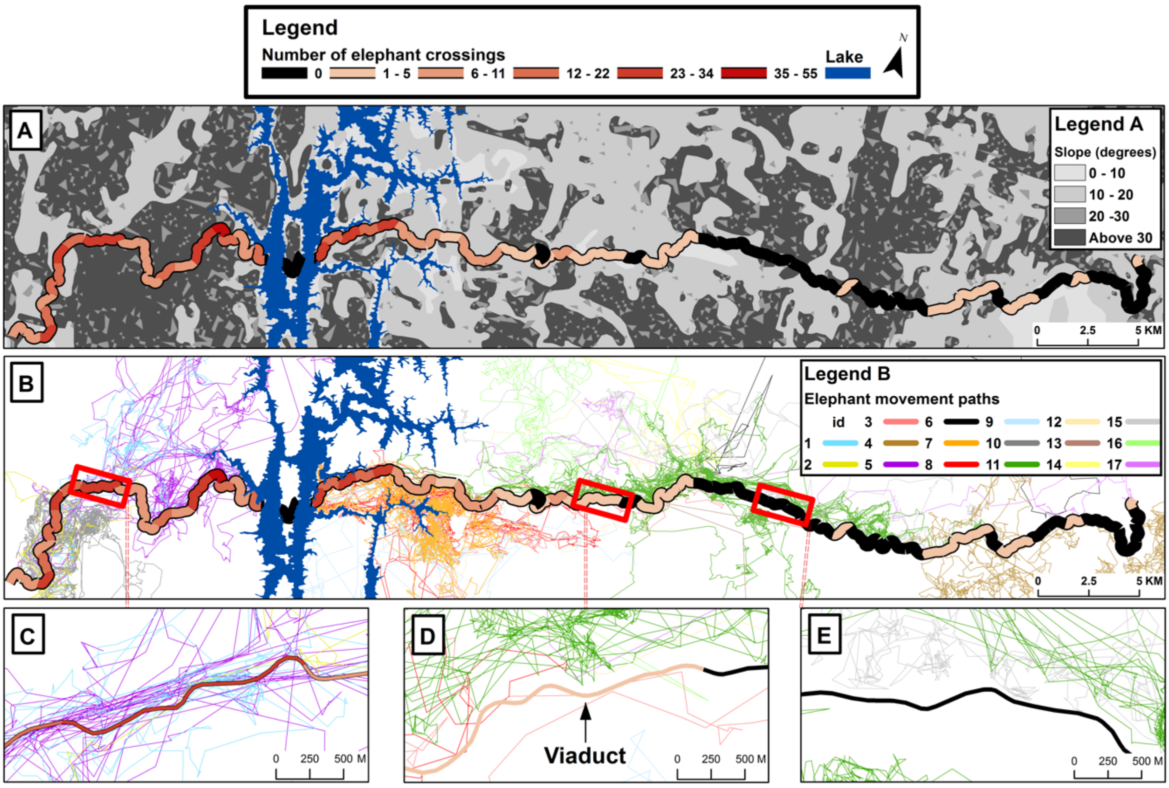


Figure 3-3. Map of elephant road-crossing frequency along the East-West Highway. Crossing frequency was calculated by segmenting the road into one-kilometre sections and using the absolute total of road-crossings per section. Background in (A) represents terrain slope in degrees. Coloured lines in (B) represent the movement paths of each of the 17 collared elephants. C: detail of an area with high frequency of crossing. D: elephant movement paths in proximity to the viaduct. E: area where elephants were present but did not cross the road.

3.4.3 Elephant habitat preference

We found strong and consistent evidence that the East-West Highway constitutes a barrier to movement for elephants. The permeability coefficient (β5; Table A3-4) was negative for all animals and the 95% confidence interval for these estimates did not overlap zero. There were, however, three individuals for which the permeability coefficient could not be estimated: two that never crossed the road and one that was very rarely near the road (id: 13, average distance to road = 49 ± 11.4 km; ; Table A3-2; Table A3-4). The average permeability coefficient among animals was −3.1, corresponding to an approximate 79.5% (range = 39.1–99.9%; N = 14 elephants) reduction in the average probability of taking a step involving crossing the road. There was also strong and consistent preference for lower wetness values: 14 of 17 individuals had negative coefficients associated with wetness and confidence intervals that did not overlap 0, while another 3 showed no significant preference (Table A3-4; Figure 3-4; Figure A3-2; Figure A3-3; Figure A3-4; Figure A3-5).

Patterns of habitat preference for the other two covariates were more variable among individuals (Table A3-4). Most animals showed preference for shallower slopes with 9 of 17 animals exhibiting negative coefficients associated with slope with confidence intervals that did not overlap 0, while another 5 showed no significant preference. Three animals had positive selection for slope. Interpretation of preference for distance to road is more complex because of the individual differences among elephants. The varied individual responses to distance from road (examples in Figure 3-4; more details in Figure A3-2; Figure A3-3; Figure A3-4; Figure A3-5) included: (i) selection for being near roads (6 of 17 elephants), (ii) avoidance of close proximity to roads (e.g. within 500 m) but also avoidance for being too far from roads (e.g. > 2.5 km) (4 of 17), (iii) preference for being far from roads (4 of 17), (iv) selection for being near the road (e.g. < 500 m) and then moving away from the road (e.g. > 2.5 km) (3 of 17). The mean distance to road for all elephants was 3.4 ± 2.8 SD km (range = 0–19 km); the average distance from the road was not different between translocated elephants (3.5 ± 2.9 SD km; range = 0–14 km; t = − 0.13, df = 10.9, P = 0.89) and local elephants (3.3 ± 2.9 SD km; range = 0–19 km). We removed a translocated female (id: 13) from the mean distance to road calculations because she moved away from the road immediately after release (average distance to road = 49 ± 11.4 SD km; range 23–60 km).

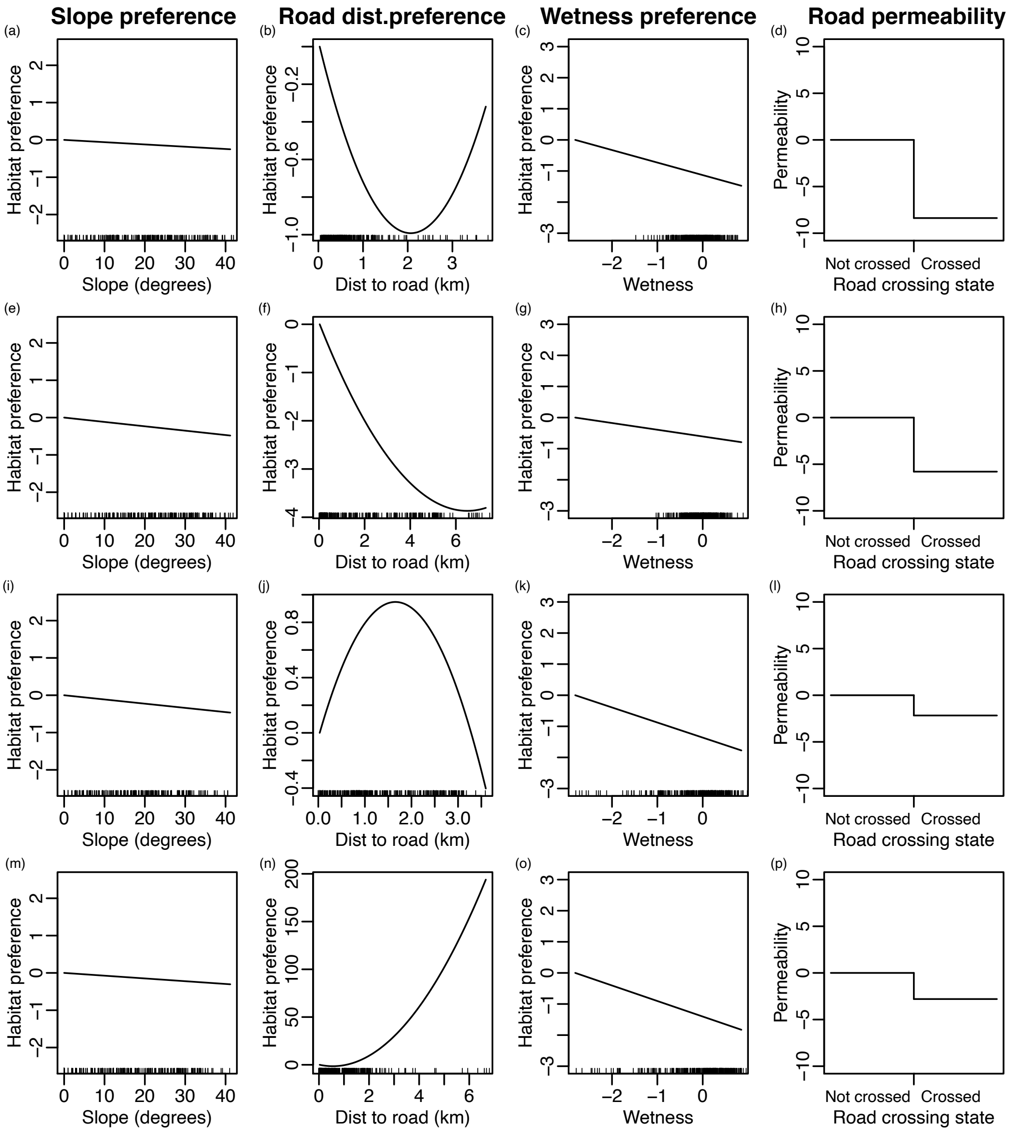


Figure 3-4. Habitat preferences of individual Asian elephants based on satellite tracking and derived resource selection functions. Rows represent a subsample of the study individuals (id: 11, 15, 7, 8); columns represent variables in ascending order: slope; distance to roads; wetness; a selection of multispectral bands as a proxy for closed canopy, disturbed and open habitat; and permeability. Solid lines are mean estimates. Rows 1 and 2 are translocated elephants. Rows 3 and 4 are local elephants. Individuals were chosen as representative examples e.g. slope, wetness and permeability showing the similar patterns by elephants; while distance to road patterns displaying the variation of selection found by the road.

3.4.4 Elephant movements

Fitted parametres describing the displacement kernel for each in- dividual indicated a mean step length of 156 m over a 2-h interval (range: 90–260 m; Figure A3-6). The mean step length of translocated and local elephants was not different ($t = -0.38$, $df = 13.3$, $P = 0.71$, Cohen's $d = 0.18$ [95% CI: -0.86, 1.24]) and there was a marginal difference in step length between sexes (females = 140 ± 26 m, males =168 ± 32m; $t = -1.9395$, $df = 14.56$, $P = 0.07$, Cohen'sd = 0.96 [95% CI: -0.15, 2.06]).

3.5 Discussion

In this study, we have found elephants interacting with a road (Peninsular Malaysia's East-West Highway) in a complex way. On the one hand, the road has a barrier effect on elephant movement (reducing permeability an average of 79.5%; Figure 3-4). On the other, elephants are still able to cross the road (with 3.9 ± 0.6 crossing events per month and individual occurring along different parts of the road; Table A3-2; Figure 3-3) and, indeed, several individuals preferred to occupy areas near the road. Based on previous studies in Africa (Stephen Blake et al., 2008; Granados et al., 2012), we expected elephants to generally avoid the road but found that elephants in BTL tended to stay close to the road (3.4 ± 2.8 SD km), suggesting that – at a landscape scale – the road is attracting rather than repelling elephants.

Road avoidance in Africa might be related to high poaching pressure and risk avoidance by elephants (Stephen Blake et al., 2008; Granados et al., 2012). In BTL, however, elephants' attraction toward the vicinity of the road is likely to be due to ecological factors, specifically, due to changes in vegetation structure and high food availability by the roadside. Yamamoto-Ebina et al. (2016) studied the food habits of elephants in BTL and concluded that the East-West Highway acts as a large linear forest gap – elephants staying near the road have a diet based on grasses and other early-succession plants, while elephants far (> 5 km) away from the road consume a higher proportion of less preferred woody plants (Yamamoto-Ebina et al., 2016). It is also possible that the road, constructed in the 1970s, disrupted ancestral elephant paths in BTL but there is no way for us to know how elephants moved in this landscape before the construction of the road.

Our habitat preference results show that elephants preferred open habitats (i.e. those with lower wetness values; Figure 3-4), which are far more common along the road compared to further away in less disturbed BTL rainforest (Figure A3-7). These open habitats along the road are the result of the heavy logging that took place until the mid-1990s and the regular road maintenance that produces patches of grasslands. A caveat in our analyses is that we used one single Landsat-8 satellite image from June 2014 to describe wetness in the study area (Methods A3-3), which means that our model is missing some details about the effect of logging during our study period. Our results regarding the effect of wetness, however, are very consistent. Asian elephants are edge specialists (Campos-Arceiz, 2013) and hence it is no surprise that they prefer these open and disturbed habitats compared with mature rainforests where fodder is less abundant. The frequent presence of elephants and other large herbivores by the roadside in Nagarahole Tiger Reserve, India, has also been attributed to grass availability along the road edges (Gubbi, Poornesha, & Madhusudan, 2012).

Understanding when and where elephants cross the road can inform the design of mitigation measures. Most (81%) of the road-crossing in BTL occurred at night (Figure 3-2), when traffic density is lower (Table A3-1). Elephants in India's Mudumalai Wildlife Reserve were mostly seen by the road just before sunset (1745 to 1845, although that study did not include observations at night; Vidya & Thuppil, 2010). In BTL, elephants could be foraging by the roadside and crossing the road at night to avoid interactions with humans. Risk avoidance has been suggested as an explanation for nocturnal crop-raiding by Asian elephants (Sukumar & Gadgil, 1988). We recorded a higher frequency of crossing events on the western portion of the study area than in the east (Figure 3-3). It is unclear why these geographical differences in the frequency of road crossing arise, especially as slope does not seem to always limit elephant crossings (Figure 3-3).

Since the completion of our study, the Malaysian government has constructed one wildlife viaduct along the East-West Highway (Figure 3-1; Figure A3-1). Our data, thus, refers to elephant movements before the via- duct was available for elephants to cross the road. The use of the area around where the viaduct was built was low – although several elephants ranged in proximity to the viaduct, we only detected one elephant crossing within the 1-km segment that included the viaduct (Figure 3-3). The construction of the viaduct may have deterred elephants from moving through the area in the last stages of our study (i.e. in 2014 and 2015). Monitoring of the use of the viaduct is necessary to understand its effectiveness in facilitating landscape connectivity for elephants and other wildlife. It is clear, in any case, that a single crossing point is not sufficient to provide landscape connectivity for elephants. The viaduct should therefore be considered as part of a suite of mitigation tools, rather than as a silver bullet to maintain permeability in BTL. The value of the viaduct in facilitating animal movement across the road may increase in the future if the road permeability decreases (e.g. due to an increase of traffic load).

Road crossing by wildlife is affected by traffic volume (Van Der Ree, Jaeger, Grift, & Clevenger, 2011). In Nagarahole Tiger Reserve, India, Gubbi et al. (2012) studied a highway with two contiguous management zones: a “no-drive zone” (1.9 vehicles/h) and a “daytime driving only zone” (44 vehicles/ h) and found lower photo-capture rates of elephants, gaur (*Bos gaurus*), and chital (*Axis axis*) beside the road in the daytime driving zone. The steady increase in traffic volume (~ 4% annually between 2005 and 2014; MoWM, 2014) along the East-West Highway in BTL could eventually prevent elephants from crossing the road and hence limit the capacity of elephants to move between Belum and Temengor. Traffic management during the night may mitigate the loss of permeability. Such management could include restricting the number of vehicles, enforcing no drive periods, or reducing speed limits.

Translocated and local elephants showed important behavioural differences in relation to the road. Local elephants crossed the road 14 times more frequently than translocated elephants (7.0 ± 0.7 vs. 0.5 ± 0.1 times per month and elephant; Table A3-2). This difference in behaviour by translocated elephants could be due to stress from the translocation process or to lack of familiarity with BTL and the East- West Highway. These results are in line with a recent endocrinology study that showed significant differences in faecal glucocorticoid concentrations between local and translocated elephants in Peninsular Malaysia (Wong, 2016). There is the potential for translocated elephants to cross the road more frequently after some time has passed. For example, one translocated elephant (id 11) was recorded to first cross the highway only after 17 months of staying within 2 km of one side of the road (Solana-mena, 2014).

The movement rate of elephants in BTL is relatively small and constant (mean of 156 m per 2 h, and a range of 90–260 m) compared to that described for elephants in southern Africa (200 to 1200 m per hour; Loarie et al., 2009). The lack of variation in these movement rates could be due to the abundance and seasonal consistency of food available along the road. In Sri Lanka and Myanmar elephants were also described to have relatively short movement rates (Campos-Arceiz et al., 2008). Male elephants in our sample had slightly higher (~20%) movement rates than females, most likely reflecting sexual dimorphism and differences in social behaviour – while females move in groups with calves, males tend to move alone or in bachelor groups (Hii, 2017). Against our expectations, there were no differences in movement rate between translocated and local individuals, which might point to an energetic optimisation of step-length or movement rates.

The East-West Highway seems to act as an attractive sink (Nielsen, Stenhouse, & Boyce, 2006) for elephants. Three out of 17 elephants (17%) died or were injured during the study period – one elephant (id: 5) was hit by a vehicle and lost a tusk (although fortunately neither elephant nor driver suffered major injuries) and two elephants (22% of the males in our sample; id: 14 & 15) were poached for their ivory within 3 km from the road. Poaching is an emerging threat for elephants in this landscape and is important to implement enforcement measures to prevent the viaduct and other parts of the road from attracting poachers. Providing poachers easy access to elephants is probably one of the most important negative impacts of the East-West Highway on elephant conservation, supporting the idea that road construction should be avoided in tropical rainforest landscapes.

A subtle indirect effect of the East-West Highway might be altering elephants' ecological function in BTL. Asian elephants play an important ecological role as agents of seed dispersal (Campos-Arceiz & Blake, 2011) in this landscape (e.g. Kromann-Clausen, 2015). Given that the road affects elephant diet (Yamamoto-Ebina et al., 2016) and movements, elephants that choose to stay near the road might consume less fruits and disperse seeds over shorter distances than elephants living in the primary rainforest.

3.6 Conclusion

Our study has direct policy and management implications for elephant conservation in Peninsular Malaysia and other elephant range states. BTL is one of the priority landscapes in Malaysia's CFS land-use masterplan (DTCP, 2014) and the National Elephant Conservation Action Plan (DWNP, 2013). We found that the East-West Highway acts as an attractive sink for elephants, attracting them to feed on abundant fodder near the road while greatly reducing landscape permeability and exposing males to poaching for ivory. Accordingly, we recommend: (1) increasing patrolling and other anti-poaching efforts along the road, especially at the viaduct and areas frequently used by elephants (Figure 3-1) to curb the concerning poaching rates suggested by our data; (2) strictly avoiding increasing the number of lanes in the East-West Highway and the creation of new roads in the landscape, as road expansion might result in further fragmentation and loss of connectivity; (3) reducing and enforcing speed limits (especially at night) through signs, speed bumps, speed traps, and strict fines to speed limit infractions; (4) consider habitat management (e.g. long-term reforestation) near the road to avoid the concentration of elephants by the roadsides; and (5) adequate monitoring of the effectiveness of the viaduct on habitat connectivity for elephants and other wildlife. Additionally, we also recommend public engagement, especially to modify drivers' behaviour in the East-West Highway and other roads crossing important wildlife habitats in Malaysia.

Overall, our results highlight the importance of considering the impact of infrastructure development on megafauna and other wildlife, especially in Southeast Asia, a region with the highest number of threatened megafauna (Ripple et al., 2016; 2017) and with large-scale infrastructure development plans for the coming decades (World Bank, 2016). The conservation of these endangered megafauna will require, among others, considering landscape connectivity and wildlife mobility and protection from poaching in infrastructure development initiatives.

3.7 Authors' contributions

ACA, JW, NO, and SS conceived the idea; ACA, JW, NO, and SS collected the data; HB, JW, and PL designed the modelling approach; ACA, JW, and HB analysed the data; ACA and JW led the writing of the manuscript; all authors contributed critically to the writing.

3.8 Acknowledgements

This study is part of the Management & Ecology of Malaysian Elephants (MEME), a joint research project between the Department of Wildlife and National Parks (DWNP) Peninsular Malaysia and the University of Nottingham Malaysia Campus. We are very grateful to DWNP, and especially to Dato' Abdul Rasid Samsudin and Dato' Abdul Kadir bin Abu Hashim, DWNP's former and current Director Generals, for the permits to conduct this research and for the continuous support in the field. Field activities were generously financed by grants from Yayasan Sime Darby (grant M0005.54.04), Wildlife Reserves Singapore (grant S0002.54.02), and Marinescape (grant M0004.54.04). HB was supported by an Australian Research Council Award (DE140101389). DWNP's elephant translocation team and Perak's elephant unit con- ducted the elephant capturing and sedation; Mohammad Rizal Bin Paimin, Steven Lim, Mei Mei Chu, Aris Mohamad Oziar, Alicia Solana Mena, Param bin Pura, Muhammad Tauhid bin Tunil, Sudin Anak lelaki Din, Rizuan Bin Angah, and many other individuals provided key as- sistance during elephant collaring and tracking activities. Alex Lechner, Natalia Huang, and Ee Phin Wong provided useful feedback on the manuscript and the Smithsonian Conservation Biology Institute provided technical support and training to JW. We are grateful to all.

