# Navigating the Night: Spatial Cognition, Locomotor and Ranging Behaviour in *Nycticebus* Species

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# Navigating the Night: Spatial Cognition, Locomotor and Ranging Behaviour in *Nycticebus* Species

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Cover photo was taken by Andrew Walmsley of Fernando, an adult Javan slow loris (*Nycticebus javanicus)*

# Abstract

In this thesis I examined the various ways physical, social, cognitive, and evolutionary factors influence ranging behaviour and spacing in *Nycticebus* species. I explored these topics with the ultimate goal of informing future conservation actions throughout Southeast Asia, especially translocations and in-situ rehabilitation. Each chapter covers topics, comprising ranging and locomotor behaviour, physical ontogeny, spatial cognition, and sociality. I worked at two field sites between 2014 and 2015 in Java and Vietnam, focused on two species of slow lorises (*Nycticebus javanicus* ,13 ind. and *N. pygmaeus,* 6 ind.); augmenting this work with data from long-term datasets and data from existing literature. Despite its frequent use, translocation can have a low success rate in *Nycticebus* species. I found that home range sizes in translocated pygmy slow loris males were larger than those reported both in wild and other translocated pygmy slow lorises, causing subsequent males to leave the release site. As a natural proxy for human-mediated translocations I analysed long-term data on natal dispersal in the Javan slow loris. I found that both males and females disperse as late as two years after birth. Offspring development and dispersal is rooted in the social interactions between family group members. The skills they acquire during this time help them to find and establish a suitable home range; skills like accessing essential food resources. In the Javan slow loris, I looked at exudate feeding to assess their preparedness. While examining the behavioural repertoire used to access tree gums and the ontogenetic development of the postures needed to access them physically, I found that the Javan slow loris acquires rapidly adult-like limb proportions to help employ vertical postures while feeding on gums highlighting their specialization for vertical clinging. The demand on individuals to locate these resources may act as an important selection pressure on the evolution of spatial cognition. I identified the use of spatial cognition and cognitive maps as tools to revisit goal locations. The distribution of stable resources throughout a home range help individuals create a map of

their environment. Another factor affecting spacing and ranging is their social interactions. To reconstruct the ancestral state of primate social organisation in primates, I found that among lorisiforms the presumed promiscuous ancestral state in mammals, then evolved into a dispersed family group at the last common ancestor of lorisiforms. In conclusion, these new data bring to light the difficulties in carrying out a successful translocation, a previously overlooked social dynamic within *Nycticebus* family groups, the importance of limb proportion in development and vertical clinging, how gum producing trees shape nightly movement, and the evolutionary history of lorisiforms social organizations. This information can be used to formulate new conservation strategies and help refine existing efforts in-situ and in captivity. Especially in translocations, which should amend practices to incorporating the complex sociality and use of spatial cognition to support natural behaviours prior to and throughout the release process.

# Acknowledgements

This thesis is dedicated to my parents, without whom none of this would be possible. From an early age, they instilled an appreciation for curiosity and academic pursuits. Despite being a mellow child, I remember an intense need to get answers and investigate anything I found mysterious. I attribute my love of primates to my frequent visits to the Brookfield Zoo, and to Binti Jua the gorilla, who rescued a small boy in 1996. Watching this report on the news, I was in awe as a 6-year-old boy fell into Binit's care and her compassion shined through despite Hollywood's constant emphasis on gorillias being big and scary. From that point on my favourite part of any holiday was a trip to the zoo and my first and last stop was always the primate house or enclosures.

Building on this childhood fasciation and through the encouragement of my parents, I went to Washington University in St. Louis for my undergraduate degree. There are a number of people that I met during those four years that helped make me into the researcher and primatologist I am today. To my academic supervisors Prof Erik Trinkause and Prof Crickette Sanz, I will be forever indebted to you for sharing your passions with me and letting me know that I too could study primates and human variation. To every professor I had the pleasure of learning from, including Prof Tab Rassmussen, Prof Robert Sussman, Prof Fiona Marshall, and Prof Herman Ponzer, thank you for giving me a strong anthropological and primatological base, from which I could build and develop into my own researcher. I have to thank the Behavioural Research Department at the Saint Louis Zoo, especially Dr Cheryl Asa and Karen Bauman. During my time as an intern I was really able to put what I learned in class into practice further strengthening my behavioural data collection skills and data entry. These skills have been an important part of my life ever since.