3.9 Data accessibility

The elephant movement data presented in this manuscript are al- ready archived at movebank.org.

3.10 Appendices

3.10.1 Methods

Methods A 3-1. Elephant tracking.

We tested for differences in the number of tracking days by using a two-sided students t-test by elephant sex and type (local vs. translocated). Tracking days were calculated from the date an elephant was collared to the last day we received a GPS location. If no locations were received for any given day, it would be subtracted from the total number of days. Collar fix success was calculated by dividing the number of received locations by the number of expected locations. Expected locations were calculated as the number expected locations in one day (i.e. 12, one every 2 hours) multiplied by the number of tracking days.

Methods A3-2. Road crossing behaviour.

The number of road crossings per month per individual. Firstly, we calculated 2-hour bins per elephant and in each bin we totalled the number of road crossings for each individual. Secondly, for each bin and individual we multiplied the number of road crossing per bin by 30 (days) and then divided that number by the number of days that elephant was tracked for. This gave an average number of road crossing events per elephant per month for each bin. Road crossing means and standard deviations were calculated on the respective bins of the road crossing per month per elephant values. We tested whether the number of road crossing per month per elephant was significantly different by using a two-sided students t-test on type (local vs. translocated) and sex.

We defined a road crossing to be at night if it occurred after 7 pm and before 7 am. While a day crossing was recorded if it occurred after 7 am and before 7 pm. We calculated the number of road crossings per individual during the day and night. We used the *glmer* function from R's *lme4* library (Bates, Mächler, Bolker, & Walker, 2015); we tested the number of road crossings with time (day or night) whilst having individual elephant id as a random factor.

The total length of the East-West highway is ~ 120 km but only ~90 km contain continuous forest on both sides. We used these 90 km of road to estimate the rate of crossing per km of road (i.e. the remaining 30 km were excluded).

Methods A3-3. Data Sources.

All raster data sets were downloaded from Earth-Explorer (https://earthexplorer.usgs.gov): Landsat 8 program 2013, Level 1 Operational Land Imager (OLI) and Thermal Infrared Sensor (TIRS). NASA EOSDIS Land Processes DAAC, USGS Earth Resources Observation and Science (EROS) Center, Sioux Falls, South Dakota (https://lpdaac.usgs.gov), accessed July 1, 2015. Habitat covariates were extracted from one satellite image acquisition date June 2, 2014, scene number: L71008058_05820031026.

3.10.2 Tables

Table A3-1. Road traffic volume expressed number of vehicles for the East-West Highway between 2005 and 2014 (MoWM, 2014). Census station number: AR803. DailyAv = average daily number of vehicles during day-time hours (0600-2200 h); VechHr = average number of vehicles per hour; NightAv = average daily number of vehicles during night hours (201-0559 h). The original report does not provide information on standard deviation.

Year	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**
DailyAv. (0600-2200)	2,609	2,906	2,846	2,946	3,078	3,337	3,148	3,944	3,796	3,636
VechHr (0600-2200)	163	182	178	184	192	208	197	247	237	227
NightAv (2201-0559)	NA	NA	NA	NA	NA	NA	NA	NA	NA	773
VechHr (2201-0559)	NA	NA	NA	NA	NA	NA	NA	NA	NA	97

Table A3-2. Summary of elephant tracking data. Ele id = elephant individual; F = female; M = male; A = Adult (~ >20 years); SA = Sub Adult (~15-20 years); Loc = local elephant; Trans = translocated elephant, Fix success = percent of successful GPS locations; Tracking period = number of days the elephant was GPS-tracked; Total crossing = total number of road crossing events per elephant; Monthly crossing = number of road crossing events per 30 days per elephant.

id	Sex	Age class	Type	Fix success (%)	Tracking period (days)	Total crossing	Monthly crossing
1	F	A	Loc	95	168	65	11.6
2	F	A	Loc	95	79	32	12.1
3	F	A	Loc	94	94	34	10.9
4	F	A	Loc	70	950	16	0.5
5	M	SA	Loc	51	875	316	10.8
6	M	SA	Loc	36	148	0	0.0
7	F	A	Loc	68	457	66	4.3
8	M	SA	Loc	81	440	116	7.9
9	M	A	Loc	48	345	28	2.4
10	F	SA	Loc	97	724	64	2.7
11	F	A	Trans	92	679	1	0.04
12	M	A	Trans	97	140	3	0.64
13	F	A	Trans	72	400	1	0.07
14	M	A	Trans	71	40	0	0.0
15	M	A	Trans	96	321	4	0.37
16	M	SA	Trans	94	134	2	0.45
17	M	SA	Trans	87	46	2	1.3
Mean				79	355	44	3.8
SD				19	296	78	0.6
Total					6040	750	

Table A3-3. Results of t-test comparing the fix success rate of the GPS telemetry and the number of GPS tracking days by elephant sex (male vs. female) and type of elephant (local vs. translocated) in Belum-Temengor Landscape.

Test	**Treatment**	**Mean ± SD**	***t***	**df**	***P***	**Cohen's d [95% CI]**
Fix success (%)	Male	75±22	0.97	14.67	0.34	0.43 [-0.62, 1.50]
	Female	84±13				
	Translocated	87±11	-1.64	13.83	0.12	-0.72 [-1.80, 1.68]
	Local	73±22				
Tracking days	Male	256±254	1.68	11.42	0.12	-0.82 [-1.9, 0.26]
	Female	496±308				
	Translocated	251±232	1.30	14.97	0.21	0.61 [-0.47, 1.68]
	Local	428±324				

Table A3-4. Maximum likelihood parametre estimates and 95% confidence intervals for 17 individual radio-collared Asian elephants (*Elephas maximus*). The parametres represent the movement kernel parametre (σ, representing the standard deviation of a normal distribution for id 1, or the rate parametre of an exponential distribution for all other animals), habitat preference for slope (β_1), distance to roads (β_2; β_3 quadratic), wetness (β_4), and permeability of roads (β_5).

id	σ	β1	β2	β3	β4	β5
1	5.25 (5.22, 5.27)	-0.01 (-0.02, -0.00)	0.15 (-0.49, 0.79)	0.02 (-0.13, 0.18)	-1.14 (-1.50, -0.79)	-1.60 (-2.03, -1.17)
2	5.31 (5.28, 5.35)	-0.01 (-0.03, 0.00)	0.04 (-0.53, 0.61)	-0.00 (-0.08, 0.08)	-2.07 (-2.78, -1.35)	-2.67 (-3.48, -1.86)
3	5.22 (5.19, 5.26)	0.00 (-0.01, 0.01)	-1.07 (-1.61, -0.52)	0.15 (0.03, 0.26)	-0.34 (-0.41, -0.26)	-1.48 (-1.86, -1.10)
4	5.18 (5.17, 5.20)	-0.03 (-0.04, -0.02)	0.19 (0.05, 0.32)	-0.01 (-0.02, -0.00)	-2.42 (-3.09, -1.74)	-3.20 (-4.13, -2.27)
5	5.61 (5.59, 5.62)	-0.01 (-0.01, -0.00)	-1.18 (-1.39, -0.97)	0.04 (0.03, 0.05)	-1.19 (-1.29, -1.08)	-1.59 (-1.77, -1.42)
6	5.30 (5.25, 5.35)	0.02 (0.00, 0.03)	-0.34 (-1.05, 0.37)	0.02 (-0.02, 0.06)	-2.07 (-3.37, -0.78)	NA (NA, NA)
7	5.13 (5.11, 5.15)	-0.01 (-0.02, -0.00)	1.19 (0.69, 1.69)	-0.36 (-0.49, -0.22)	-2.08 (-2.52, -1.65)	-2.17 (-2.66, -1.68)
8	5.18 (5.17, 5.20)	-0.01 (-0.02, 0.00)	-5.84 (-7.96, -3.73)	5.25 (3.46, 7.03)	-2.15 (-2.64, -1.66)	-2.80 (-3.33, -2.28)
9	5.48 (5.46, 5.51)	0.01 (0.01, 0.02)	-0.69 (-1.00, -0.38)	0.03 (0.01, 0.05)	-1.87 (-2.26, -1.48)	-2.89 (-3.82, -1.97)
10	4.74 (4.73, 4.75)	0.00 (-0.01, 0.01)	0.20 (-0.12, 0.52)	-0.03 (-0.07, -0.00)	-2.03 (-2.44, -1.62)	-2.40 (-3.06, -1.74)
11	5.14 (5.13, 5.15)	-0.01 (-0.01, -0.00)	-0.99 (-1.60, -0.37)	0.24 (0.03, 0.44)	-1.73 (-2.02, -1.45)	-8.38 (-10.42, -6.34)
12	5.09 (5.06, 5.11)	0.05 (0.03, 0.07)	0.41 (-0.13, 0.94)	-0.05 (0.09, -0.01)	-1.44 (-2.06, -0.82)	-4.13 (-6.35, -1.92)
13	5.41 (5.39, 5.43)	-0.05 (-0.06, -0.03)	-3.83 (-3.93, -3.74)	0.04 (NA, NA)	-3.09 (-3.78, -2.40)	NA (NA, NA)
14	5.63 (5.47, 5.79)	-0.03 (-0.06, -0.00)	1.18 (-1.22, 3.58)	-0.17 (-0.47, 0.14)	-0.41 (-1.86, 1.05)	NA (NA, NA)
15	5.15 (5.13, 5.16)	-0.01 (-0.02, -0.01)	-1.20 (-1.80, -0.61)	0.09 (-0.01, 0.20)	-0.93 (-1.27, -0.59)	-5.80 (-6.86, -4.73)
16	5.27 (5.24, 5.29)	0.00 (-0.00, 0.01)	-0.51 (-1.00, -0.01)	0.09 (0.03, 0.14)	-0.19 (-0.44, 0.06)	-1.87 (-3.29, -0.45)
17	5.32 (5.27, 5.37)	-0.01 (-0.02, -0.00)	-1.28 (-2.13, -0.44)	0.09 (-0.08, 0.25)	-0.04 (-0.29, 0.21)	-2.46 (-3.62, -1.30)

3.10.3 Figures

Figure A3-1. Wildlife viaduct in the East-West Highway. The viaduct was completed in September 2015 and its dimensions are 17.4 m width, 8.1 to 11 m height, and 200 m length.

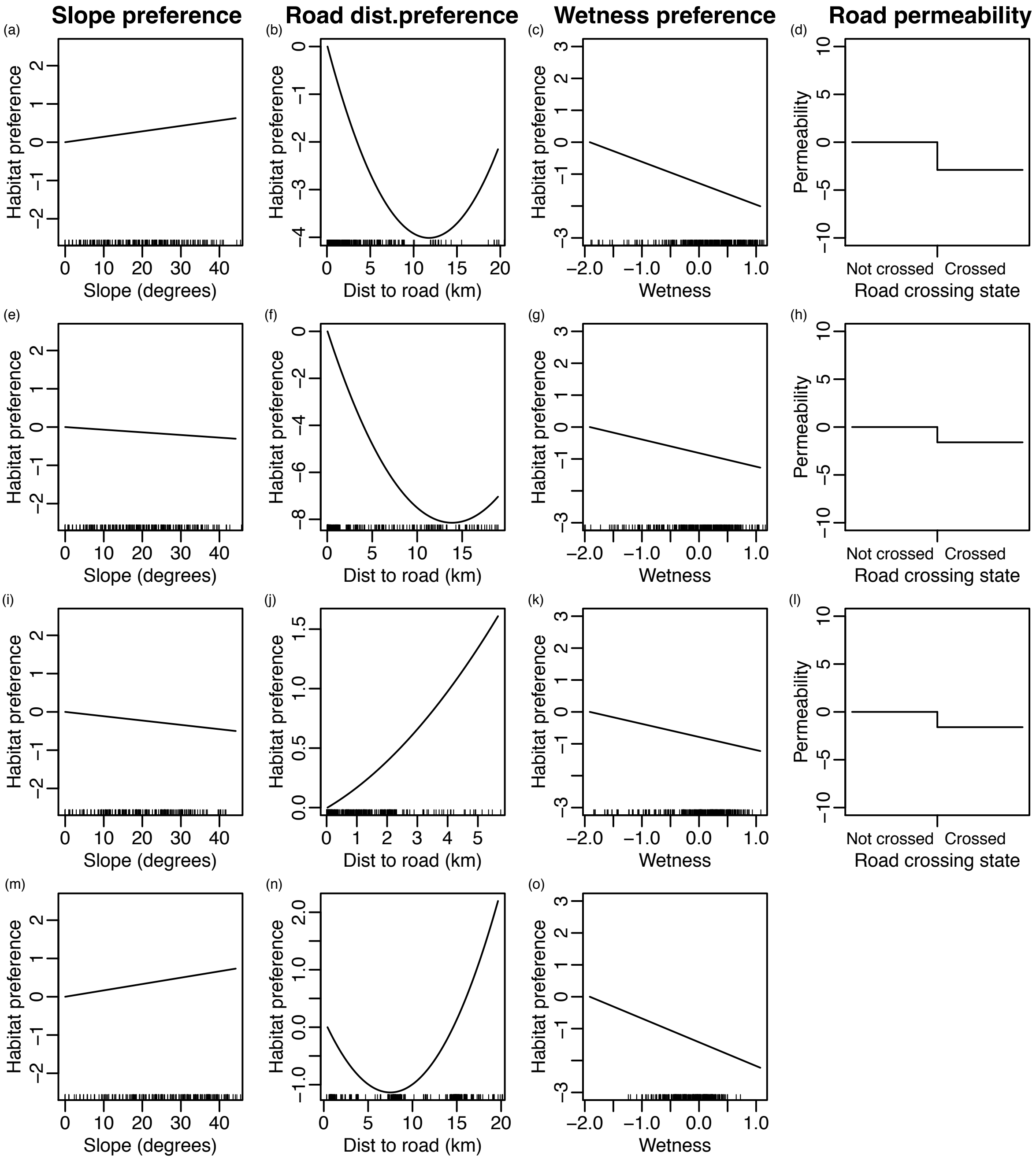


Figure A3-2. Habitat preferences of individual Asian elephants based on satellite tracking and derived resource selection functions. Rows represent a study individual (id: 9, 5, 1, 6); columns represent variables in ascending order: slope; distance to roads; wetness (a selection of multispectral bands as a proxy for closed canopy, disturbed and open habitat); and permeability. Solid lines are mean estimates. Road permeability was not estimated for id 6 because individuals never crossed the road. All individuals are local elephants.

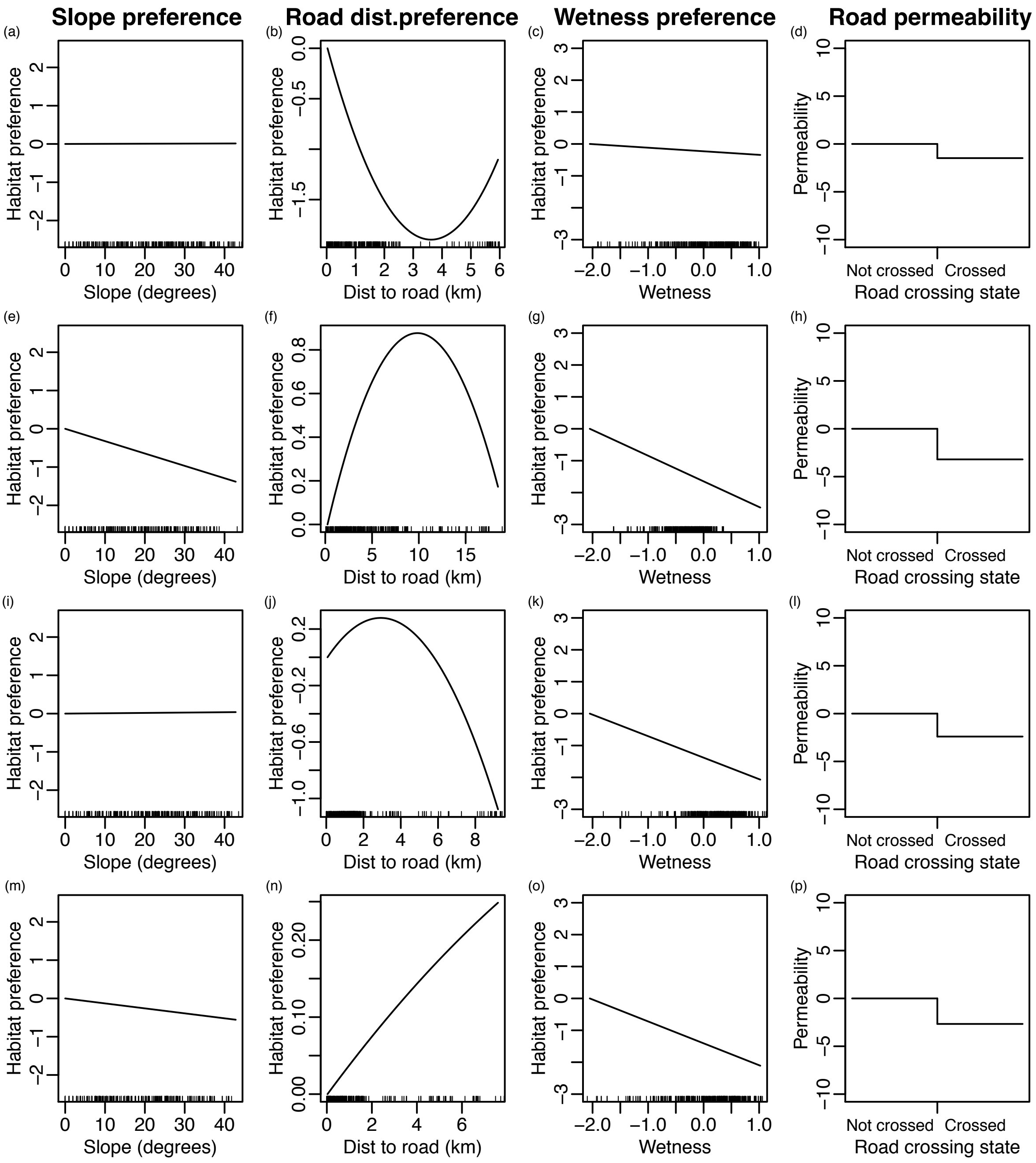


Figure A3-3. Habitat preferences of individual Asian elephants based on satellite tracking and derived resource selection functions. Rows represent a study individual (id: 3, 4, 10, 2); columns represent variables in ascending order: slope; distance to roads; wetness (a selection of multispectral bands as a proxy for closed canopy, disturbed and open habitat); and permeability. Solid lines are mean estimates. All individuals are local elephants.