Moving to the UK was one of the best decisions I have ever made and I will always remember my time in Oxford as the best four years of my life. To Anna and Vincent, I have never met two people so dedicated to research and to sharing what they know with others.

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The Little Fireface Project in Indonesia will always hold a special place in my heart. I saw my first wild loris there, learned to attach radio collars, and use radio telemetry. It is quite a unique experience to wonder around the forest at night to find a small arboreal animal; I could not have been in better hand than with Dendi Rustandi, Adin Nunur, Aconk Ahmed, and Yiyi Nazmi. I hope that you always remember that bizarre student who swooped in at various times throughout 2014-2016, and left behind various ‘Chicago” trinkets. Thank you to Wirdatete Wirdateti, Richard Moore, Eva Johanna Rode, Denise Spaan, Francis Cabana, Robert O’Hagan, Daniel Bergin, Muhammad Imron Ali, Sharon McCabe and Marie Sigaud, you made looking at a long-term dataset much easier than I know it could have been, so I truly appreciate every moment of work you did to help me in any way.

In addition to logistical, emotional, and academic support, this project would not have happened without the generous funding agencies. The translocation of lorises into Cuc Phuong National Park was generously supported by an anonymous donor. For the comprehensive studies on lorises we thank Amersfoort Zoo, Augsburg Zoo, Brevard Zoo, Cleveland Zoo and Zoo Society, Columbus Zoo, Conservation

International Primate Action Fund and Margot Marsh Biodiversity Fund, Cotswold Wildlife Park, Disney Worldwide Conservation Fund, European Human Behaviour and Evolution Society, Henry Doorly Zoo, International Primate Protection League, Leverhulme Trust, Longleat Safari & Adventure Park, Mazuri Zoo Feeds, Mohamed bin al Zayed Species Conservation Fund (152511813), Memphis Zoo, Nacey Maggioncalda Foundation, National Geographic (GEFNE101-13), People's Trust for Endangered Species, Phoenix Zoo, Primate Society of Great Britain, the Royal Geographic Society with IBG, Shaldon Wildlife Trust, Sophie Danforth Conservation Biology Fund, University's Federation for Animal Welfare, Whitley Wildlife Conservation Trust, ZGAP, and the European Human Behaviour and Evolution Association.

Finally, I have to thank the slow lorises. I have enjoyed following your majestic movements in Vietnam and in Indonesia. I have seen individuals arrive at the field site and unfortunately pass away, but I remember each one of you as a pair of unique rubies floating in the night's sky.

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***Euoticus:** Jewell and Oats, 1969; Charles–Dominque, 1977; Ambrose, 1999; ***Galago:*** Smithers, 1971; Izard and Nash, 1988; Pullen, 2000; Butynski and de Jong, 2004; Bearder et al., 2008 ***Galagoides:*** Kingdon, 1971; 1997; Charles –Dominque, 1977; Ambrose, 1999; Olson and Nash, 2002-2003; ***Paragalago:*** Harcourt and Nash, 1986; Bearder et al., 2003; Butynski et al., 2006; ***Otolemur:*** Bearder, 1974; Doyle, 1979; Nash et al., 1990; Perkin, 2004; Bearder, 2007 ***Sciurocheirus*:** Pimley, 2002 ***Arctocebus:*** Jewell and Oates, 1969a; 1969b; Charles-Dominique, 1977; ***Perodicticus:*** Pimley, 2002; Pimley et al., 2005; Pimley and Bearder, 2013; ***Loris:*** Nekaris, 2000; Nekarsi, 2003; Nekaris and Jayewardene, 2003; Kar Gupta, 2005; Kar Gupta and Katti, 2007; ***Nycticebus:*** Gupta, 2001; Wiens, 2002; Nekaris and Bearder, 2006; Pilosungnoen et al., 2010; Nekaris and Bearder, 2007.