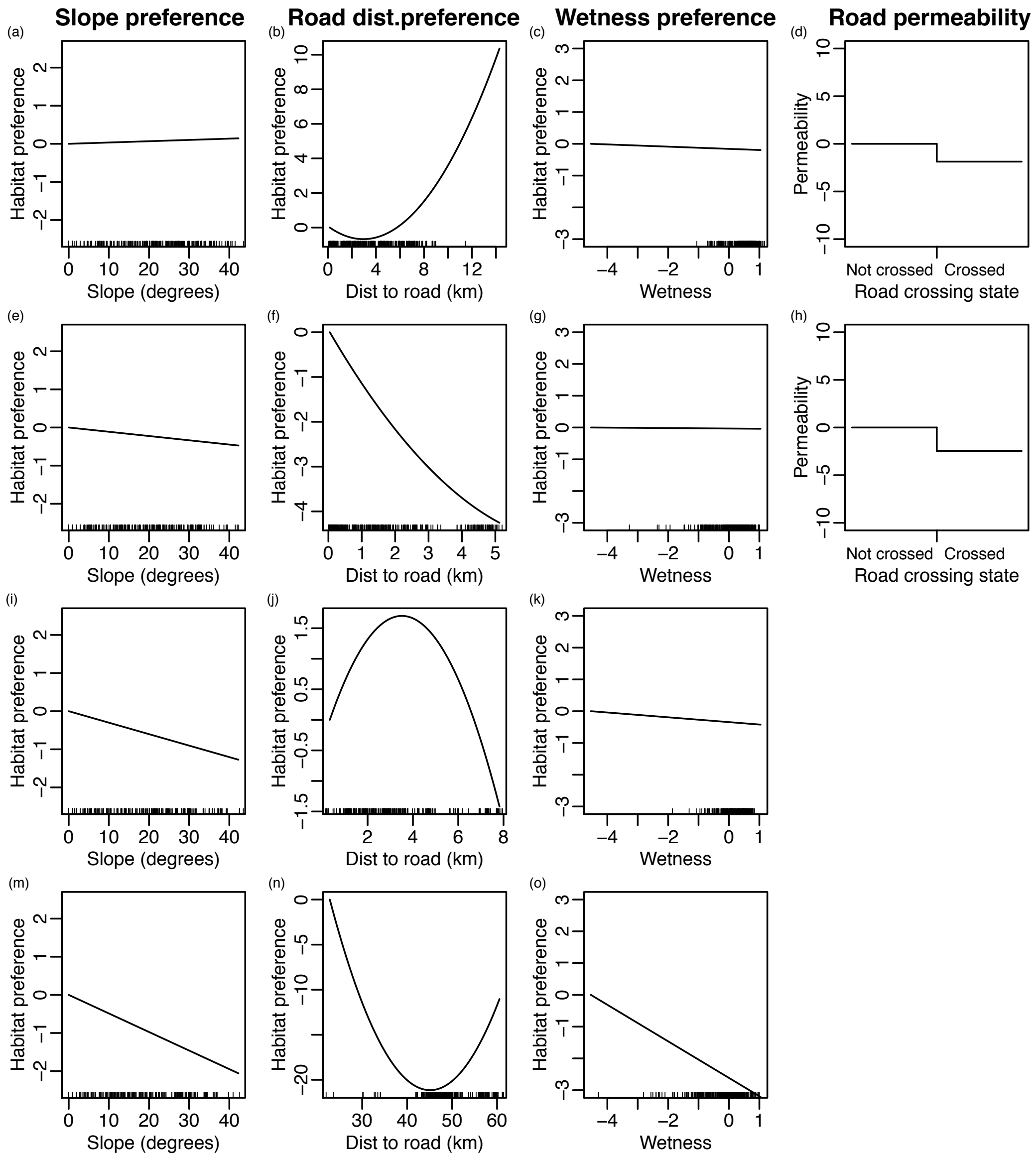


Figure A3-4. Habitat preferences of individual Asian elephants based on satellite tracking and derived resource selection functions. Rows represent a study individual (id: 16, 17, 14, 13); columns represent variables in ascending order: slope; distance to roads; wetness (a selection of multispectral bands as a proxy for closed canopy, disturbed and open habitat); and permeability. Solid lines are mean estimates. Road permeability was not estimated for id: 14 because he never crossed the road; while id: 13 moved away from the road immediately after release (average DRD = 49±11.4 SD km; range 23-60 km). All individuals are translocated elephants.

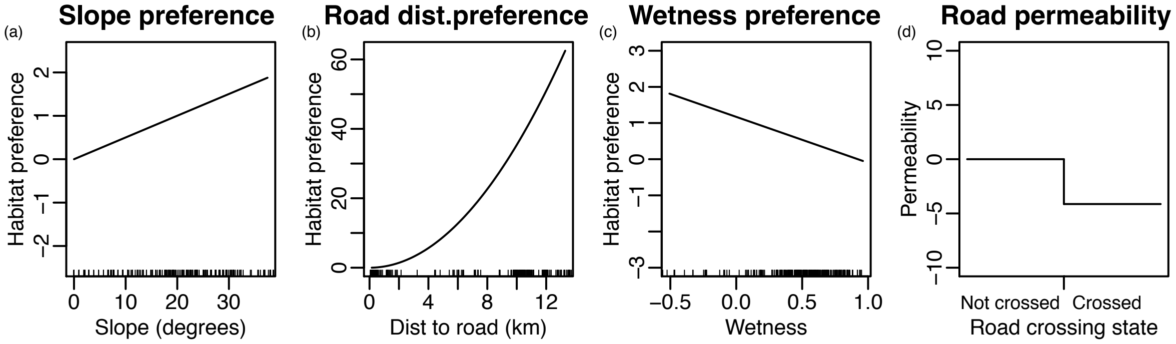


Figure A3-5. Habitat preferences of an individual Asian elephants based on satellite tracking and derived resource selection functions. Rows represent a study individual (id: 12); columns represent variables in ascending order: slope; distance to roads; wetness (a selection of multispectral bands as a proxy for closed canopy, disturbed and open habitat); and permeability. Solid lines are mean estimates. The elephant is a translocated individual.

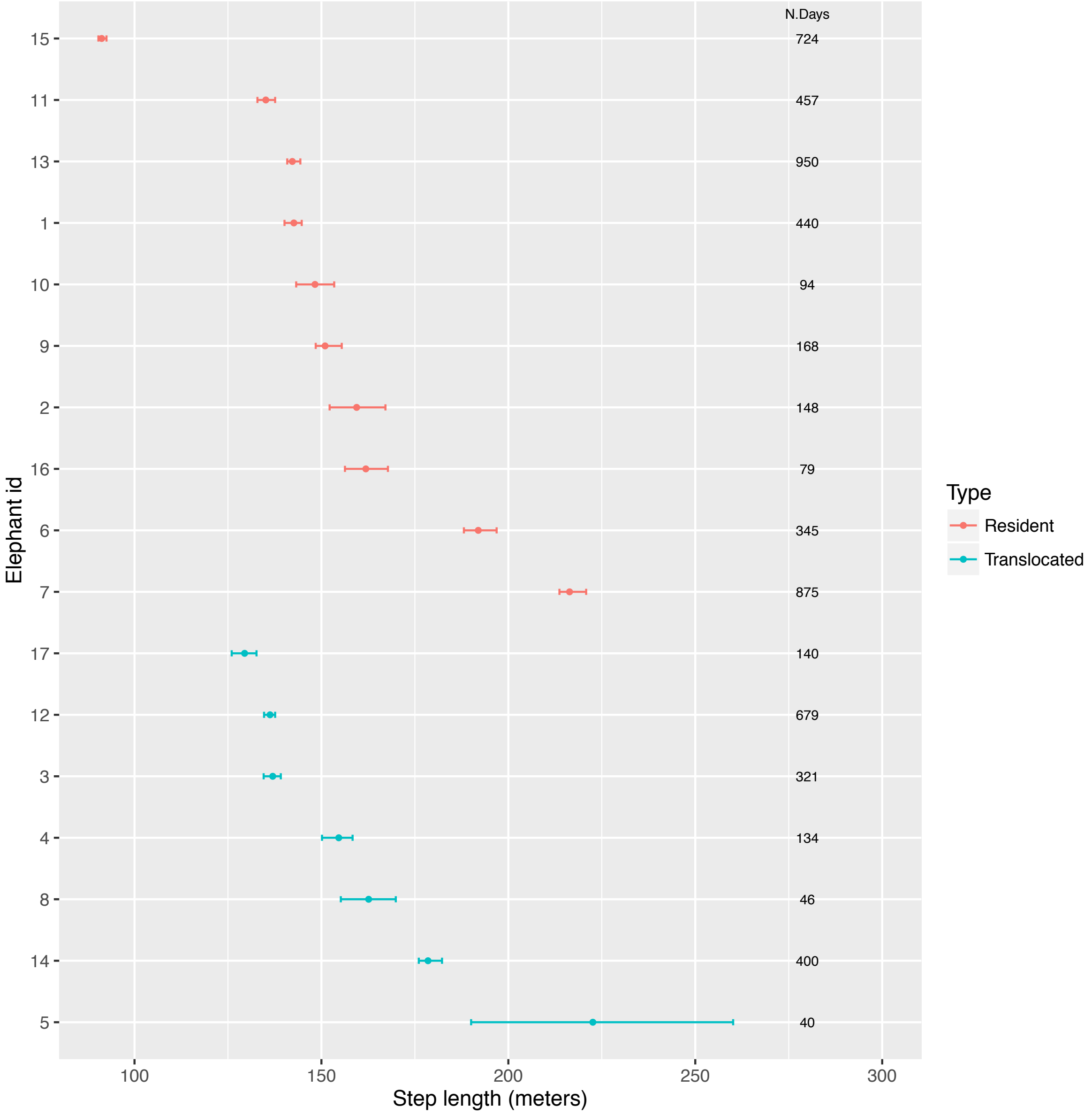


Figure A3-6. Elephant average step lengths. Step length values were calculated by taking the exponent of the parametre estimate from a random normal distribution of observations (N=100,000) and then calculating the mean of those observations. N. Days = number of days an individual was GPS collared. Elephant id = identification number of each elephant (see Table A3-2).

Figure A3-7. Distribution of wetness values with distance from the East-West highway. Points were randomly generated (n=2000) throughout the study area and then randomly subset (N=100).

Chapter 4: Movement responses of translocated elephants in Peninsular Malaysia

Authors: Wadey, Jamie[1]; Singh, Navinder[2]; Othman, Nasharuddin[3]; Saaban, Salman[3], Leimgruber, Peter[4], Campos-Arceiz, Ahimsa[1,5,*]

Affiliations:

[1] School of Environmental and Geographical Sciences, University of Nottingham Malaysia Campus, Jalan Broga, Semenyih 43500, Kajang, Selangor, Malaysia; [2] Department of Wildlife, Fish and Environmental Studies, Swedish University of Agricultural Sciences, Umeå, SE-90183, Sweden; [3] Department of Wildlife and National Parks Peninsular Malaysia, Km. 10, Jalan Cheras, 56100 Kuala Lumpur, Malaysia; [4] Smithsonian Conservation Biology Institute, Front Royal, Virginia, United States of America; [5] Mindset Interdisciplinary Centre for Tropical Environmental Studies, University of Nottingham Malaysia Campus, Jalan Broga, Semenyih 43500, Kajang, Selangor, Malaysia.

[*] **Corresponding author.** Email: ahimsa@camposarceiz.com

4.1 Abstract

Translocating elephants is a common practice in an attempt to resolve human-elephant conflict. We used GPS telemetry to explore movement responses following translocation. We collared 34 translocated and 15 local Asian elephants (*Elephas maximus*) throughout Peninsular Malaysia. In 34 translocations, 56% either returned home or left the release area, with 44% remaining at the release site. The movement behaviour of translocated elephants differed from local elephants, with no resident behaviour and higher proportions of dispersal and nomadic behaviour. Based on the total area used, local elephants settled seven months after collaring, while translocated elephants were estimated to settle 20 months post-translocation. Our step length analysis also revealed differences between groups. Translocated elephants consistently maintained higher levels of exploratory behaviour compared to locals, while translocated encamped behaviour was initially at lower levels but increased to levels similar to locals by the end of the first year. Unfortunately, (14%) male elephants, all translocated, were poached for their ivory during the study period. The results from this study reveal critical patterns of response by Asian elephants to translocation. Translocated elephants varied in their response, with a high proportion of elephants returning to the original human-conflict area and taking long periods to settle. We suggest the appropriateness of elephant translocation programs - as a human conflict mitigation method - to be seriously reconsidered.

Keywords: translocation, *Elephas maximus,* movement ecology, policy, net squared displacement, space use, home range, human-elephant conflict, HEC.

4.2 Introduction

Terrestrial megafauna are in rapid decline globally due to anthropogenic pressure (Ripple et al., 2016). In a world where human-pressure on the environment is showing no signs of abating (Venter et al., 2016), large animals are continually competing and coming into conflict with people for space and resources (Allan et al., 2017; Kareiva et al., 2007). Historically, competition and conflict between people and megafauna have resulted in megafauna population declines and extinction (Dirzo et al., 2014). Translocating megafauna, i.e., capturing individuals and relocating them to a non-conflict area (Blanc, 1998), has been widely used to mitigate the conflict and competition between humans and megafauna (Wolf, Griffith, Reed, & Temple, 1996). Although the movement responses are not well-studied, most case studies suggest translocation does not resolve the conflict (Athreya, Odden, Linnell, & Karanth, 2010; Boast, Good, & Klein, 2015; Fernando et al., 2012; Weilenmann, Gusset, Mills, Gabanapelo, & Schiess-Meier, 2010; Weise, Wiesel, Lemeris, & Vuuren, 2015). The effectiveness of translocation as a mitigation technique is concerning for megafauna, animals that are amongst some of the most threated species world-wide (Ripple et al., 2016; 2017).

Our ability to detect the impacts of translocation on megafauna can be improved with advancements in GPS technology and quantitative methods (Nathan et al., 2008). For example: (1) estimating a non-bias home range over time (Bekoff & Mech, 1984; Fleming et al., 2015a), which can help understand if and when home ranges settle (Fernando et al., 2008); (2) ability to classify large scale movement behaviour (e.g. resident, nomadic or dispersing behaviour) through net-squared displacement modelling (Bunnefeld et al., 2011; Singh, Börger, Dettki, Bunnefeld, & Ericsson, 2012) has assisted quantifying long term behavioural impacts; and (3) at smaller scales, differences in step length and turning angles can now be linked to fine scale behaviours, such as exploratory and encamped behaviour (Fryxell et al., 2008; Michelot, Langrock, & Patterson, 2016), which can demonstrate how individuals initially respond to a new environment.

There are limited studies that have monitored movements responses of megafauna post-translocation, especially elephants, a species that is commonly translocated throughout its range (Blanc, 1998). One study from Sri Lanka (Fernando et al., 2012) found: 1) out of 16 elephant translocations, five instances were recorded as ‘homers’ where elephants returned to the original conflict site; 2) six individuals as ‘wanderers’, elephants that left the national park they were released in and showed no signs of an established home range; and 3) five elephants as ‘settlers’, individuals that established a home range, however, all home ranges were established outside the national park. In addition, 12 out of 16 translocated elephants killed five humans; and 3) translocation increased elephant mortality, with 5 of 12 (42%) translocated elephants being killed (shot or poisoned). Fernando et al. (2012) concluded that translocation in Sri Lanka does not resolve human-elephant conflict (HEC) nor meet elephant conservation goals. Another study in Kenya found similar negative impacts from 150 translocated African elephants (*Loxodonta africana*) - 24 elephants died (16%) within 55 days of release, while 11 left the national park and 6 returned to the capture site (Pinter-Wollman et al., 2009). These few studies indicate similar responses have been found between African and Asian elephants, suggesting translocation may not mitigate HEC.

Southeast Asia contains the greatest number of threated megafauna from human pressure world-wide (Ripple et al., 2016; 2017). It is also a region of rapid population and economic growth (World Bank, 2016). The expected increases in the human population and economic growth will likely continue to intensify the region’s threat on native megafauna, including Asian elephants, the largest terrestrial animal in Southeast Asia. Habitat loss and HEC are the primary factors responsible for this endangered megafauna's rapid population decline and range reduction (Choudhury et al., 2008; Fernando & Pastorini, 2011). Habitat loss does not necessarily kill elephants; however, it brings humans and elephants into regular contact through the reduction of available habitat. This can lead to an increase in the availability of desirable food along forest edges and cleared areas, for example, grass patch's and agricultural crops. Inevitably resulting in HEC where elephants are regularly: 1) shot; or 2) poisoned in retaliation to the conflict and/or crop damage; and 3) translocated to mitigate HEC, with translocated effectiveness usually unknown because of the lack of post-translocation monitoring.

Within Southeast Asia, Peninsular Malaysia is an important stronghold for Asian elephants and other large megafauna (Rostro-García et al., 2016; Saaban et al., 2011). Recent reduction in forest cover in Peninsular Malaysia has resulted in persistent conflict between elephants and humans (Saaban et al., 2011). In 1974, Peninsular Malaysia set up an elephant translocation unit to mitigate this conflict (Daim, 1995). A total of 600 elephants were translocated between 1974 and 2010 (Saaban et al., 2011). Only two studies have followed the movements of translocated elephants in Peninsular Malaysia, each study tracking two translocated elephants to assess the response of translocation. One study found elephants roamed over an area of 350 and 7000 km^2 from the release point (Stüwe et al., 1998). The other study found elephants to select secondary forest over primary forest, which were regularly outside protected areas (Aini et al., 2017).

There are still key questions about elephant translocation that remain unanswered, for example: what is the return rate of translocated elephants? Does translocated distance affect the return rate? Do elephants settle (e.g. movements are similar to non-translocated elephants) in their new environment? The general aim of our study was to gain a better understanding of the movement responses following translocation. We used GPS telemetry to explore three specific issues: **A) Do translocated elephants stay at the release site?** We predict most elephants will return home or leave the PA in search of their capture location. We augmented an existing categorical framework by including the home range size of non-translocated elephants (Fernando *et al.* 2012). **B) Do translocated elephant home range size and movement patterns settle?** and **C) If settling occurs, how long does it take to occur?** We hypothesize that translocated elephants will take more than one year to settle. To answer questions **B)** and **C)** we used a combination of: i) net squared displacement modelling that quantifies the dominant movement behaviour (Bunnefeld et al., 2011); ii) accumulation curves of the total area over time; iii) changes in step length over time; and iv) classification of exploratory and encamped behaviour over time (Michelot et al., 2016). Results from this work will be informative for future elephant translocations, policies and management within Peninsular Malaysia and other Asian elephant range countries.

4.3 Materials and methods

4.3.1 Study area

This study was conducted in several landscapes of Peninsular Malaysia (Figure 4-1). Natural vegetation in these landscapes is dominated by lowland and hill dipterocarp forests with presence of some human settlements and crops, mostly oil palm and rubber plantations. Translocated elephants were captured in or near plantations and human settlements and subsequently released at one of the four following landscapes: (1) Belum-Temengor, a landscape that occupies an area of ~ 4,000 km^2; (2) Kenyir State Park (300 km^2), an area connected to Taman Negara, Malaysia's first and largest national park (4,343 km^2); (3) Endau-Rompin State Park (870 km^2); and (4) Lenggor Forest Reserve, which is part of the Johor Wildlife Conservation Protection Site, a network of interconnected forest reserves (2,000 km^2; Figure 4-1). Local elephants were tracked in four landscapes: (1) Belum-Temengor, a large mature primary dipterocarp rainforest (~ 4,000 km^2); (2) Siput-Lenggong, an area within the main range that is mostly mature secondary forest (~ 2,000 km^2), which is 75 km south of Belum-Temmengor; (3) the Gua Musang mosaic, located 10 km north of Taman Negara (Kelantan) where no continuous forest exist, and is dominated by oil palm and rubber plantations with small patches of fragmented regrowth forest (~ 300 km^2); and (4) Temerloh Forest Reserve, which consists of a mixture of logging concessions and Acacia plantations (536 km^2; Figure 4-1).

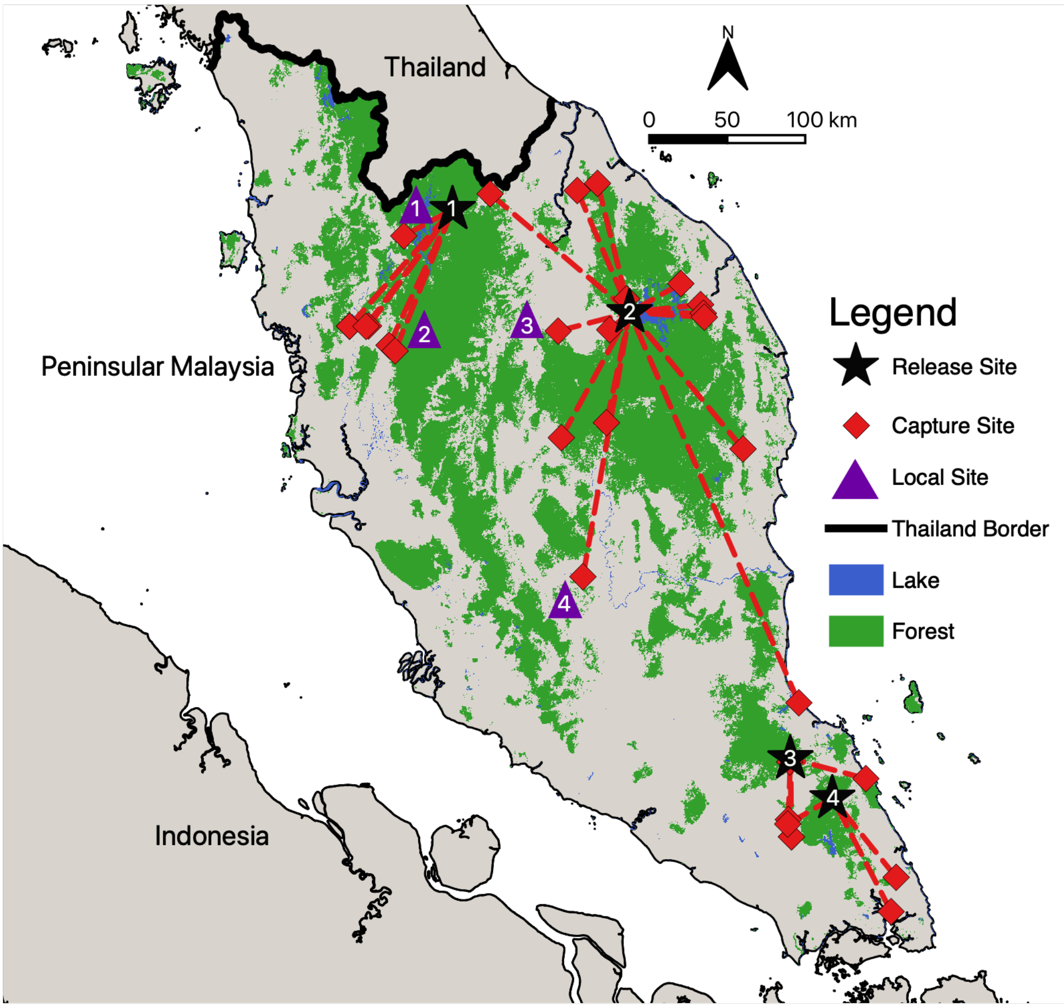


Figure 4-1. Study area in Peninsular Malaysia. Red diamonds are capture sites for translocated elephants. Black stars are release sites for translocated elephants. For release sites: 1 = Belum-Temenggor complex and main range, 2 = Kenyir state park and Taman Negara, 3 = Endau Rompin National Park, and 4 = Lenggor Forest Reserve. Purple triangles are locations of local elephants. For local sites: 1 = Belum-Temenggor and main range, 2 = Siput-Lenggong complex and main range, 3 = Gua Musang Mosaic, 4 = Temerloh Forest Reserve.

4.3.2 Elephant tracking

We tracked elephant movements using Inmarsat satellite GPS collars (10D cells, Africa Wildlife Tracking, Pretoria, South Africa) programmed to collect one GPS location every two hours. All elephants were immobilised by DWNP as described in (Daim, 1995). We complied with research and ethics requirements by the Malaysian government (permit #JPHL%TN(IP): 80-4/2).

We collared and tracked two types of elephants – "local" and "translocated". Local elephants were collared and released in the same place within a few hours of being captured. They represent the control (i.e. non-translocated) group. Translocated elephants were captured at areas of human-elephant conflict and relocated to one of the aforementioned landscapes (Figure 4-1). We tracked elephants of both sexes (male vs. female) and types (local vs. translocated). The total number of elephants tracked and their totals within these groups (male vs. female and local vs. translocated) could not be decided *a priori* because it was dependent on the success of collaring operations and DWNP's translocation program.

4.3.3 Analysis decision making

Preceding analyses were selected based on the flow chart in Figure A4-14. This section will provide a brief description behind the decision making for each research question. The first question: **A) Do translocated elephants stay at the release site?** The nature of this question requires a spatial limit where elephants are considered to have '*left*' the release site. We assumed if an elephant stays at the release site, the release site should be within its home range. Thus, we used the radius of a circular home range (of local elephants) as our distance threshold. The second and third question:

B) Do translocated elephant home range size and movement patterns settle? and **C) If settling occurs, how long does it take to occur?** We assumed if translocated elephants produced similar home range and movement values to local elephants, they could then be regarded as ‘settled’. Therefore, we plotted home range size and key movement metrics (e.g. step length) over time between to observe if the translocated elephants displayed differences and if these differences changed over time. Additionally, movement metrics (e.g. turning angles and or net squared displacement) can be used to infer behaviour of an individual. Since behavioural decisions are made at different temporal scales, we selected a fine scale (hidden Markov modelling) and course scale (net squared displacement modelling) to investigate behavioural differences between locals and translocated.

4.3.4 Home range size

We calculated each individual’s home range size, or area used, to investigate differences in the use of space between local and translocated elephants. We calculated the cumulative area used for each elephant at one-month intervals using the *rhrMCP* function in *R*’s *rhr* package (Signer & Balkenhol, 2015). Investigating the effects of home range over time has previously been used for ranging behaviour of local elephants in Sri Lanka and translocated giraffes in Namibia (Fernando et al., 2008; Flanagan, Brown, Fennessy, & Bolger, 2016). To be temporally comparable, elephant track lengths were restricted to 1 year or excluded if there was less then 1 year of data, based on a previous study that found elephant home range size reached an asymptote by 1 year (Fernando et al., 2008). We then calculated the asymptote of the cumulative area (Haines, Hernández, Henke, & Bingham, 2006) using the functions *nls*() and *SSasym*() in *R*’s *stats* package (R Core Team, 2016). Predicted values of the asymptote line were derived from the expression: cumulative used area = *Asym* + (*R0*-*Asym*) **exp*(-*exp*(*lrc*) * *x*, in which *x* is a value of the independent variable (elephant tracking time), *R0* is the cumulative area when x is zero, and *lrc* represents the natural logarithm of the rate constant.

4.3.5 Movement rates

We analysed elephant movement rates using step lengths, i.e., the geometric straight-line distance between successive locations at two-hour intervals. We estimated elephant step lengths using the function *as.ltraj* in *R*'s *AdehabitatLT* package (Calenge, Dray, & Royer-Carenzi, 2009). We first calculated the mean step length per elephant per day and then we averaged individual daily means by elephant type (local or translocated) to get a grand mean step length per day. We limited movement tracks to 1 year in length for temporal comparisons, as mentioned in the home range size methodology. We tested whether step lengths differed between both elephant groups (local vs. translocated) and whether they changed over time (i.e. since release) using linear mixed effect model using the *lme* function (Pinheiro & Bates, 2000). The model included step length as the response variable, time (day since release, 1-365) and elephant type (local vs. translocated) as well as their interaction as fixed factors, and individual elephant as a random factor.

4.3.6 Homing, settling, and wandering behaviours

We modified Fernando et al.'s (2012) approach to classify elephants in three categories (i.e. homers, settlers, and wanderers) based on where they went after being collared and released. We defined 'homers' as translocated elephants that returned to within 17.2 km of their original capture site. We used the threshold of 17.2 km because it represents twice the radius of a circle as large as the local elephants' maximum spatial coverage (95% MCP, which we previously estimated to be 232 ± 212 km^2 based on the movements of seven local elephants tracked for one year). 'Settlers' were elephants (both local and translocated) that did not move more than 17.2 km from their release location (which for local elephants was also their collaing location). 'Wanderers' were elephants (both local and translocated) that moved more than 17.2 km away from the release point but, in the case of translocated elephants, did not return to within 17.2 km of their capture site. We validated our classifications (*homer*, *settler,* and *wanderer*) by plotting the distance to release site and capture site (two response variables) over time (one explanatory variable). After a translocated elephant was released, we calculated both the distance (km; straight line distance) to the release and capture site for all GPS locations over time.

4.3.7 Individual elephants' dominant movement mode

We used net squared displacements (NSD) to classify each elephant's dominant movement mode as either resident, nomadic, dispersing, or migratory. NSD is the distance from a location to the first location measured (i.e. the release location). Dominant movement modes were modelled using existing movement models for each behaviour (Bunnefeld et al., 2011; Figure A4-1). 'Resident' are individuals that remain within a defined home range, which is represented by NSD values remaining constant after reaching an asymptote (Figure A4-1). 'Nomadic' individuals have no defined home range and are consistently increasing the total area used, which corresponds with NSD values increasing linearly over time (Figure A4-1). 'Dispersing' individuals are individuals that display a temporary defined home range then shift their home range to a new area. The NSD values of dispersing individuals initially remain constant, which then follow a vertical increase and subsequently more constant NSD values (Figure A4-1). 'Migratory' individuals are the same as disperses, however, they display two dispersal events, the second of which returns back to the initial home range over an annual cycle. This is represented by NSD values following that of dispersers, with the addition of NSD values decreasing on the second dispersal event as the individual returns back to the original area. Dispersal and migratory models are able to estimate the distance and duration of dispersing and migratory behaviour, while for resident and nomadic, distance and duration estimates are not possible. Since dispersal and migratory models can estimate the duration of the behaviour, we were able to re-run the movement models to investigate what the dominant movement mode were after the dispersal or migration period.

We fitted all NSD movement models to nonlinear mixed effects models, using the *nlme* function from *R*'s *nlme* package with REML settings (Pinheiro & Bates, 2000). The NSD of an elephant's movement path was estimated using the *as.ltraj* function in *R*'s *adehabitatLT* package (Calenge et al., 2009). We limited the number of days an individual was tracked to 100 days and maximum of 1 year, as small sample periods are known to cause overfitting (Pinheiro & Bates, 2000). Additionally, we also compared individuals with one year of data to confirm whether of variable track length approach is suitable. Model fit for each individual was evaluated using the concordance criterion (CC; Huang et al., 2009), which measures the level of agreement between observed and predicted values. CC is a combined measure of the degree of accuracy and precision of pairs of values (Huang, Meng, & Yang, 2009; Singh et al., 2012) and it ranges from -1 to 1, whereby negative values indicate lack of fit and higher positive values indicate improved fit. 'Mixed' behaviours can occur if the highest CC values are similar between different movement modes (Huang et al., 2009).

4.3.8 Daily proportion of encamped vs. exploratory behavioural states

We identified different behavioural states along movement paths using hidden Markov models (HMMs; Patterson, Basson, Bravington, & Gunn, 2009). We modelled two different behavioural states: (1) encamped behaviour, which involves movements with many turns and mostly short step lengths; and (2) exploratory behaviour, which involves less frequent turns (straighter movements) and larger step lengths. We followed the workflow of Michelot et al. (2016) using the *moveHMM* package and fitted HMM models using the function *fitHMM*. Initial parametres for the gamma and von Mises distributions were selected as recommended by Michelot et al. (2016). We then calculated the daily proportion of encamped and exploratory behaviour per elephant per day and averaged all individual proportions by type (local or translocated) to get a grand mean percentage of behaviour (exploratory and encamped) per day. We limited movement tracks to 1 year in length for temporal comparisons, as mentioned in the home range size methodology. We tested whether there was an effect of time since release on the distribution of behavioural states (encamped and exploratory) by fitting a linear mixed effect model using the *lme* function (Pinheiro & Bates, 2000). The model included percentage of behavioural state (encamped or exploratory) as the response variable, time (day since elephant release, 1-365), elephant type (local or translocated), and their interaction as fixed factors, and individual elephant as a random factor.

4.4 Results

4.4.1 Elephant tracking

We collared a total of 49 wild Asian elephants between 2011 and 2018 including 34 translocated (6 female and 28 male) and 15 local (10 female and 5 male) individuals (Table A4-1). Translocated and local elephants were tracked for an average (± SD) of 303 ± 232 (range = 11-924) and 431 ± 344 (72 - 1016) days respectively, giving total tracking periods of 10,334 days (125,787 GPS fixes) for translocated elephants and 6,470 days (66,119 GPS fixes) for local elephants. There was no difference in the number of tracking days between local and translocated elephants ($t = 1.30$, $df = 19.85$, $P = 0.20$) but female elephants were tracked for a period 1.6 times longer than males (469 ± 312 vs. 281 ± 235 days; $t = 2.12$, $df = 23.53$, $P = 0.04$). Only 18 elephants were tracked for a continuous period of at least one year: seven local (two males and five females) and 11 translocated (seven males and four females; Table A4-1) individuals. Translocated elephants were relocated an average distance of 76 ± 46 (range = 16-271) km away from their capture point (Table A4-1). There was no difference in translocation distance between sexes ($t = -0.53$, $df = 12.30$, $P = 0.60$). Four out of the 28 (14%) male elephants, all translocated, were poached for their ivory during the study period (Table A4-1). We did not record any human death or injury caused by the collared elephants.

4.4.2 Home range size

Local and translocated elephants displayed very different behaviours in their use of space. The average home range size or area used by local elephants (n = 15 elephants) reached an asymptote at 153 ± 17 km^2 after seven months, while translocated elephants (n = 34 elephants) used an area three times bigger and required more than double the time to cover it (they reached the asymptote at 817 ± 151 km^2 after 20 months; Figure 4-2). The goodness of fit for the asymptote regression line produced r^2 values of 0.43 and 0.56 for translocated and locals. This suggested that on average, our regression models predicted around half ($r^2 = 0.43$ and 0.56) of the variability in our data. The maximum home range size for translocated elephants (2,279 km^2) was nearly six times larger than the maximum home range for a local elephant (387 km^2; Figure 4-2). The maximum displacement from the release site was 84 km for translocated elephants and 23 km for local elephants (Figure A4-2). We excluded abnormal data of one local elephant (month 16 to 29; id:13;Table A4-1; Figure A4-3) after it was hit by a vehicle (at month 15) and lost a tusk (fortunately neither elephant nor driver suffered major injuries). The increase in area for the elephant (id:13) was a result of leaving the area of the vehicle collision (northern Malaysia) and resettling (~60 km) away in southern Thailand.

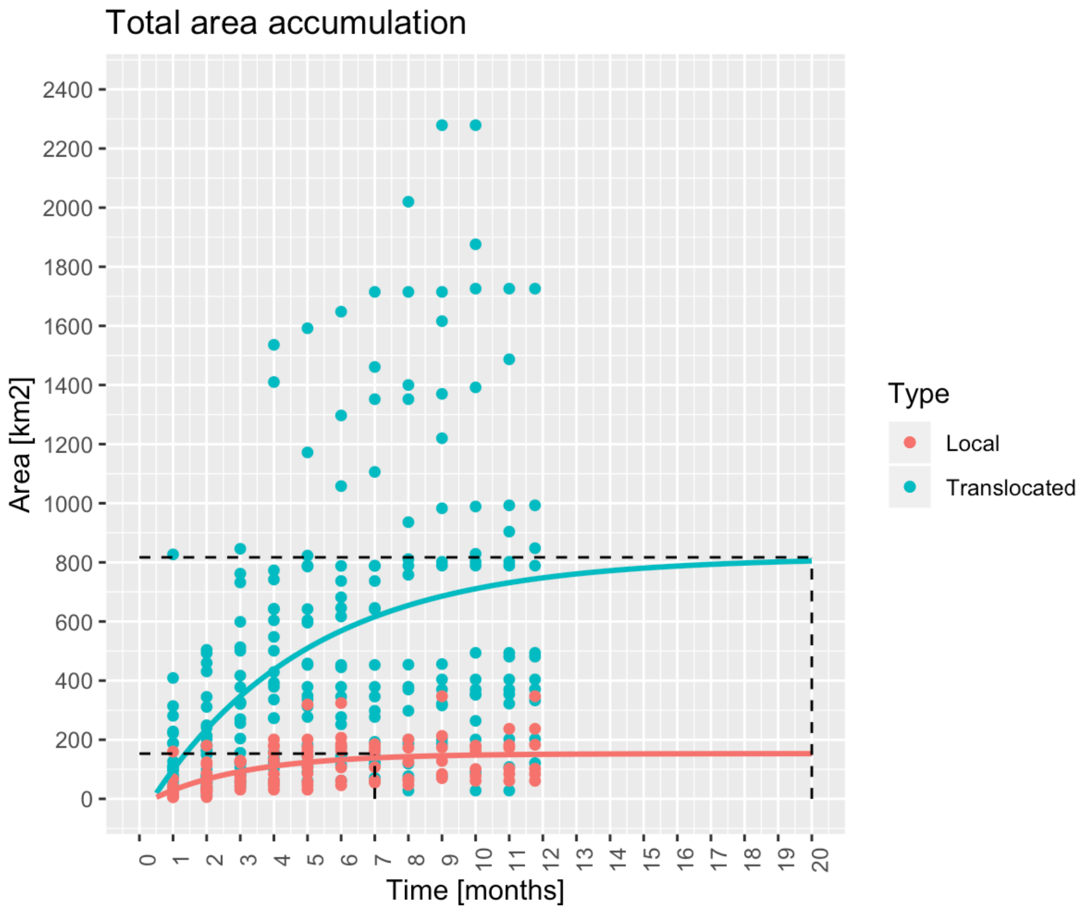


Figure 4-2. Total area accumulation of local and translocated elephants over time. Points are total area calculations for individuals, while smoothed lines represent the grand mean.

4.4.3 Movement rates

Translocated elephants (mean step length = 244 ± 51 m; n = 34 elephants) had higher movement rates than local elephants (183 ± 39 m; *b* = 54.1, SE = 6.8, df = 350, t = 8.1, p << 0.0001; n = 15 elephants; Figure A4-4), although the difference between both groups declined over time, as indicated by the interaction between ‘elephant type’ and ‘time since collaring’ (*b* = -0.09, SE = 0.03, df = 350, t = -2.2, p = 0.005; Figure A4-4). At this rate, we estimate that it would take 1.6 years for translocated elephants to exhibit similar movement rates to local elephants. We also found variation within daily step lengths to remain constant over time (Figure A4-5), suggesting the use of a daily average to be justifiable.

4.4.4 Homing, settling, and wandering behaviours

In 34 translocations, eight (24%) elephants responded as homers (returned to the capture site), 15 (44%) as settlers (stayed at the capture site), and 11 (32%) as wanderers (left the release site and did not return to the capture site; Figure 4-3; Table A4-1). All 15 local elephants responded as settlers (Figure 4-3; Table A4-1). Neither translocation distance ($f = 2.4$, $df = 2$, $P = 0.1$; Figure A4-6) nor the length of the period tracked ($f = 0.35$, $df = 2$, $P = 0.7$; Figure A4-7) affected the type of elephant response to translocation (see Table A4-1; Figure A4-6; Figure A4-7). Our validation method (comparing patterns between distance to release site and capture site over time) revealed the same patterns within each classification (*homer*, *settler,* and *wanderer*): for all *homers*, the distances from the capture site decreased over time while distance from release site increased over time; for all *settlers*, the distance to both capture and release site remained horizontally parallel; and for all *wanderers*, both distances increased over time without intersection (Figure 4-3).

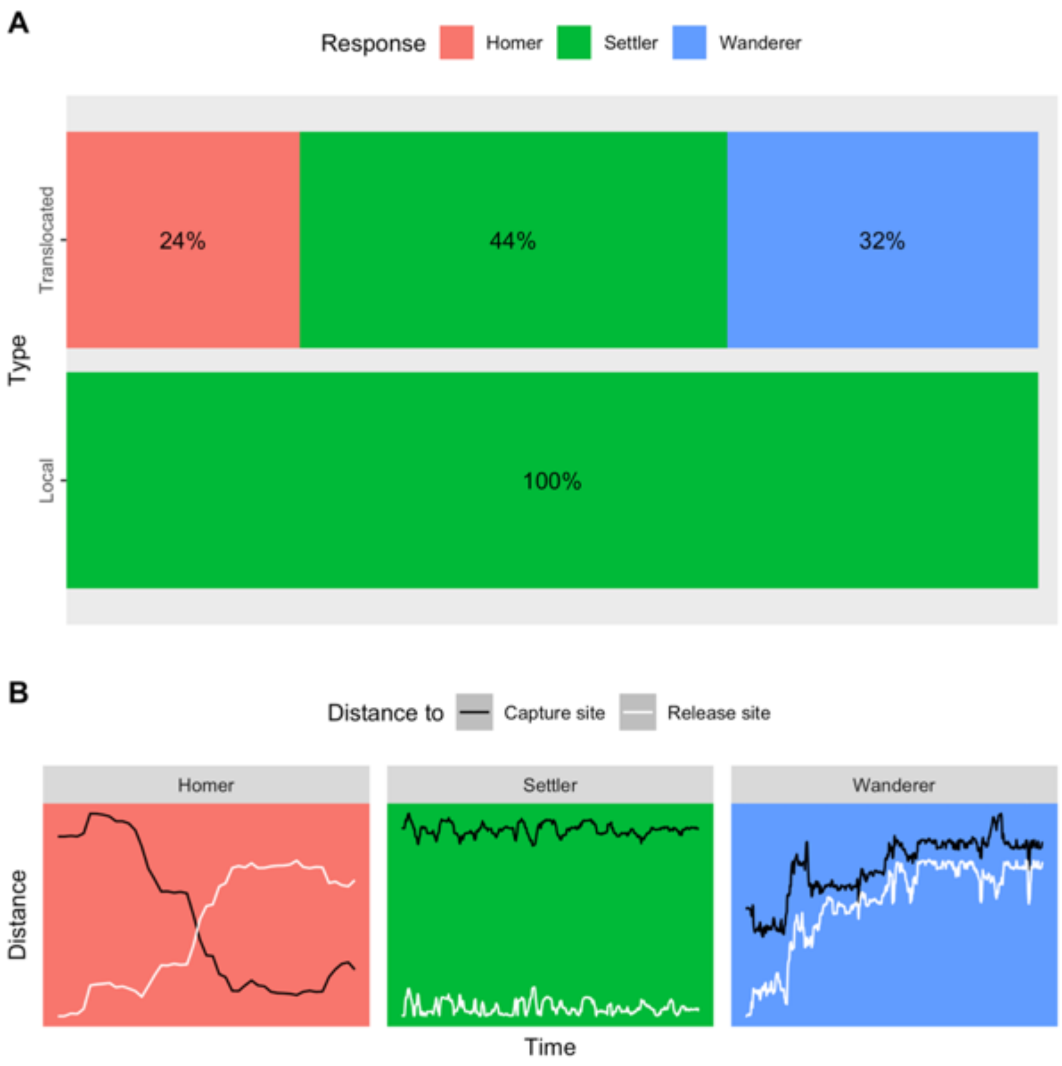


Figure 4-3. Proportions of homer, settler, and wanderer behaviours. (A) Local '*settler*' n = 15 out of 15 (100%). Translocated '*homer*' n = 8 out of 34 (24%), '*settler*' n = 15 out of 34 (44%), and 'other' n = 11 out of 34 (32%). (B) The distance relationship from capture and release sites for homers, settlers and wanderer.