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## Abbreviations

CITES- Convention on International Trade in Endangered Species of Wild Fauna and Flora
CPT- Change Point Test
CVA-Canonical Variate Analysis
DBH- Diameter at Breast Height
DPL- Daily Path Length
DOB- Date of Birth
EPRC- Endangered Primate Rescue Centre
EAST- Endangered Asian Species Trust
GIS-Geographical Information System
GLM- General Linear Model
GPS-Geographical Position System
HPA - hypothalamic–pituitary–adrenal
ICD- Incremental Area Development
IUCN- International Union for the Conservation of Nature
KC-Kernel Contour
LFP- Little Fireface Project
LS- Least Square (Regression)
MCP-Minimum Convex Polygon
NGO- Non-Governmental Organisation
NHPI - Natal Habitat Preference Induction
NPL- Nightly Path Length
VCL-Vertical Clinging and Leaping

**Box 1.1:**Key terms and definitions used throughout the thesis.

| Term | Definition |
|---|---|
| Allometric scaling | When two variables do not scale proportionally. |
| Distal (distance) | Situated away from the point of origin or attachment |
| Exudates | Plant exudates include saps, gums, latex, and resin. |
| Exudativore | An animal that specialises in eating exudates. |
| Folivore | An animal that specialises in eating leaves. |
| Frugivore | Animals that eat a large proportion of fruit. |
| Isometric scaling | When two variables scale proportionally |
| Lorisiformes | A taxonomic infraorder within the order Primates including the lorises, pottos and galagos. |
| Ontogeny | The origination and development of an organism, usually from the time of fertilization of the egg to the organisms mature form. |
| Prosimian | Various primates of the suborder Strepsirrhini (formerly Prosimii), as well as the tarsiers, often considered the most primitive primates. |
| Proximate (distance) | Next or nearest in space or time |
| Proximate causation | The immediate influential factors effecting biological functions (eg. environmental cues). |
| Retia mirabilia | Complex of arteries and veins lying very close to each other; the retia mirabilia utilizes countercurrent blood flow within the net to maintain blood circulation. |
| Tapetum lucidum | A biologic reflector system that provide the light-sensitive retinal cells with a second opportunity for photon-photoreceptor stimulation, thereby enhancing visual sensitivity at low light levels. |
| Territory | The area that an animal defends against intruders, especially of the same species. |
| Triangulation | The tracing and measurement of a series or network of triangles in order to determine the distances and relative positions of points |

# Chapter 1: General introduction

**Figure 1.1:** Javan slow loris (*Nycticebus javanicus*) in a cloth bag after a health check at the Little Fireface Project in West Javan, Indonesia. Photo provided by the Little Fireface Project.

## 1.1 Preface

The term biodiversity has varying definitions, but each of these definitions largely focuses on the concept of the variation of life (Gaston, 1998). Following this broad description, people from a range of disciplines have looked to quantify, study, and protect biodiversity. To conserve biodiversity, conservation biology has emerged as a scientific field tasked with providing the information and advice needed to create and execute effective conservation practices, which in turn help maintain natural biodiversity (Cowlishaw and Dunbar, 2000). Conservation biology as a discipline has grown enormously over the last few decades and has increased our awareness and understanding of the intersection of human action, natural ecosystems and biodiversity.

Margoluis and Salafsky (1998) emphasised that in order to conserve biodiversity, we must use indicators that are measurable, consistent, and sensitive to proximate and ultimate influential factors. To create these indicators, we must fully understand the natural bounds of each species we wish to conserve. Conservation efforts and practices created using generalized data cannot fully address the concerns of individual species in ever changing environments. Primates are among the most threatened taxa on the planet and for decades concentrated efforts have focused on ways to conserve their current populations and reverse population decline. These conservation efforts are of particular importance throughout Southeast Asia where rapid human population increase alongside a decrease in suitable forested habitat for primates, have led to a loss in biodiversity. This region is populated with a unique and remarkable array of primate species, including strepsirrhines like the slow loris.

## 1.2 Aims and structure

In this thesis I examine four main themes regarding resource acquisition through successful nightly movements and spacing in *Nycticebus* species (Primates, Strepsirrhini, Lorisiformes) (Figure 1.2). Using direct observational data from the Javan slow loris (*N. javanicus*) and the pygmy slow loris (*N. pygmaeus*), as well as pre-existing data on other lorisiforms, I examine how locomotor and ranging behaviour and spatial cognition can impact *Nycticebus* spp. in the wild and their conservation through translocation. While covering these themes I also address their ecological and evolutionary value to understanding the emergence of aspects of behavioural ecology in nocturnal and diurnal primates. First I provide background information on the key themes addressed throughout the thesis (Chapter 1), then I describe in detail the methods used to collect, manage, and analyse included data (Chapter 2). In Chapter 3, I assess the ranging behaviour and spacing in a group of translocated pygmy slow lorises (*N. pygmaeus*) in Vietnam, highlighting the psychological and social aspects that influence the outcomes of this conservation tool. In Chapter 4, I look at a wild Javan slow loris population in Indonesia and assess natal dispersal. In Chapter 5, I focus on ontogenetic variation in morphometric measures and vertical substrate access in the Javan slow loris (*N. javanicus*) in Indonesia; in Chapter 6, I assess the Javan slow loris' capacity for large-scale spatial cognition through cognitive map use while securing resources. Next, I look at the social aspects of spacing and ranging behaviour in *Nycticebus* spp. and its broader evolutionary context in lorisiforms and all primates (Chapter 7). Finally, I provide general conclusions and applications to conservation based on the novel information provided in Chapters 3-7.