4.4.5 Individual elephants' dominant movement mode

The behaviour of local elephants (n = 12 individuals) was predominantly resident (67% of elephants), with just two elephants (17%) displaying a mixed behaviour (resident-nomadic and resident-dispersal) and another two elephants (17%) displaying nomadic behaviour (Figure 4-4; Figure A4-8; Table A4-2). No local elephants displayed a dominantly dispersal behaviour (Figure 4-4; Figure A4-8; Table A4-2). The behaviour of translocated elephants (n = 26 individuals) was very different with 50% of them exhibiting a dominantly dispersal behaviour, 34.6% exhibiting nomadic behaviour, 7.7% nomadic-resident, and 7.7% mixed dispersal-resident (Figure 4-4; Figure A4-8; Table A4-2). No translocated elephant displayed a dominantly resident behaviour, and neither local nor translocated, displayed a migratory behaviour (Figure 4-4; Figure A4-8).

Translocation distance did not affect the type of the dominant movement mode (*f* = 1.96, *df* = 2, *P*= 0.16; n = 34 elephants; Figure A4-9). The elephants with a dominant dispersing behaviour (n = 13 elephants) showed average dispersal phases of 87 ± 79 days (range 6-264 days) and maximum displacement distances of 36 ± 20 km (range 18-97 km) away from their release site (Figure A4-10). After dispersal, 40% of them displayed a nomadic behaviour, 20% settled down, and the remaining 40% exhibited mixed behaviours (Figure A4-11; Table A4-3). After completing their dispersal, elephants moved on average 18 ± 10 km (range 5-38 km) from the newly dispersed area (Figure A4-12). Two translocated elephants contained dispersal phases in its mixed behaviour (dispersal-resident), which corresponded to dispersal distance of 29 and 12 km over 22 and 27 days (Figure A4-12). While one local elephant exhibited a dispersal phase in their mixed behaviour (resident-dispersal), this individual dispersed 21 km over 36 days (Figure A4-2). On average local elephants moved 13.8 ± 4.3 km (range 10-23 km) from the release site, while translocated elephants were greater at 38.0 ± 22.2 km (range 14-97 km), which was found to be statistically different (*f* = 8.32, *df* = 1, *P* = 0.01; Figure A4-2). In addition, we did not find large differences of behavioural classifications between elephants with only one-year tracking data and elephants with a minimum of 100 days and maximum of one-year (See Analysis A4-1 in the Appendices for further details).

Figure 4-4. Behaviour classification of the dominate movement behaviour using NSD modelling approach for local and translocated elephants. (A) Local '*dispersal*' n = 0 out of 12 (0%), '*mixed*' n = 2 out of 12 (17%), '*nomadic*' n = 2 out of 12 (17%), '*resident*' n = 8 out of 12 (67%). Translocated '*dispersal*' n = 13 out of 26 (50%), '*mixed*' (resident-nomadic) n = 2 out of 26 (7.7%), '*mixed*' (dispersal-resident) n = 2 out of 26 (7.7%), '*nomadic*' n = 9 out of 26 (34.6%), and '*resident*' n = 0 out of 26 (0%). (B) The movement signatures for the different movement behaviours, with NSD as the response variable and time as the explanatory variable.

4.4.6 Distribution of behavioural states in the year after release

Local elephants (n = 15 elephants) showed a relatively constant distribution of behavioural states within a day compared with translocated elephants (n = 34 elephants; Figure A4-13). Both local and translocated elephants showed signs of exploratory and encamped behaviour in the first day post-release (Figure A4-13). The maximum number of days an individual elephant took to display its first encamped and exploratory movement was 23 and 20 (locals) and 55 and 16 (translocated) respectively. On average local elephants took less time to display their first encamped behaviour (2.3 ± 5.1 days) compared to translocated elephants (4.5 ± 11.0 days), whereas, for exploratory behaviour, translocated elephants on average took less time to display their first exploratory behaviour (1.9 ± 2.5 days and 3.2 ± 4.4 days). The percentage of encamped behaviour for translocated elephants remained lower in the first 150 days, then increased above local elephant levels following a decrease to a similar percentage of encamped behaviour by the end of the first year (Figure A4-13).

We found a significant difference in the proportion of encamped behaviour of translocated and locals (*b* (fixed effect estimate) = -4.4, SE = 1.5, df = 350, t = -3.1, p = 0.003); and the interaction between elephant type (local and translocated) and time was also significant with translocated elephants over time (*b* (fixed effect estimate) = 0.04, SE = 0.01, df = 350, t = 3.1, p = 0.0000001).

The overall daily percentage average of encamped behaviour in the first year for local and translocated elephants were similar at 71 ± 13 % and 62 ± 8 % respectively, while translocated exploratory behaviour was on average greater than locals (49 ± 7 % and 44± 11 %). There was no difference in exploratory behaviour of translocated and locals (*b* (fixed effect estimate) = 1.1, SE = 0.9, df = 350, t = 1.3, p = 0.9) and the interaction between elephant type (local and translocated) over time (*b* (fixed effect estimate) = 0.05, SE = 0.001, df = 351, t = 2.1, p = 0.11).

4.5 Discussion

We show the movement responses of a megaherbivore to translocation. We also demonstrate how individuals may exhibit different behaviours over time in new environments initially, while some may settle, whereas others may continue to be nomadic for long periods of time. This study has found translocation to have both short and long-term effects on elephant space use and movement patterns. In the short-term, the majority of translocated elephants did not remain at the release site, with more than half (56 %) either leaving the protected area or returning back to the capture site (up to 80 km away; Figure 4-3). The number of individuals returning to the capture site or leaving the PA is significant, however, we predicted this proportion to be greater. We also found unsustainable rates of translocated males being poached (14 %; out of 28), whereas none of the local males were poached (0 %; out of 5). We found evidence to support our hypothesis that translocated elephants would take more than one year to settle. For example, the dominant movement behaviour of translocated elephants still differed one-year post-translocation, with higher rates of dispersal and nomadic behaviours, plus no resident behaviour - which was the dominant behaviour for local elephants (Figure 4-4). Additionally, home range size of translocated elephants did not settle (reach an asymptote) in the first year whereas local elephants had settled (reach an asymptote) by the seventh month (Figure 4-2).

Distance from the capture site did not determine if an individual would return (Figure A4-6; Table A4-1). The maximum distance we recorded an individual returning to its capture site was 80 km (Figure A4-6; Table A4-1); with the maximum translocated distance being 270 km and average 77±48 km. Our maximum homing distance was within the maximum known homing distance of 300 km in South Africa (Viljoen et al., 2008) and 180 km in India (Choudhury, 1993). We assumed that all elephants preferred their capture site compared to their release site and, as such, we expected more elephants to return home (24 %; out of 34), especially elephants for which translocation distance was within the distance travelled by other elephants that returned home. Topography may be a reason why some elephants did not return home. Despite being translocated short distances, mountainous areas between capture and release sites were common. This is supported by a previous study in Kenya Africa that found even minor hills were significant energy barriers for elephants (Wall et al., 2006).

Multiple theories exist on what mechanism animals use for navigation. Spatial memory is suggested to be the navigational mechanism behind some returning behaviour in elephants, with a previous study finding highly directional movements through minimising travel distance when returning to a known location (Polansky et al., 2015). We suggest spatial memory is likely to be involved with the returning behaviour as we also found that our homing elephants' paths home were highly directional. If spatial memory is the mechanism behind homing behaviour, we postulate two possible reasons why some elephants did not return home: 1) They were translocated within their home range and have no preference between the two locations; or 2) They were translocated to an area outside their home range and thus have no spatial memory to return home.

Based on the strong social bonds that female elephants have within their family herds (de Silva & Wittemyer, 2012), we expected higher proportions of females to return home to re-join their herd compared to males, which are generally solitary in nature. We found one out of five females (20 %) returning home compared to seven out of 20 males returning home (35 %; Table A4-1). One reason why males returned more often could be due to larger home ranges, which would suggest the navigational mechanism to possibly be spatial memory. As elephant herds are led by older females, we suspect being translocated without their group leader(s) would negatively impact homing behaviour of other female members of the herd. The lack of a matriarch in African elephants is known to have negative effects on the individuals by increasing stress levels and lowering reproductive output (Gobush, Mutayoba, & Wasser, 2008). In our study it is unclear why males returned more often; one possible reason could be related to a preference of resources and mates; another reason could be that males range over larger areas within a lifetime (more than one annual home range estimate).

Whether an elephant leaves a PA following translocation is unpredictable. In this study, 45 % of elephants remained in the PAs. This is considerably higher when compared to Sri Lanka, where 0 % of elephants (n =16) remained in the PA (Fernando et al., 2012), but markedly lower when compared to Kenya where almost all elephants stayed in the PA (92 %, n =109; Pinter- Wollman et al., 2009). One reason could be the size of the PA in the Kenyan study being larger than in the Sri Lankan and Malaysian studies and therefore able to support greater number of elephants. Another possible reason why the Kenyan elephants did not leave the PA could be due to the high poaching pressure outside the PA (Blake et al., 2008; Coutu, Lee-Thorp, Collins, & Lane, 2016; Granados et al., 2012).

In our study, 14 % of translocated males were poached outside a PA or within 3 km of a park boundary. Therefore, elephants that remained in the PA could be doing so as a means of avoiding risk. Previous crop-raiding behaviour may also be a key factor in determining whether an elephant stays in a PA. Elephants in shared landscapes are usually preferential feeders rather than obligate crop raiders (Ekanayaka, Campos-Arceiz, Rupasinghe, Pastorini, & Fernando, 2011), and by translocating an elephant with obligate crop-raiding behaviour, we suggest the likelihood of reform and staying in a PA is low. This is particularly evident in

Sri Lanka where 84 % of translocated elephants resumed crop-raiding behaviour when they were moved to an area outside a PA (Fernando et al., 2012).

This is the first study that has quantified when translocated elephants have ‘settled’ using space use and movement patterns, which makes comparisons to other samples difficult. Based on our local elephants, we expected similar proportions of ‘resident’ behaviour with the translocated elephants. Initially, we did not record any ‘resident’ behaviour following translocation (Figure 4-4). However, one translocated elephant started showing resident behaviour after completing their dispersal phase (Figure A4-11). We suggest the movement behaviour of translocated elephants to be influenced by the need to learn the distribution of resources and conspecifics in their new environment and avoid conflict. The lack of resident behaviour and increased proportions of dispersal and nomadic behaviours is likely due to a learning phase which probably requires exploring a larger area. This explanation is supported by the total area used for translocated elephants, which was estimated to take around 20 months to asymptote, compared to locals needing only seven months.

Little is known about the factors that influence movement rates for translocated elephants. In Africa, local elephants recorded larger step lengths in the dry season when walking towards water (Wato et al., 2018), while another study found increases in step length at night when poaching levels were higher (Ihwagi et al., 2018). We expected translocated step lengths to be initially larger than local elephants but to reduce over time to that of local levels. We found evidence that translocated step lengths would require around 1.7 years before they would be indistinguishable from locals. We suggest the gradual decrease in step length over time could be a result of an increasing spatial memory, leading to less exploratory behaviour when locating resources. This is further supported by Fryxell et al. (2008), who found exploratory behaviour of reintroduced elk to have larger step lengths, while smaller steps lengths were related to encamped behaviour.

We showed that translocated elephants consistently maintained higher levels of exploratory behaviour throughout the first year compared to locals. Initially, the translocated individuals exhibited encamped behaviour less often than locals. However, by the end of the first year they had increased to similar levels, suggesting some sign of settling (Figure A4-13). The consistent availability of food and water throughout the year is a possible explanation as to why local elephants had higher and stable proportions of encamped behaviour. We expected exploratory behaviour of translocated elephants (especially in the early stages of the release e.g. first month) to be lower than locals, largely due to the stress of translocation. However, we did not find any evidence to support this (Figure A4-13).

We acknowledge several caveats with our study. Firstly, some of our 'settler' classifications could be misclassified due to small tracking periods. There were five elephants which were tracked for less than 60 days. Less than 60 days of tracking may not be long enough to classify the 'true' response - in our study, we found one elephant (id 21; Table A4-1) that spent more than 60 days (~85 days) at the release site before making directional movements back to the capture site. In any case, our 'settler' classifications are conservative and likely to be less than the 44% we recorded, which only strengthens our findings that translocated elephants are unlikely to remain or settle in protected areas. Secondly, our translocation data was biased towards males, with 28 out of 34 elephants being males. However, in Peninsular Malaysia, this may be an artefact of the translocation process where males cause more HEC than females (Saaban et al., 2011) and inevitably more males are translocated than females. Thirdly, comparing NSD behavioural classifications where track length varied between individuals can be misleading and often affected by confounding factors, such as, seasonality. However, we have shown even when comparing elephants with one-year track length, variation in behavioural classifications were minimal (Table A4-4). The lack of seasonality in Peninsular Malaysia is unlikely to influence the movement of elephants as food and water is plentiful all year round. Lastly, it is a possibility that elephants who were translocated were not the individual(s) causing the conflict. Correct identification of elephants in dense tropical forest could obscure direct sightings of a whole family unit or individuals that are causing HEC.

4.6 Conclusion

Our study has direct policy and management implications for elephant conservation in Peninsular Malaysia and other elephant range states. All translocated elephants were released in landscapes that are important ecological linkages in Malaysia's CFS land-use masterplan (DTCP, 2014). This study will inform the National Elephant Conservation Action Plan, which will assist in achieving long term translocation goals (DWNP, 2013). This study found: (i) translocated elephants took long periods to settle; (ii) the majority of translocated elephants either returned to the original conflict area or left the protected area; and (iii) high rates of translocated males were poached (14 %). Hence, translocation of elephants in Peninsular Malaysia defeats both HEC mitigation and conservation goals. Accordingly, we recommend: (1) translocations only be used for management of small size herds that are not genetically viable; (2) if they must be translocated then the release site should be further than the largest known homing case in Peninsular Malaysia (i.e., > 80 km); (3) neighbouring locations to release sites should be low in human density; (4) if elephants are to be translocated, monitoring through GPS-telemetry is essential; and (5) public awareness and education efforts to increase the tolerance of elephant presence and co-existence to ease the demand for translocation as a HEC mitigation method. However, there may be situations where translocation might be necessary as a last resort, for example, human-killer elephants, systematic fence-breakers or reintroducing elephants into forests where they have become locally extirpated.

Overall, our results highlight the importance of considering movement responses when translocating megafauna and other wildlife, especially with a species that persists in a region where the primary threat to survival – human-elephant conflict – is showing no signs of abating. The conservation of these endangered megafauna will require, among others, habitat protection, landscape connectivity, increasing people’s tolerance, and protection from poaching.

4.7 Authors' contributions

ACA, JW, NO and SS conceived the idea; ACA, JW, NO, and SS collected the data; JW, NS and PL designed the modelling approach; ACA, JW and NS analysed the data; ACA, and JW led the writing of the manuscript; all authors contributed critically to the writing.

4.8 Acknowledgements

This study is part of the Management & Ecology of Malaysian Elephants (MEME), a joint research project between the Department of Wildlife and National Parks (DWNP) Peninsular Malaysia and the University of Nottingham Malaysia Campus. We are very grateful to DWNP, and especially to Dato' Abdul Rasid Samsudin and Dato' Abdul Kadir bin Abu Hashim, DWNP's former and current Director Generals, for the permits to conduct this research and for the continuous support in the field. Field activities were generously financed by grants from Yayasan Sime Darby (grant M0005.54.04), Wildlife Reserves Singapore (grant S0002.54.02), and Marinescape (grant M0004.5404). DWNP's elephant translocation team and Perak's elephant unit conducted the elephant capturing and sedation; Mohammad Rizal Bin Paimin, Steven Lim, Mei Mei Chu, Aris Mohamad Oziar, Alicia Solana Mena, Param bin Pura, Muhammad Tauhid bin Tunil, Sudin Anak lelaki Din, Rizuan Bin Angah, and may other individuals provided key assistance during elephant collaring and tracking activities. The Smithsonian Conservation Biology Institute provided technical support and training.

4.9 Data Accessibility

The elephant movement data presented in this manuscript are already archived at movebank.org

4.10 Appendices

4.10.1 Tables

Table A4-1 Descriptives of GPS collared elephants. ID = individual elephant; Translocated = translocated elephant; Local = local elephant (not translocated); No.Days = number of days the elephant was GPS-tracked; Trans. Dist = distance [km] elephant was translocated from the capture site. Here we tabled whether elephants were locals or translocated, their response to translocation and other attributes, such as, sex and distance translocated.

ID	Type	Response	Sex	Trans.Dist	No.Days	Name
1	local	settler	female	NA	353	Dayang Siput
2	local	settler	female	NA	168	Mama Kay
3	local	settler	female	NA	102	Mek Banun
4	local	settler	female	NA	581	Mek Fish
5	local	settler	female	NA	1016	Mek Kamsul
6	local	settler	female	NA	931	Mek Pergau
7	local	settler	female	NA	889	Puteri Rafflesia
8	local	settler	female	NA	77	Rafflesia
9	local	settler	female	NA	204	Yong Chepor
10	local	settler	female	NA	190	Yong Jalong
11	local	settler	male	NA	484	Awang Banun
12	local	settler	male	NA	355	Awang Mendelum
13	local	settler	male	NA	875	A S Kedah
14	local	settler	male	NA	86	Castello
15	local	settler	male	NA	72	Yeob Bendang
16	translocated	homer	female	37	398	Mek Gawi
17	translocated	homer	male	33	568	Awang Illham
18	translocated	homer	male	17	259	Awang Putih
19	translocated	homer	male	39	137	Awang Seri Timur
20	translocated	homer	male	65	70	Awang Waha
21	translocated	homer	male	39	222	Baung
22	translocated	homer	male	84	481	Cherang
23	translocated	homer	male	54	28	Limau Kasturi
24	translocated	wanderer	female	96	481	Mek Polis
25	translocated	wanderer	female	99	206	Yong Jalong1
26	translocated	wanderer	male	85	362	Awang Jenor
27	translocated	wanderer	male	48	315	Ajit
28	translocated	wanderer	male	171	484	Awang Bakti
29	translocated	wanderer	male	35	923	Awang Kapak
30	translocated	wanderer	male	50	11	Awang Sindora
31	translocated	wanderer	male	113	339	Awang Teladas
32	translocated	wanderer	male	50	303	Pak Malau
33	translocated	wanderer	male	33	92	Kudong
34	translocated	wanderer	male	80	148	Awang Chepor
35	translocated	settler	female	46	230	Mek Dusun
36	translocated	settler	female	94	679	Mek Jalong
37	translocated	settler	female	47	827	Mek Kemat
38	translocated	settler	male	48	510	Awang Badur
39	translocated	settler	male	91	394	Awang Halim
40	translocated	settler	male	87	351	Awang Sedili
41	translocated	settler	male	271	23	Awang Sindora1
42	translocated	settler	male	72	505	Awang Tahan
43	translocated	settler	male	99	134	Sauk
44	translocated	settler	male	52	53	Awang Belitung
45	translocated	settler	male	91	40	Awang Lasah
46	translocated	settler	male	96	60	Awang Udin
47	translocated	settler	male	84	130	Cherang Hangus
48	translocated	settler	male	117	44	Jerek
49	translocated	settler	male	80	251	Tok Giring

Table A4-2. Best Concordance Criterion (CC) values for ranking the different movement behaviours under the NSD modelling framework. Values are bounded from 0-1 with the highest-ranking value denoted as the best model. Mixed best models are assigned when CC values are within 20% of the best model (Huang et al., 2009).

Nam	Type	Resident	Null	Nomadic	Dispersal	Disp.Dist	Disp.Day	Top.Model
Yong Chepor	Local	0.12	0.00	0.00	0.14	21.00	36	Mixed
Puteri Rafflesia	Local	-0.10	0.00	-0.12	0.00	0.00	0	Mixed
Awang Mendelum	Local	0.17	0.00	0.34	0.00	0.00	0	Nomadic
Dayang Siput	Local	0.17	0.00	0.60	0.00	0.00	0	Nomadic
Awang Banun	Local	0.07	0.00	-0.05	0.00	0.00	0	Resident
Awang S Kedah	Local	0.89	0.00	0.44	0.00	0.00	0	Resident
Mama Kay	Local	0.03	0.00	0.00	0.00	0.00	0	Resident
Mek Banun	Local	0.17	0.00	0.06	0.00	0.00	0	Resident
Mek Fish	Local	0.04	0.00	0.02	0.00	0.00	0	Resident
Mek Kamasul	Local	0.05	0.00	0.03	0.00	0.00	0	Resident
Mek Pergau	Local	0.10	0.00	0.01	0.00	0.00	0	Resident
Yong Jalong	Local	0.27	0.00	0.03	0.00	0.00	0	Resident
Ajit	Translocated	0.28	0.00	0.48	0.69	41.00	220	Dispersal
Awang Bakti	Translocated	0.27	0.00	0.62	0.95	29.00	264	Dispersal
Awang Illham	Translocated	0.73	0.00	0.86	0.88	32.00	98	Dispersal
Awang Jenor	Translocated	0.40	0.00	0.10	0.48	24.00	38	Dispersal
Awang Kapak	Translocated	0.63	0.00	0.89	0.95	33.00	143	Dispersal
Awang Teladas	Translocated	0.29	0.00	0.31	0.58	28.00	177	Dispersal
Buang	Translocated	0.81	0.00	0.65	0.91	40.00	50	Dispersal
Cherang	Translocated	0.67	0.00	0.69	0.93	97.00	72	Dispersal
Kudong	Translocated	0.11	0.00	-0.12	0.19	22.00	28	Dispersal
Mek Gawi	Translocated	0.20	0.00	0.06	0.21	37.00	6	Dispersal
Mek Polis	Translocated	0.37	0.00	0.13	0.74	57.00	28	Dispersal
Pak Malau	Translocated	0.38	0.00	0.39	0.49	39.00	93	Dispersal
Sauk	Translocated	0.88	0.00	0.75	0.96	20.00	40	Dispersal
Awang Putih	Translocated	0.12	0.00	0.14	-0.13	0.00	0	Mixed
Awang Tahan	Translocated	-0.14	0.00	-0.05	-0.16	29.00	22	Mixed
Cherang Hangus	Translocated	0.38	0.00	0.30	0.39	12.00	27	Mixed
Mek Kemat	Translocated	-0.17	0.00	-0.16	-0.04	0.00	0	Mixed
Awang Badur	Translocated	0.00	0.00	0.35	0.00	0.00	0	Nomadic
Awang Chepor	Translocated	0.42	0.00	0.81	0.06	0.00	0	Nomadic
Awang Halim	Translocated	0.04	0.00	0.40	0.00	0.00	0	Nomadic
Awang Sedili	Translocated	0.53	0.00	0.54	0.32	0.00	0	Nomadic
Awang Sri Timur	Translocated	0.08	0.00	0.16	0.00	0.00	0	Nomadic
Mek Dusun	Translocated	0.16	0.00	0.23	0.00	0.00	0	Nomadic
Mek Jalong	Translocated	0.01	0.00	0.02	0.00	0.00	0	Nomadic
Tok Giring	Translocated	0.01	0.00	0.12	0.00	0.00	0	Nomadic
Yong Jalong1	Translocated	0.08	0.00	0.13	0.09	0.00	0	Nomadic

Table A4-3. Best Concordance Criterion (CC) values for ranking the different movement behaviours under the NSD modelling framework for elephants after dispersal. Values are bounded from 0-1 with the highest-ranking value denoted as the best model. Mixed best models are assigned when CC values are within 20% of the best model (Huang et al., 2009).

Name	Type	CC.Res	CC.Null	CC.Nomad	CC.Disp	Top.Model
Ajit	Translocated	0.01	0.000	0.32	0.00	Nomadic
Awang Bakti	Translocated	0.71	0.000	0.78	0.00	Nomadic
Awang Illham	Translocated	0.13	0.000	0.14	0.00	Mixed
Awang Jenor	Translocated	0.12	0.000	0.11	0.00	Mixed
Awang Kapak	Translocated	0.41	0.000	0.81	0.00	Nomadic
Awang Putih	Translocated	0.21	0.000	0.19	0.00	Mixed
Awang Teladas	Translocated	0.20	0.000	0.68	0.00	Nomadic
Buang	Translocated	0.83	0.000	0.13	0.00	Resident
Cherang	Translocated	0.12	0.000	0.10	0.00	Mixed
Cherang Hangus	Translocated	0.04	0.000	0.03	0.00	Mixed
Kudong	Translocated	0.12	0.000	0.11	0.00	Mixed
Mek Gawi	Translocated	0.30	0.000	0.38	0.00	Nomadic
Mek Polis	Translocated	0.65	0.000	0.52	0.00	Resident
Pak Malau	Translocated	0.08	0.000	0.77	0.00	Nomadic
Sauk	Translocated	0.49	0.000	0.02	0.00	Resident

4.10.2 Figures

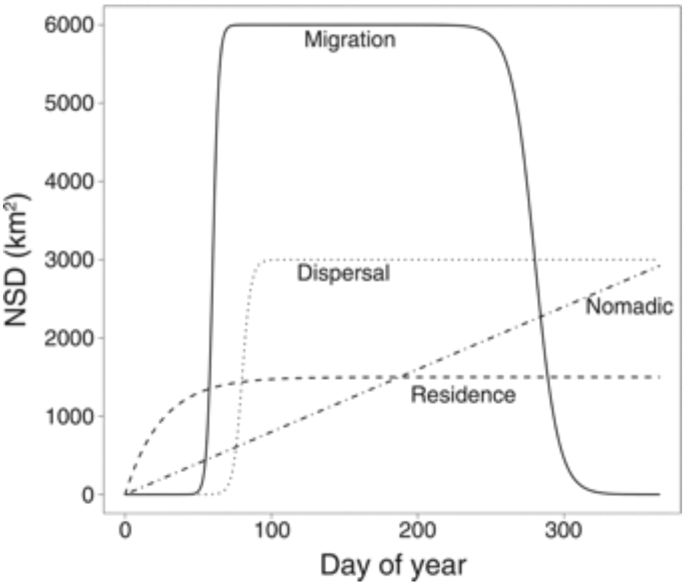


Figure A4-1. Expected net squared displacement (NSD) plots for different movement behaviours (Bunnefeld et al., 2011).

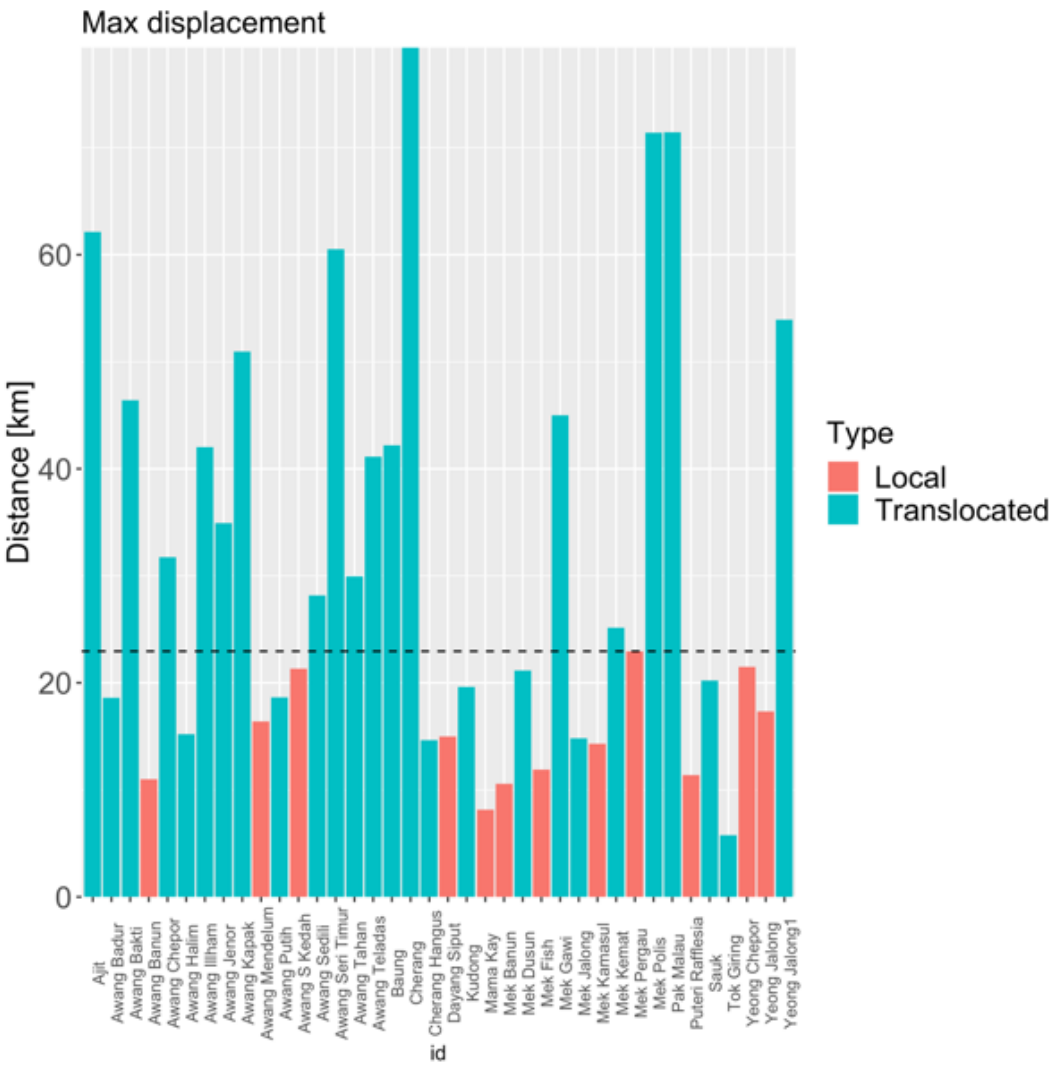


Figure A4-2. The maximum displacement for local and translocated elephants. Dotted line represents the largest local elephant displacement at 23 km.

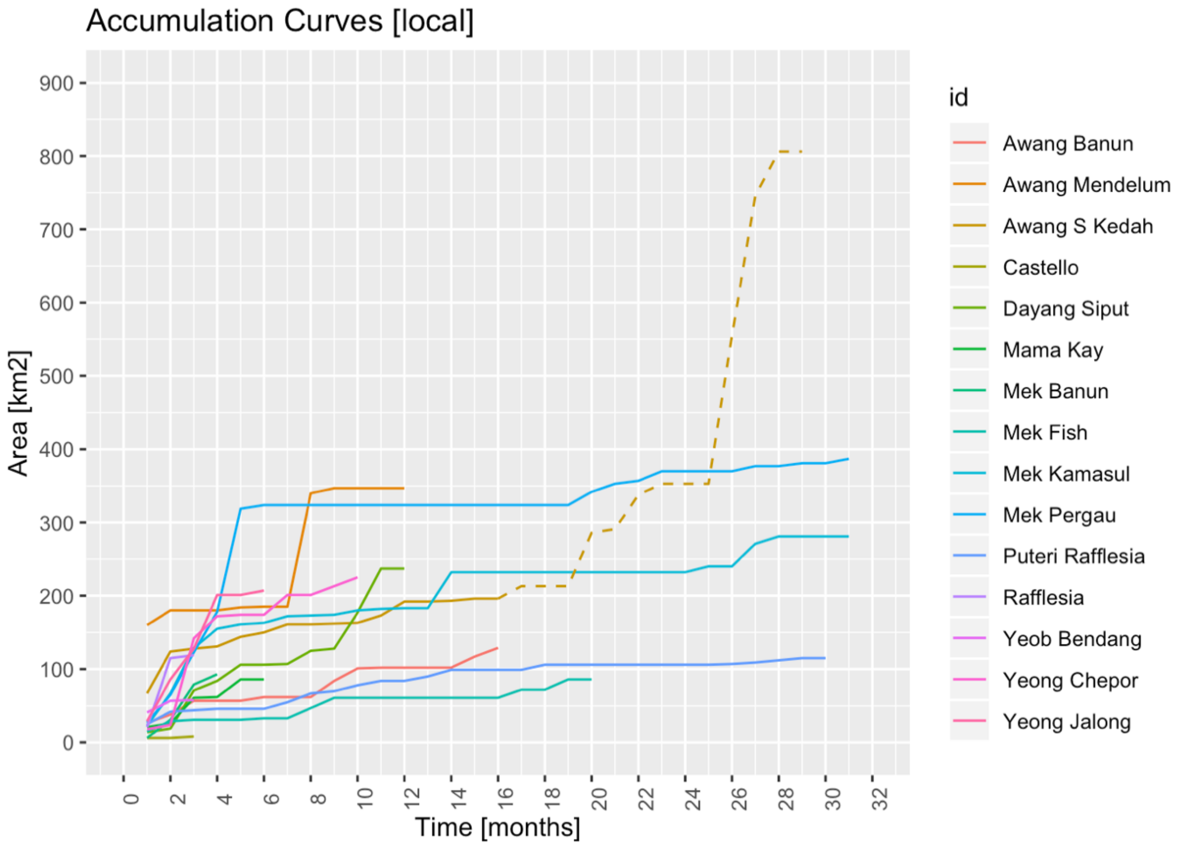


Figure A4-3. Individual local accumulation curves for local elephants in square kilometres. Elephant id 'Awang S Kedah' (ASK) movement track from 16 months to 29 months (dashed line) was excluded from the analysis due to being hit by a car and losing a tusk on 15th month. Consequently, this resulted in ASK leaving Malaysia permanently and roaming in southern Thailand, which resulted in a sharp increase in area (dashed line).

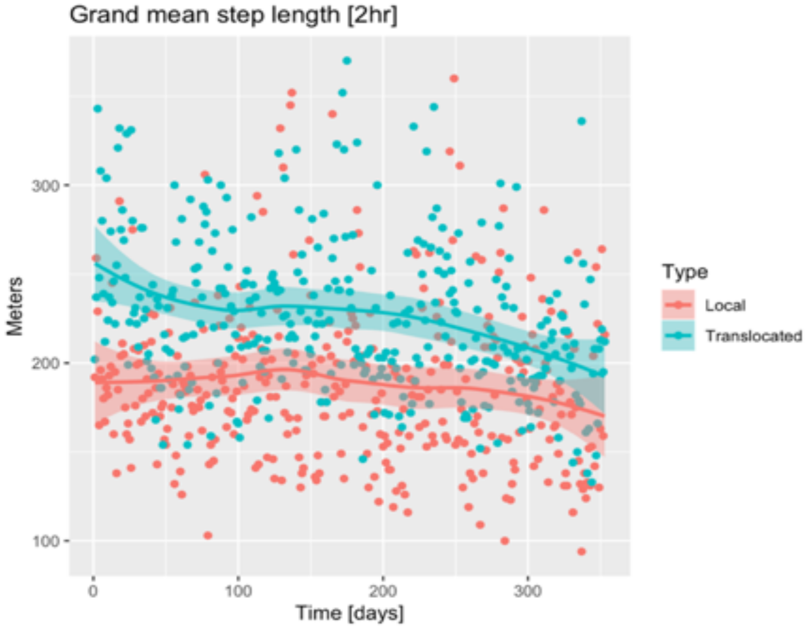


Figure A4-4. Grand mean step length in metres over time from two-hour fixes.

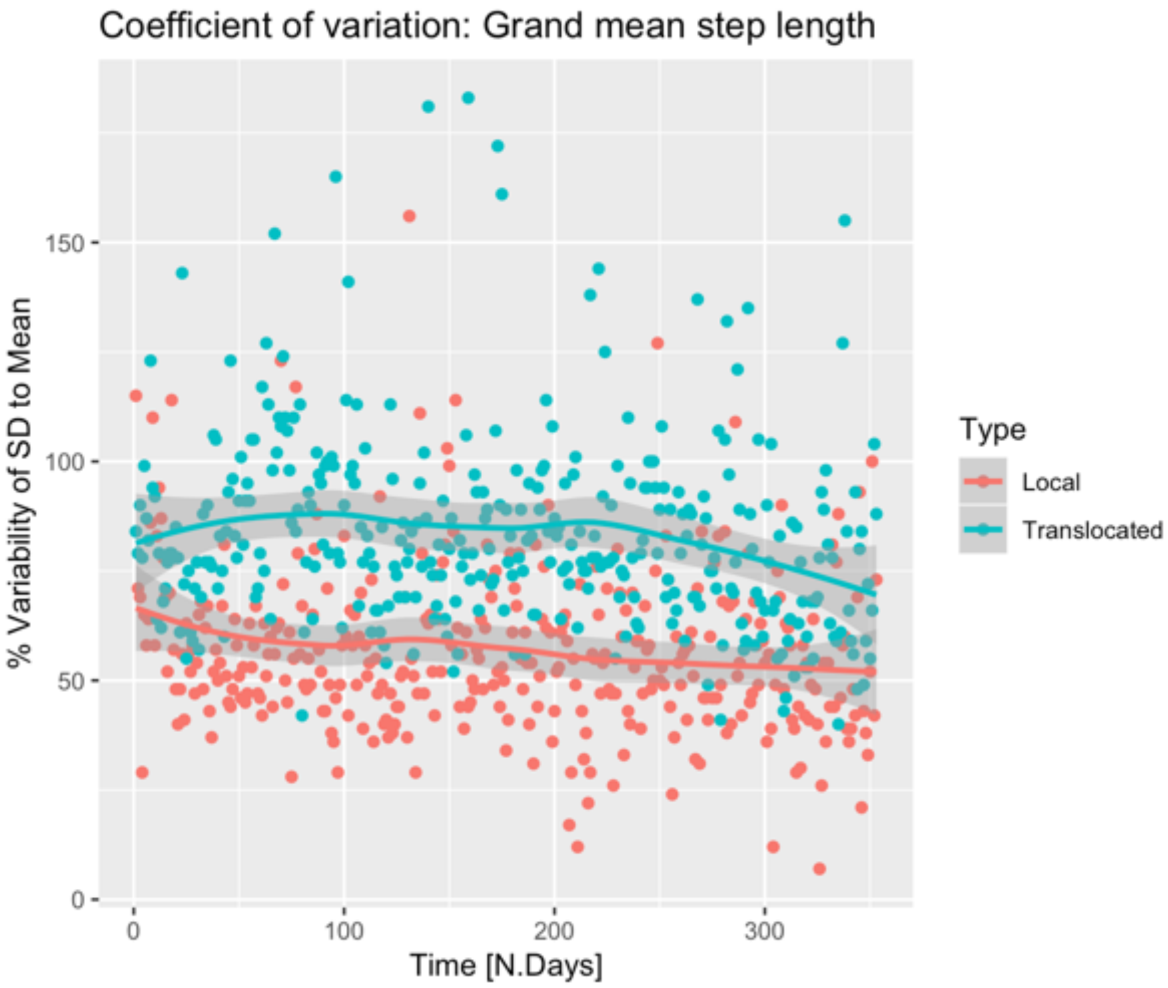


Figure A4-5. Coefficient of variation (CV) to the grand mean step length. CV = standard deviation of grand mean divided by grand mean.

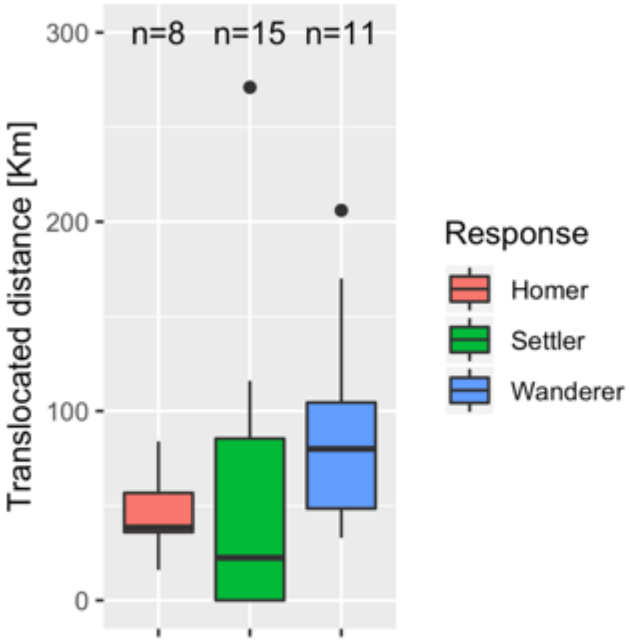


Figure A4-6. Categorical response to translocation and the relationship with translocation distance.

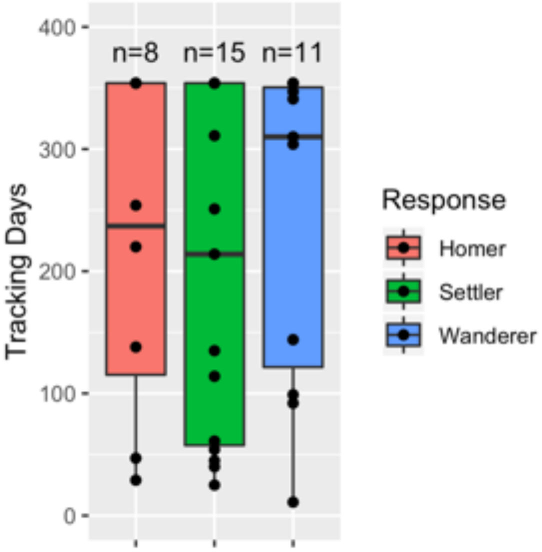


Figure A4-7. Categorical response to translocation and the relationship with tracking days.