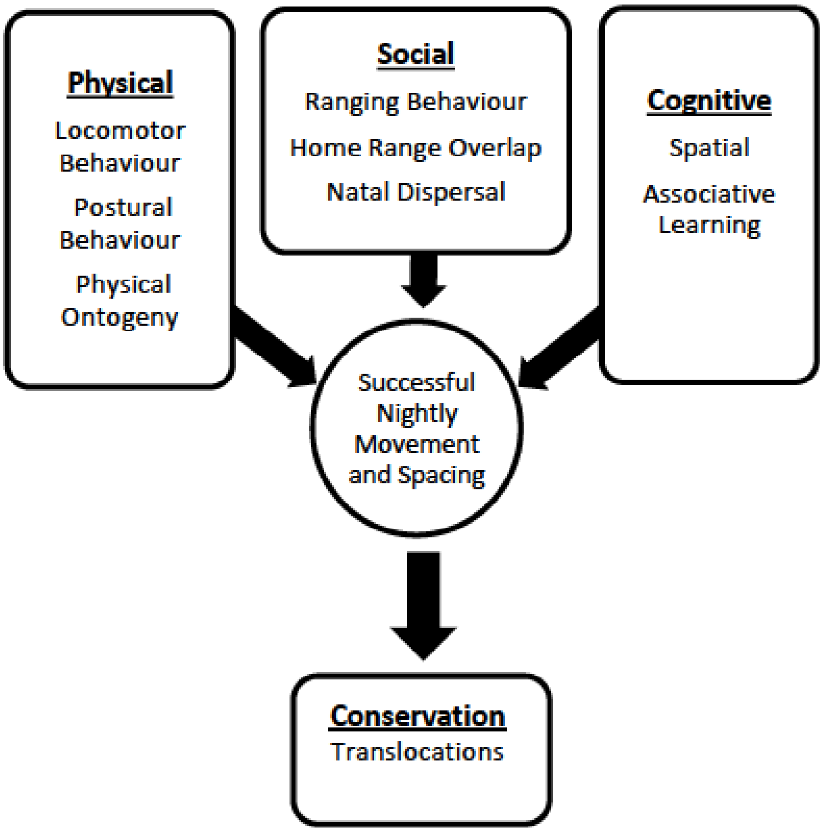


**Figure 1.2:** Visual representation of the thesis framework, highlighting how the varying topics, all contribute to understanding translocations, a conservation tool.

## 1.3 Topic overview

### 1.3.1 Ranging behaviour

The home range represents the area habitually traversed by an individual or group of animals during normal daily activities such as feeding, resting, and reproductive behaviour (Burt, 1943). When this range is defended against conspecifics, it is referred to as a territory (Noble, 1939; Burt, 1943). To survive and reproduce an animal must adapt its behaviour to the environmental conditions it experiences

(Krebs and Davies, 1993). Primatologists have long investigated the relationship between these ranging patterns and ecological variables (Clutton-Brock and Harvey, 1977; Leighton and Leighton, 1982; Terborgh, 1983; Symington, 1988; White and Wrangham, 1988; van Schaik, 1989; Chapman, 1990; Koenig et al., 1998; Stevenson et al., 1998; Dias and Strier, 2003).

An understanding of the way animals move through their habitat can help researchers understand the way they perceive; their umwelt (Powell, 2000). In an effort to quantify ranging behaviour, studies typically focus on two measurements: home range and daily path lengths (DPL), which vary within and across species (Turner et al., 1969; Horne et al., 2008; van Beest et al., 2011). Understanding why home range size varies continues to be a prominent question among zoologists and ecologists (McLoughlin and Ferguson, 2000; Börger et al., 2008). Home range size and overlap can shed light on the social and ecological lives of a given species. Researchers regularly use home range and DPL to address questions about how animals survive in their wild environments.