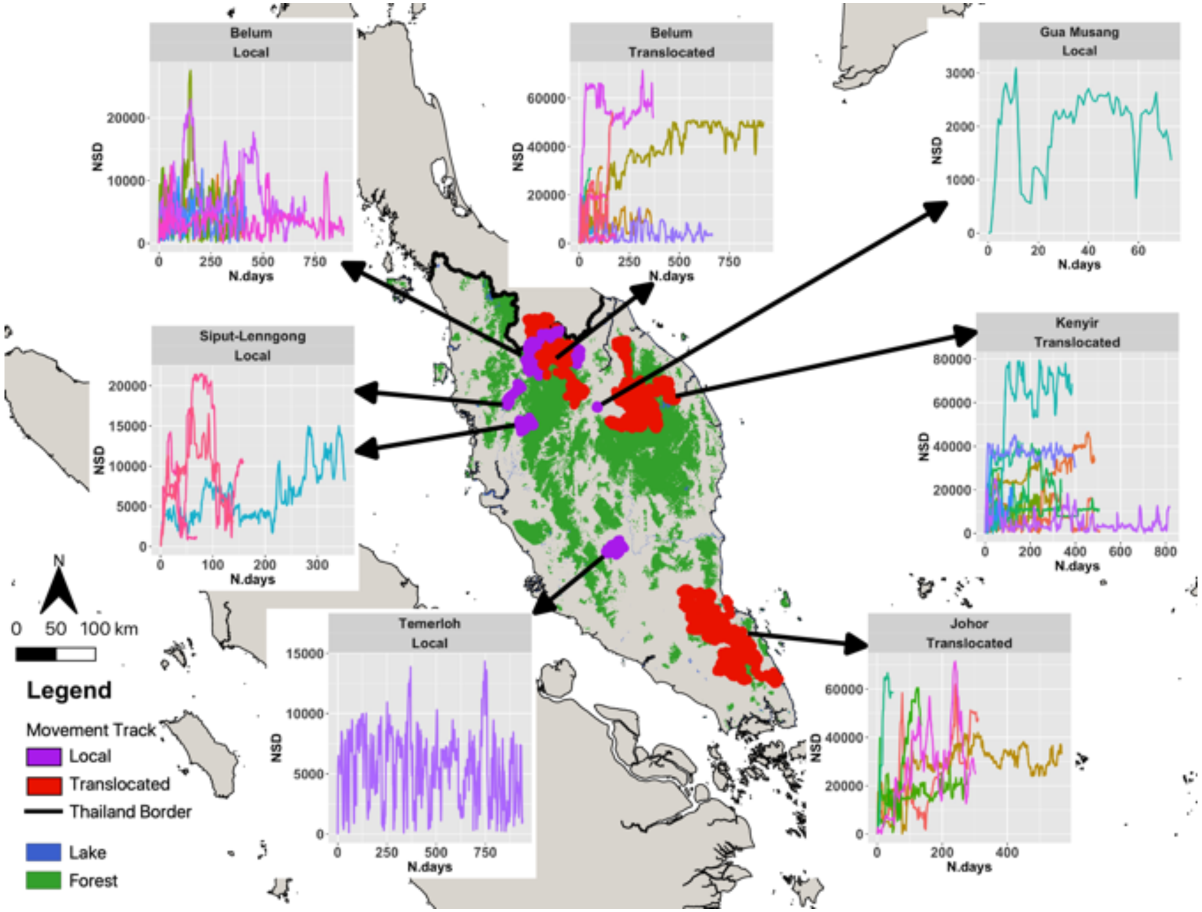


Figure A4-8.Net squared displacement patterns (km^2) for individual elephants at each study area in Peninsular Malaysia. Red colour within Peninsular Malaysia denotes translocated movement tracks, while Purple colour represents local elephants. Within NSD plots, line colours are unique for each elephant.

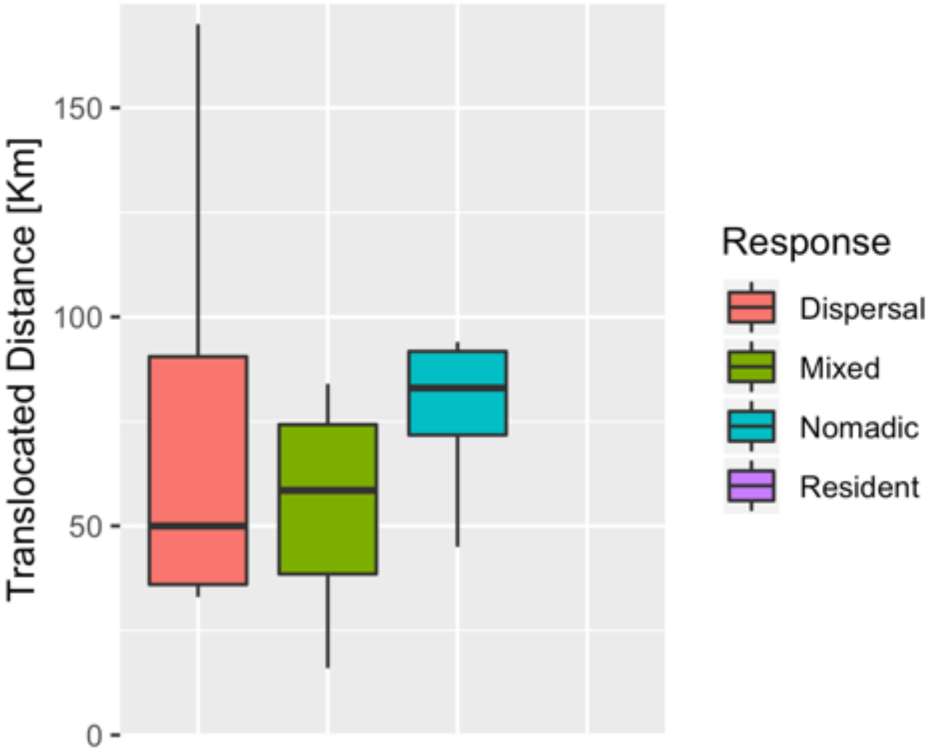


Figure A4-9. NSD Response to translocation and the relationship with translocation distance.

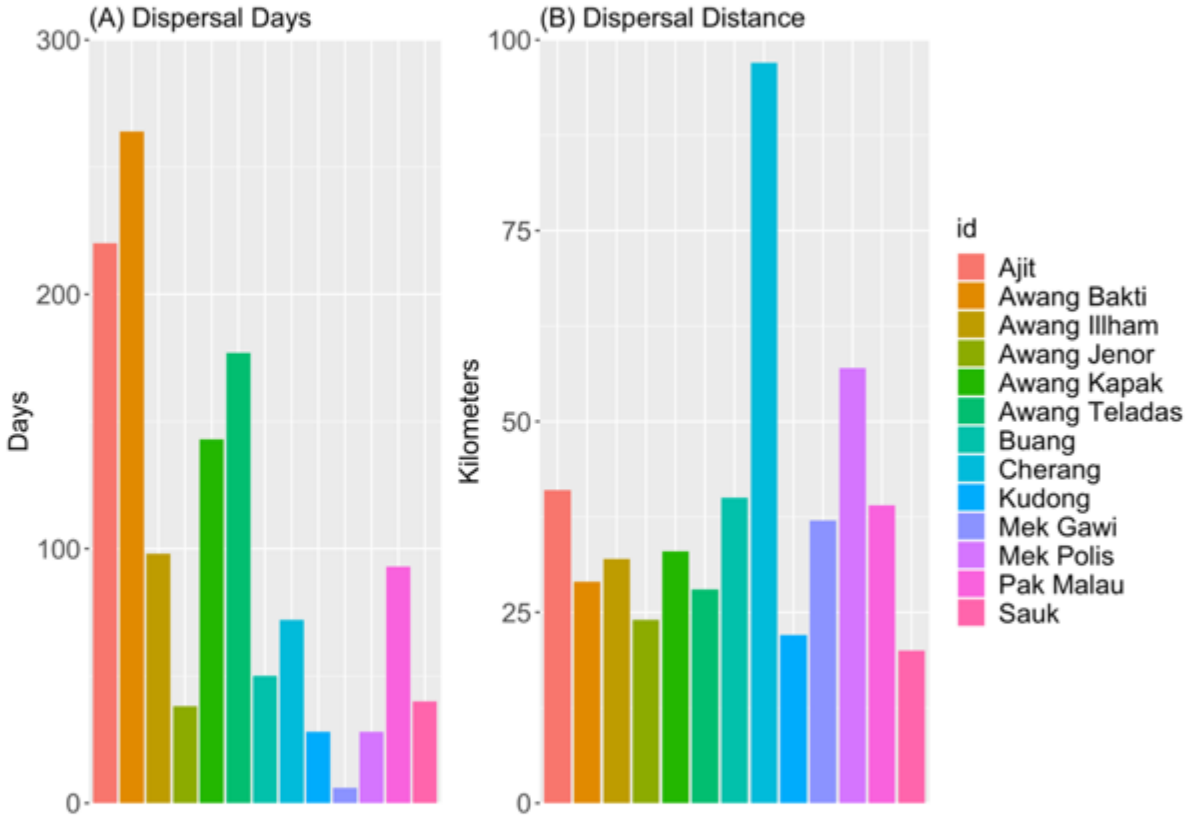


Figure A4-10. (A) Number of days elephants dispersed from release site. (B) Dispersal distance (km) for the release site.

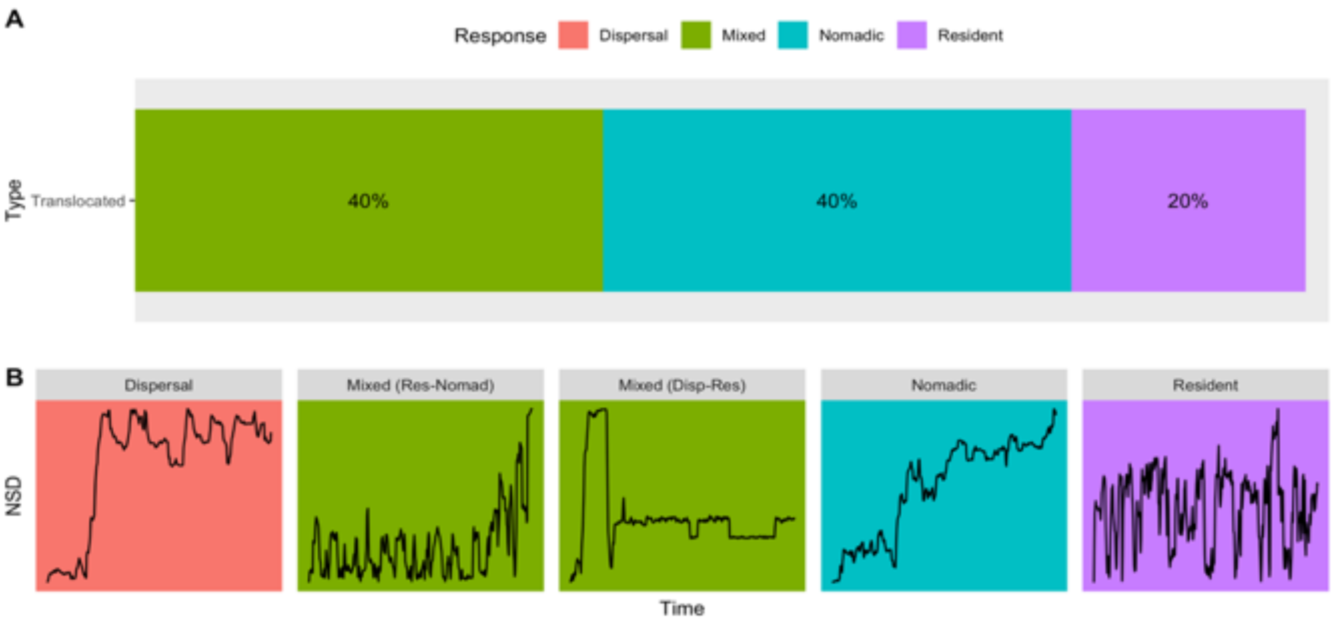


Figure A4-11. Behaviour classification of the dominate movement behaviour using the NSD modelling approach for translocated elephants that completed their dispersal phase. Translocated ‘*dispersal*’ n = 0 out of 15 (0%), ‘*mixed*’ (resident-nomadic) n = 6 out of 15 (40%), ‘*nomadic*’ n = 6 out of 15 (40%), and ‘*resident*’ n = 3 out of 15 (20%). We increased our dispersal sample size from 13 to 15 with the inclusion of two ‘*mixed*’ translocated elephants that included a dispersal phase within the dominate movement behaviour. (B) The movement signatures for the different movement behaviours, with NSD as the response variable and time as the explanatory variable.

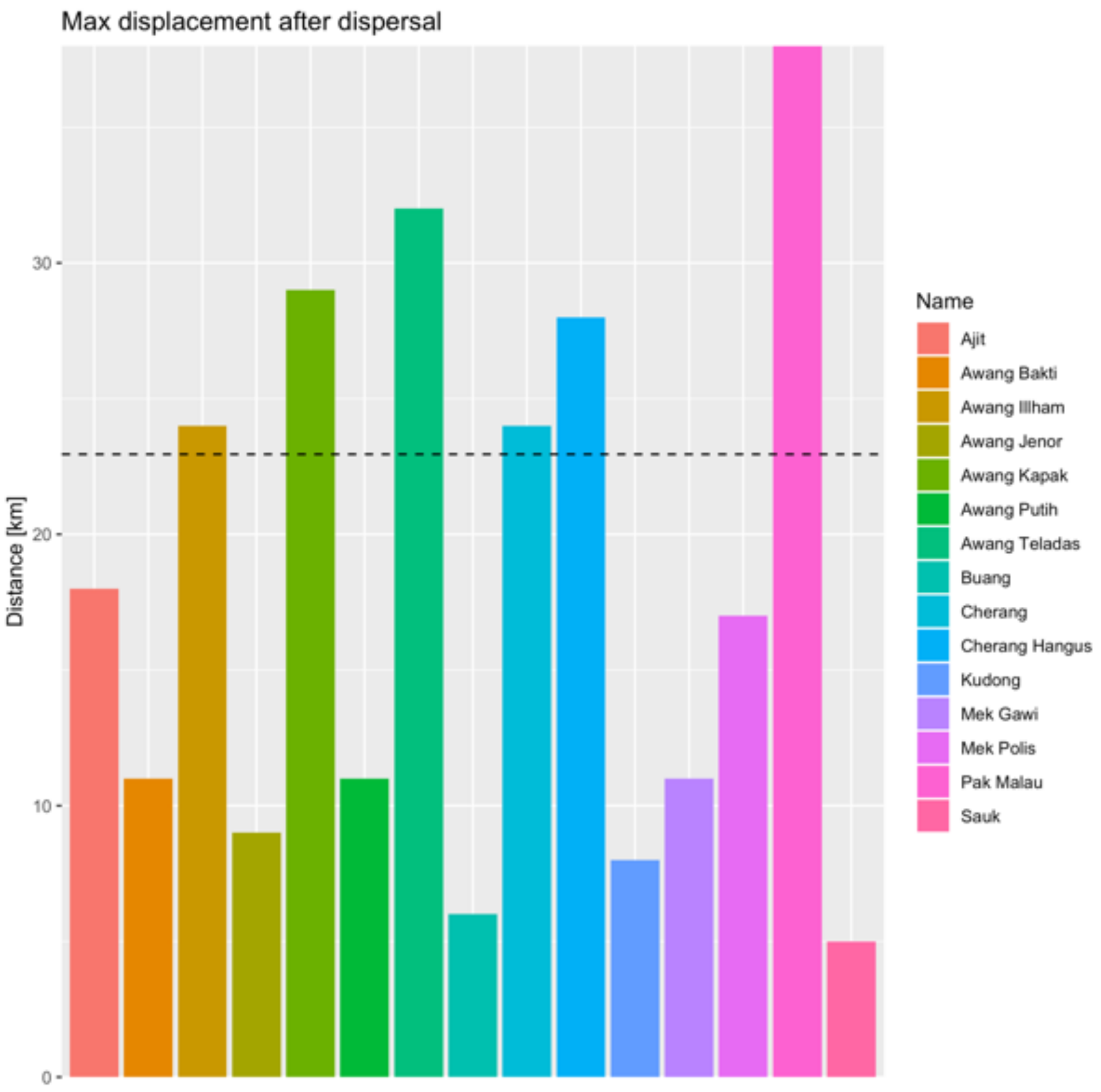


Figure A4-12. The maximum distance [km] for translocated elephants are dispersing. Dotted line is the maximum displacement of local elephants (23 km).

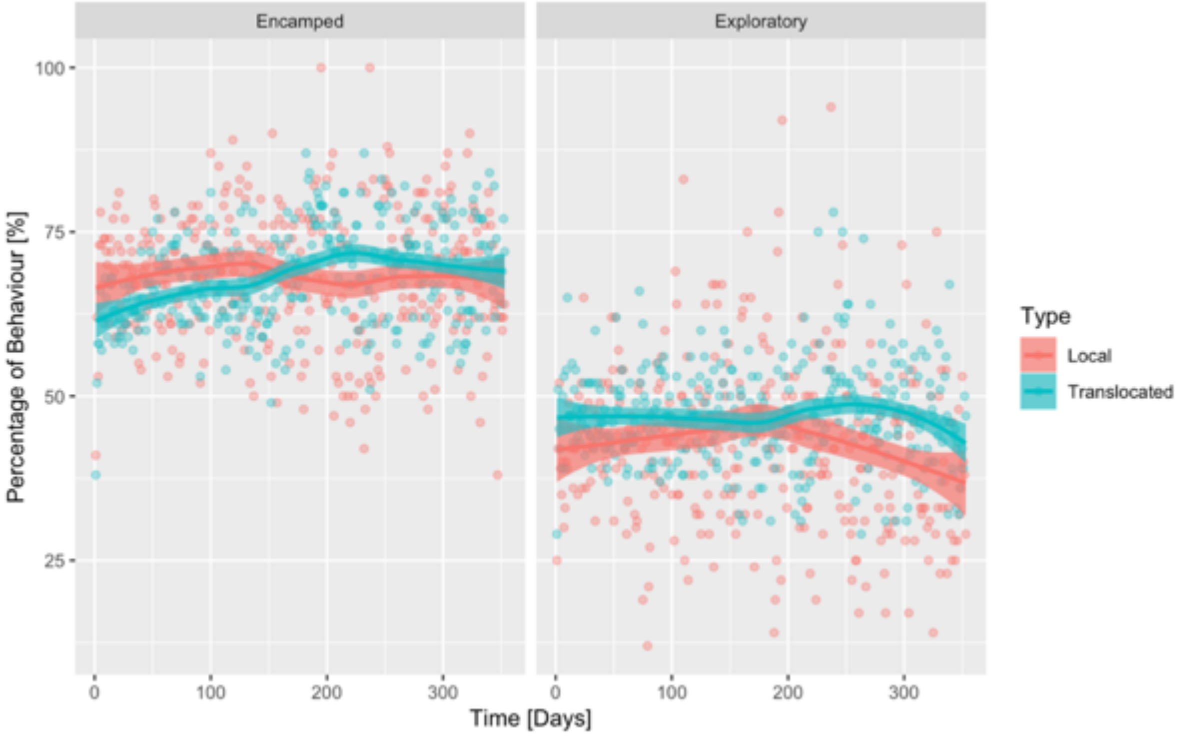
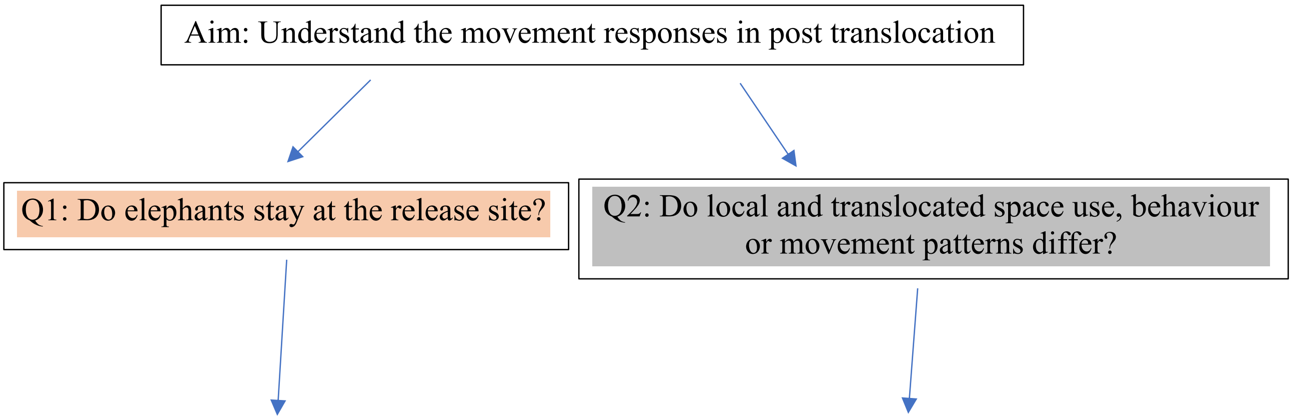


Figure A4-13. Daily percentage of encamped and exploratory behaviour over time from two-hour fixes.