### 1.3.2 Locomotor behaviour

Postures are defined as a state where an animal’s centre of mass remains static, whereas locomotion is the act of moving from one place to the next involving body mass displacement (Prost, 1965). To be able to negotiate an arboreal habitat, organisms require a large array of movement types. Napier and Walker (1967) were the first to attempt to categorize the different movement patterns used by primates. They defined four principal locomotor categories: vertical clinging and leaping (VCL), quadrupedalism (which includes ground running and walking, branch running and walking, and climbing), brachiation (swinging from branch to branch only using the arms) and bipedalism. In connection with what modes of locomotion an animal is performing, another useful piece of information is how often the animal is engaging in different forms of movement. Since the first primate locomotor classifications very few efforts have been made to improve upon Napier and Walker's (1967) groupings. Hunt et al. (1996) defined biomechanically distinct modes and sub-modes of locomotion and posture based on the body orientation; the main weight-bearing body parts; method of weight bearing; and gait pattern for modes of locomotion. By providing a standardised method of recording primate positional locomotor behaviour, Hunt et al. (1996) facilitated cross comparisons of these behaviours between study sites and primate species.

### 1.3.3 Postural behaviour

Similar to the function of locomotor modes, primates that live in arboreal environments utilize a wide range of positional strategies to aid in the successful navigation of their habitat (Garber, 2007). Postural and locomotor behaviours (here after referred to as locomotor behaviours) impact the musculoskeletal system in varying ways; the force exerted on this system can be higher during more specialized locomotor and postural modes, such as leaping or vertical clinging (Warren and Crompton, 1997; Demes et al., 1999; Isler and Thorpe 2003). In general, primates spend the majority of their time in postures (Rose 1974; McGraw 1998). While engaging in prolonged locomotor and postural modes, it is expected that locomotor behaviours will affect the individuals' morphologies (Preuschoft, 1979; Hunt, 1991). Thus locomotor behaviours are essential aspects of understanding the morphology and physical competence of individual species.

### 1.3.4 Natal dispersal

Natal dispersal is a major factor in the dynamics and genetic structure of a population (Hamilton and May, 1977; Johnson and Gaines, 1990; Whitlock, 2001). Dispersal time and distances vary based on individual characteristics, linkage, group size and environmental cues. Natal dispersal patterns may influence social and ecological behaviours. Furthermore, the absence of dispersal, known as philopatry, is often a prerequisite for kin-selection (Hamilton, 1987). Historically, researchers have focused on the importance of home ranges and daily movements (Ehrlich and Macbride, 1989) in relation to foraging and resource selection (Moorcroft et al., 1999; Borger et al., 2008; Barnett and Moorcroft, 2008; Smouse et al., 2010). Though in actuality it is the less frequent movements, such as dispersal that can be more essential to survival (Pärt and Doligez, 2003; Van Dyck and Baguette, 2005; Cox and Kesler, 2012; Ponchon et al., 2013; Delgado et al., 2014). Although the study of individual animal movements and populations has been carried out for over 100 years, there is increased interest in the study of different types of movements (Dalziel et al., 2008; Haydon et al., 2008;Nathan et al., 2008; Barton et al., 2009; Gurarie et al., 2009; Humphries et al., 2010; Morales et al., 2010; Jeltsch et al., 2013), particularly in response to climate change, the introduction of invasive species, habitat fragmentation, and the importance for land management and conservation.

### 1.3.5 Ontogeny

Incorporating an ontogenetic analysis into behavioural and ecological observations acknowledges the importance of developmental patterns on evolution and the individual's interaction with the environment (Gould, 1977). One of the most important achievements for a juvenile is surviving to adulthood and successfully reproducing (van Noordwijk et al., 1993). The relationship between mammalian mothers and their offspring is critical, and the actions that mothers take to shield their infant from the external environment can contribute to an offspring's death or survival (Hinde, 1971; Peripato and Cheverud, 2002). The mother's investment in her offspring allows development to happen in an environment that is shielded from typical ecological constraints. Physical and behavioural competencies are key factors that help researchers understand how life history traits and ecology facilitate successful development (Milton and May, 1976; Clutton-Brock and Harvey, 1977, 1983; Western, 1979; Eisenberg, 1981; Fleagle, 1984). As immature primates are smaller and less skilled compared to adults, they are at greater risk from malnutrition or predation (Janson and van Schaik, 1993). While these problems mainly relate to their small body size, they can be overcome by growing faster; researchers classify primates as taxa that grow at a slower rate (Jones, 2011). By reducing their metabolic needs through such slow growth, they increase long-term survival. Studying ontogenetic variation in individual behavioural ecology and morphology offers the opportunity for researchers to understand better the development from juvenility to adulthood.