Translocation Analysis Flow Chart



Question	Analysis Type	Method description	Why this method?
1	Categorical Response	Use a distance threshold from release site to see if elephants stay. Threshold based on the radius local HR.	Simple. Answers the question. Better understand the area needed for a release site.
2	Behaviour	NSD modelling to describe the dominant movement behaviour	Provides a behavioural comparison between local and translocated. Able to estimate dispersal distance and time. Links space use and behaviour at large scale.
2	Space Use	HR Accumulation Curves	It can calculate number of days it takes for HR to become stable.
2	Movement Patterns	Step Length (2hr)	Provides insight to small scale movements (2 hours). Quantify the difference in movements between local and translocated.
2	Movement Patterns	Proportion of Exploratory & Encamped behaviour over time (2hr)	Links the step length to behaviour (encamped or exploratory). Provides a small scale understanding of behaviour.

Figure A4-14. Flow chart to determine choice of analyses.

4.10.3 Analysis

Analysis A4-2. NSD modelling of elephants with one-year track length.

We analysed the movement data of elephants with one year of tracking data. The total number of elephants equated to seven locals (two male and five female) and eleven translocated (seven male and four female). We used net squared displacements (NSD) to classify each elephant's dominant movement mode as either resident, nomadic, dispersing, or migratory (see section 4.3.7 for more details on NSD modelling).

The behaviour of local elephants (n = 7 individuals) was predominantly resident (43% of elephants) and mixed resident-nomadic (43%), and to a much less extent nomadic (14%). Local elephants displayed no dispersal behaviour. The behaviour of translocated elephants was very different and was dominated by dispersal (55% of individuals), followed by nomadic (27%), and mixed resident-nomadic behaviour (18%). None of the elephants, neither local nor translocated, displayed any migratory behaviour.

Translocated elephants that displayed dispersal behaviour moved an average of 32 ± 20 km (range 10-72 km) from the release site with an average dispersal period of 115 ± 90 days (range 6-264 days). The maximum dispersal distance from the release site was 84 km. Translocation distance did not affect the type of response to translocation ($f = 1.3$, $df = 2$, $P = 0.87$; Fig. S5). The maximum displacement distance for elephants after completing the dispersal phase was 30 km with a total of three (24, 25, 30 km) elephants surpassing the maximum displacement for local elephants (23 km). After dispersing we found the dominant behaviours to be nomadic (50%), followed by mixed resident-nomadic (33%) and resident (17%).

Elephants with one-year tracking data did not show large differences in behavioural when compared to individuals with less than one-year track length (minimum of 100; See Table A4-4 for details).

Table A4-4. Comparing NSD behavioural classifications between individuals with tracking period of 100-365 days and individuals with 365 days only. Res-Nom = Resident – Nomadic; Res-Dis = Resident – Dispersal.

Tracking Period (days)	**Type**	**Sample Size**	**Resident**	**Nomadic**	**Dispersal**	**Mixed (Res-Nom)**	**Mixed (Res-Dis)**	**Migratory**
100-365	Local	12	67%	17%	0%	17%	0%	0%
100-365	Trans	26	0%	34.5%	50%	7.7%	7.7%	0%
365	Local	7	43%	14%	0%	43%	0%	0%
365	Trans	11	0%	27%	55%	18%	0%	0%

Chapter 5: General Discussion

5.1 Studying Asian elephants with GPS telemetry

The rapidly declining trend of Asian elephant populations across all range states is of great concern. Understanding the movement ecology of Asian elephants through GPS telemetry offers an insightful tool for researchers to link their findings to conservation and management actions. However, data from GPS telemetry on elephants still remains scarce or non-existent, particularly for most Asian elephant range states. The lack of GPS telemetry data is often due to the resources required to collect such data, such as financial and labour resources to find, capture, immobilise and collar an elephant, activities which are often at high risk to both the elephant and people involved. This can result in government agencies viewing GPS projects as 'risky' endeavours, which can lead to difficulties obtaining research permits. Additionally, the temporal scale of elephant GPS telemetry studies is normally insufficient. As elephants can live for more than 50 years, studies would benefit from being long-term, however, research projects usually last a few years at best. This thesis has generated GPS data to provide novel and supportive information about the movement ecology (e.g. home range size and habitat selection) and threats (e.g. roads and translocation) to Asian elephants in Peninsular Malaysia.

5.2 Movement ecology

Chapter 2 of this thesis contributed to numerous new findings about the movement ecology and spatial requirements of Asian elephants whilst simultaneously addressing the lack of scientific knowledge about elephant movement in Peninsular Malaysia. Firstly, we supported previous findings that the home range of Asian elephants are generally smaller than their African counterparts (Alfred et al., 2012; Blake et al., 2008; Fernando et al., 2008; Galanti et al., 2006; Lindeque & Lindeque, 1991; Ngene et al., 2010; Williams et al., 2008). Secondly, this thesis provided the first conclusive evidence that male home ranges were consistently larger than females, while proximity to water did not drive movements of elephants, as it does for African savannah elephants (Ndaimani et al., 2018; Polansky et al., 2015; Wato et al., 2018). Thirdly, elephants showed a preference for disturbed habitat, which was unsurprising because elephants are known to be edge specialists and consume large varieties of food that grow in disturbed habitats, e.g., grasses and early successional plants (Terborgh et al., 2018; Yamamoto-Ebina et al., 2016). This finding further strengthens the argument that protected areas alone cannot sufficiently protect elephants because: 1) protected areas usually cover intact mountainous habitat and not lowland disturbed habitat; and inadvertently 2) the size of many protected areas are smaller than home ranges of individual elephants and or populations.

In Peninsular Malaysia, the Central Forest Spine (CFS) project aims to create ecological linkages throughout the country to secure future connectivity of biodiversity (DTCP, 2014). Based on the results of habitat selection and home range results of this thesis, we strongly recommend protecting large areas of disturbed habitat in and around ecological linkages. An essential part of the National Elephant Action Plan (NECAP) is to secure and protect high quality elephant habitat (DWNP, 2013). Integrating our results about elephants using shallower slopes and lower elevation can improve the robustness of identifying the high-quality elephant habitat that remains in Peninsular Malaysia. Lastly, the methods used in this thesis can be applied to a multitude of different animal species and or movement research topics, particularly with building baseline information about movement ecology of Asian and African elephants.

5.3 Roads

Chapter 3 of this thesis provided the first GPS telemetry study to investigate the impacts of roads on Asian elephant movements. The evidence uncovered by this GPS telemetry study has revealed critical differences between Asian and African forest elephants - Asian elephants are attracted to roads for food but African forest elephants are repelled by roads. We speculate the differences could be due to the higher poaching pressure in Africa and that Asian elephants are more specialized at grazing grasses, which are common by the roadside, compared to their African relatives that focus on gleaning leaves, bark, and green stems from plants (Cerling, Harris, & Leakey, 1999). However, our results still found roads to be deleterious to elephants by facilitating poaching, with high proportions of elephants being poached within short distances to the road. Additionally, our approach to quantify permeability, which we showed was dramatically reduced (on average by 79.5%), was novel for both African and Asian elephants.

Our results have local implications in Peninsular Malaysia for the future road network, which will likely lead to further reduction of permeability and connectivity for elephant populations and may transform some roads into impermeable barriers for elephants and other wildlife. Internationally, China's Belt and Road Initiative (BRI), has the potential to negatively impact the movements of Asian elephants across multiple range countries (Lechner, Chan, & Campos-Arceiz, 2018), however, rezoning road networks to accommodate for environmental impacts can also reduce economic costs of road construction (Mahmoud et al., 2017). The knowledge from this chapter can provide useful implications for road planners and developers in Peninsular Malaysia and throughout Asia. For example, we now know the consequence of a road being built through elephant habitat, and that is, elephants will be attracted to the roadside for the grasses but will not cross the road frequently which may fragment populations in the long term.

5.4 Translocation

The evidence revealed by Chapter 4 highlights the clear limitations of translocation as an HEC mitigation tool. This thesis builds on a growing body of literature from both Asia and Africa that elephant translocation defeats both elephant conservation and HEC mitigation goals, with high mortality rates, regular returns to the capture site and HEC being created at the release area (Choudhury, 1993; Fernando et al., 2012; Pinter-Wollman et al., 2009). With this information, there is the opportunity for Peninsular Malaysia to shift the focus away from translocation as the primary mitigation method and focus on developing a holistic approach using several approaches simultaneously.

We suggest one possible approach to be: (1) appropriate land-use planning to ensure suitable habitat and large areas are protected from future development and habitat pressure; (2) crop protection using electric fences, which have already been proven to be successful in Peninsular Malaysia when designed and maintained properly (Ponnusamy, Chackrapani, Lim, Saaban, & Campos-Arceiz, 2016); (3) economic tools, such as compensation schemes; these have shown success in China where insurance payouts were based on a cost-sharing mechanism which incorporated shared payments from government, farmers and tourists to improve co-existence between elephants and people (Chen, Yi, Campos-Arceiz, Chen, & Webb, 2013); and (4) increasing public tolerance of elephants through education; this is a critical step towards co-existence, such as addressing common misconceptions about HEC and possible mitigation options – for example, translocation being an ineffective mitigation option. Additionally, showing GPS data of elephants returning to the capture site could be used as powerful visuals to educate villagers, agricultural companies and policy makers to discourage the demand for translocation. Sharing such information could lead to a decrease in pressure on the government to translocate elephants.

This study has provided clear evidence of the shortfalls of elephant translocation in Peninsular Malaysia with: (1) translocated elephants taking long periods to settle; (2) the majority of translocated elephants either returning to the original conflict area or leaving the protected area; and (3) high rates of translocated males being poached (14 %). Hence, translocation of elephants in Peninsular Malaysia defeats both HEC mitigation and conservation goals. However, there may be situations where translocation might be necessary, for example, human-killer elephants, systematic fence-breakers or reintroducing elephants into forests where they have become locally extirpated.

5.5 Future research

Since a baseline understanding of the movement ecology and spatial requirements has been established from this thesis, future research should focus on generating new information to mitigate the threats to elephants and humans involved in HEC. HEC is the main factor that is responsible for the rapidly decreasing population trend of Asian elephants, and future research goals should aim at reversing this trend. In Peninsular Malaysia, crop-raiding is the number one HEC incident reported (Saaban et al., 2011), which generally leads to translocation of problem elephants. However, there are small numbers of elephant mortalities from poisoning and shootings by locals in retaliation to HEC (Saaban et al., 2011).

Future research could explore the issue of crop-raiding, such as the use of GPS telemetry to provide real-time data on the location of elephants and when they may be likely to raid crops. This can help plantation owners, farmers and villages know when to start non-violent crop-guarding efforts (Shaffer et al., 2019). Audio and light-based deterrents are new HEC mitigation approaches that could be combined with GPS telemetry. Initial studies in India have found promising results with audio play backs of felids, which have reduced 90% of crop raiding attempts (Thuppil & Coss, 2015). Additionally, GPS telemetry can be trialled as an early warning system, where stakeholders can be automatically notified when elephants breach a pre-determined distance threshold - countries such as Kenya and India are already exploring this approach. Studying the social aspect of humans in regard to crop-raiding will also be beneficial, such as understanding the degree of tolerance by various stakeholders before retaliating, which can assist how government resources are distributed across multiple reported HEC incidents.

Elephant mortality from vehicle collisions is increasing in Peninsular Malaysia (Wong et al., 2018). With the extensive network of new roads planned across the country and internationally, including the implementation of the BRI (Lechner et al., 2018), elephant-vehicle collisions are likely to continue to be a threat across range states. Future research could explore methods to mitigate wildlife-vehicle collisions which are specific to the psychology and culture of the country and locality of the road. For example, using life size elephant statues and audio can overcome '*inattentional blindness*', which is suggested to be a main reason behind wildlife-vehicle collisions (Wong et al., 2018). In addition, this thesis found poaching rates to be higher in close proximity to roads. Future research could explore the effectiveness of car patrols along highways and roads for providing intelligence to authorities and the effectiveness or appropriateness of night road closures, the latter of which was found to lead to a decrease in poaching in India (Gubbi et al., 2012). Decreasing the threats to elephants by the roadside (e.g. poaching and vehicle collisions) will both benefit elephant numbers and likely lead to increases in connectivity between elephant habitats (Wadey et al., 2018).

There are still large tracts of forest in Peninsular Malaysia where elephants have not been GPS-collared, such as Taman Negara (the country's largest national park), which covers an area of approximately 4,343 km^2. Collaring elephants in such areas of low disturbance would cement our findings of elephant movement ecology and spatial requirements. Additionally, the majority of elephants collared in this thesis were in close proximity to roads and forest edges. As elephants in this study were found to spend time in disturbed areas to forage on their preferred foods, collaring elephants that are deep inside forests is of high interest as there is the possibility that these elephants move differently to those along the forest edge. Do they stay within the forest, finding preferred foods in naturally created disturbed areas (such as those created by natural treefall), or do they emerge from the forest regularly to visit disturbed areas which occur everywhere, as a result of the fragmentation prevalent across the country? We suspect elephants use the forest interiors as temporary refuges and emerge to the forest edge, however there are no data to support this. Gaining such information would be useful for mangers designing protected areas to maintain connectivity for elephants.

In this study there was a bias towards males in the translocated group due to the tendency for male elephants to cause HEC and therefore be captured and collared. Further research should focus on GPS-collaring females, in particular, older females of a herd that are not the matriarch (to avoid putting the herd at risk). This can provide more information about how herds of elephants use the landscape. The ideal situation would be to GPS-collar an older female of every herd in Peninsular Malaysia to monitor the movement of each herd across the country, which would allow adaptive and live management of elephants. The main barrier to achieve this scale of elephant collaring for Peninsular Malaysia would be to finance a project long enough (10+ years) and sourcing expert collaring personal to complete the collaring deep within the forest interior. Such a project would require DWNP staff and indigenous trackers to be full-time staff of the project.

Elephant are long-lived animals, living more than 50 years of age. The longest amount of time an elephant was GPS-collared from this thesis was 2.7 years. Repeated GPS collaring of the same individual is important to understand how much our findings vary throughout the life span of an elephant. Furthermore, as elephants are non-territorial and food is the limiting factor in Peninsular Malaysia, it is likely that elephant home ranges will shift or expand over their large life span to deal with changes in the distribution and availability of food resources. Collecting longitudinal data can be important when managers are considering the size of protected areas, as we suspect protected areas will need to be larger than the home range size estimated in this thesis to accommodate the likelihood that elephant home ranges may be flexible over time.

GPS telemetry of elephants in Peninsular Malaysia could be used to foster future international collaboration and research with its neighbouring country -Thailand. In this thesis, three elephants in northern Peninsular Malaysia moved back and forth between both countries, demonstrating that some elephant populations may require joint responsibility in their conservation and management. Other benefits from this future collaboration could be the securing of forest connectivity between Thailand and Peninsular Malaysia, with some forests in northern Peninsular Malaysia are only connected by forests from southern

Thailand. As wildlife do not recognise political borders, such inter-border management of forests is important for elephant movement and consequent existence.

5.6 Challenges and limitations

Challenges and limitations were covered throughout the various chapters; however, these were case-specific and analytically focused. Here, the overarching challenges and limitations will be discussed with respect to conducting an elephant GPS telemetry study for a doctoral thesis in Peninsular Malaysia. The timeline for the modern thesis (3 years plus 1 year write up) is generally not enough time for a student to raise funds for equipment (e.g. GPS collars), write permits, build vital relationships with partners, conduct collaring operations, collar a reasonable sample size of wild elephants over a long enough period of time, carry out detail analyses and write up the findings. Before this thesis began, elephant collaring, funds, permits, partnerships, and field work was established by the Management and Ecology of Malaysian Elephants (MEME) research project. This made it possible to achieve our large sample size of 51 elephants over 8 years (2011 to 2018), while the thesis was conducted from late 2014 to 2019.

The success of collaring operations was dependent on several components which proved to be challenging. The two main factors were the experience of the operation team and the alibility to act in a timely manner upon opportunistic information of elephant presence. The operation team was a mixture of academic researchers, indigenous people and Department of Wildlife and National Parks staff. The researchers were mainly responsible for attaching the collar to the elephant, while the DWNP staff carried out the sedation and immobilisation, and the indigenous people were critical in tracking elephant herds on the ground. Each state in Peninsular Malaysia have their own sedation personnel with varying experience, which influenced operational success. Furthermore, all personnel who were involved in the collaring operations had various external responsibilities and therefore were not always available to act on opportunistic information, which reduced the number of opportunities to collar wild elephants.

Re-capturing elephants to replace drained GPS batteries was a challenge - several attempts were made on different individuals, but all with no success. Anecdotally, the collared elephants seem to have learned from the first collaring and either moved to areas where it was unsafe for the operation team to access them, for example, on the side of a ridge, or displayed continuous fast movements away from the collaring team. Dense tropical rainforest and steep terrain made it physically challenging and also at times unsafe, with many occasions resulting in the operation team running away from charging elephants.

There are various limitations of using GPS collars in Peninsular Malaysia, however, none great enough to forgo future research. The moist and humid environment can degrade the belts and GPS units. The first few elephant collars experienced torn belts or GPS units detaching from the belt. This required communication with the manufacturers to trial different belt materials that could withstand the tropical conditions. Additionally, elephants were able to remove the GPS collar with their trunks if the collar was too loose. Learning the ideal tightness was a challenge to avoid over-tightening and causing distress to the elephant. Large male elephants (>50 years of age) exposed a limitation, as some were strong enough to tear the belt with their trunks, regardless of the belt material.

Another limitation is the terrain and habitat in Peninsular Malaysia which made tracking a herd to collar another elephant in the field difficult. In steep terrain we relied on

GPS locations to get within 500 – 1000 metres of the collared elephant and its herd, and then use VHF to pinpoint their live location. Using VHF beyond 1000 metres from the collar generally produced weak to no signal in the dense forest. The steep terrain and dense canopy cover also regularly blocked the reception of GPS; which left the operation team on the ground without information. This delay in location uploads could take hours or weeks, the longest delay of which was over one month. Such delays in GPS uploads significantly reduced the opportunities of re-collaring or collaring another elephant.

There may be some scenarios where elephant wellbeing might be at risk. For example, if a GPS collar is too loose, too tight or attached for too long, it could result in deterioration of the skin. In our study we did not find evidence of skin deterioration around the GPS collar, even for one individual that had a GPS collar attached for three years. Secondly, there is the possibility that GPS collars could interfere with social dynamics. As elephants are intelligent animals, a foreign object attached to an individual may result in decreased bonds between females or decreased mating opportunities for males, however, there are no evidence to support this, which includes over 20 years of intensive elephant tracking in Africa.

5.7 Final remarks

The continual downward trend of elephant populations in Peninsular Malaysia is of grave concern. However, there is definitely room for optimism as compared to other countries in the region where environmental, financial, demographic and governmental conditions are favourable for the conservation of elephants and biodiversity in general. For example: i) Peninsular Malaysia forest cover is still largely connected, and covers a significant proportion of the land surface (~ 37%); ii) Peninsular Malaysia houses a strong economy that is relying less on agricultural products, e.g. oil palm and rubber, as a primary commodity and more on manufacturing which uses less land; iii) the country has a low population density which is coupled by the majority of Malaysians living in cities; and iv) there is high governmental capacity and intention, generating policy and legislation for elephants and other endangered species. The implementation and enforcement of policy and legislation will be the linchpin to the survival of elephants in Peninsular Malaysia and will be heavily reliant on the political desire of the country (Nagulendran et al., 2016).

The constitutional structure of Malaysia is worth noting due to the implications of implementing policy and legislation. The state governments in Malaysia have legal revenue rights over natural resources, such as, land, water and forest, while the federal government hold the revenue rights over non-natural resources, for example, trade, education, tax, health care, criminal law and tourism. The difference in revenue rights result in 90% of the country's revenue being channelled through the federal government. This impacts elephants and biodiversity enormously as the state governments becoming highly dependent on exploiting natural resources for revenue, for example, by converting forest to agriculture, which has resulted in large-scale habitat loss and massive decreases in elephant population numbers. Importantly, the federal government has little constitutional power when implementing elephant or other biodiversity policy as it falls under the state's jurisdiction. Amendments to the constitution which decrease the state governments reliance on natural resources, in combination with increased state funding for elephants and biodiversity would likely see greater implementation of policy and legislation.

This thesis was generated for a doctoral degree; however, the main purpose was to produce relevant knowledge about Asian elephants to assist in their conservation. Therefore, the knowledge generated here will only be meaningful if it is transformed into on-the-ground action that changes the direction of elephant population declines in Peninsular Malaysia.

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