#### 1.3.5.1 Developmental landmarks in *Nycticebus* species

In slow lorises, our understanding of developmental landmarks stems from captive research; these studies focus on the life history and reproduction of slow lorises in captivity (e.g. Ehrlich and Musicant, 1977; Rasmussen, 1986; Rasmussen and Izard, 1988; Ehrlich and Macbride, 1989; Nash, 1993; Weisenseel et al., 1998; Fitch-Snyder and Schulze, 2001; Fitch-Snyder and Ehrlich, 2003; Fuller et al., 2014). Most slow lorises give birth to singletons, but pygmy slow lorises regularly have twins. Newborn slow lorises are relatively tiny (9-30 g) and depend entirely on the mother, until they are parked throughout the night. Slow lorises have one of the longest life histories of all primates for their body size with long inter-birth intervals (6-12 months), gestation (157-205 days) and lactation (120-200 days), offspring dependency periods (up to 20 months), and a life expectancy of between 15-26 years (Rasmussen and Izard, 1988; Martin, 1990; Hakeem et al., 1996; Kingdon, 1997; Nekaris, 2017).

### 1.3.6 Spatial cognition

Spatial Cognition is a branch of cognitive science focused on how one perceives, interprets, mentally represents, and interacts with their spatial environment (Garling and Golledge, 1993; Thinus-Blanc, 1996; Freksa et al., 1998; Montello, 2001; Waller and Nadel, 2013). Parts of the environment that are highly relevant within the process of navigation are called landmarks or cues. Most landmarks are relative in a sense that they are defined in relation to other reference points or landmarks (Evans and Garling, 1991). Navigation is goal-directed and oriented travel through space (Montello, 2001). A key feature of navigation is the idea of travel routes, upon which linear travel can occur, such as continuously connected vegetation in arboreal animals, or cleared paths in terrestrial animals. Routes represent directional patterns of movements either on formal paths or beyond them. A cognitive plan of routes is a prerequisite for travelling distances during navigation. This plan represents an internalised knowledge that allows inferences about the spatial features and relations of the external world (Gallistel, 1990). Spatial information about locations or objects can be integrated into the cognitive system in two different ways, depending on the dominant frame of reference (Berthoz, 1991; Levinson, 1996; Klatzky, 1998). When the new information is relative to the observer's own location, it is called egocentric or viewer-centred representation. In contrast, if the referencing is independent from the observer and relative to other external places or objects, it is referred to as allocentric or object-centred. These two frames of reference are essential to understanding variations in spatial cognition, both in terms of how the information is processed and how it is updated into previously existing knowledge.

#### 1.3.6.1 Wayfinding

A sub-topic within spatial cognition known as wayfinding emphasises the travel element in spatial behaviour, or the process of exploring and processing available spatial information, planning, deciding and executing a spatial action (Thinus-Blanc, 1996; Chen and Stanney, 1999). Wayfinding describes an animal's ability, both cognitively and behaviourally, to reach spatial destinations. Wayfinding is often used interchangeably with the term navigation, especially when the environment in question has more than one goal location and the navigator is assumed to be visiting more than one. In this thesis, I discuss multi-goal environments, thus I will use the term navigation. Navigation emphasizes goal-directedness as a purposeful action of determining and maintaining a course or trajectory from one place to another (Gallistel, 1990). Regarding the spatial elements of navigation, they are represented as routes, landmarks, and nodes, (Lynch, 1960). There are three recognized cognitive process associated with wayfinding and navigation in complex environments: cognitive mapping, decision-making, and decision-execution (Chen and Stanney, 1999).

#### 1.3.6.2 Cognitive maps

Over the past 40 years, researchers in a variety of fields have examined questions relating to the nature of cognitive maps, from the psychological process of acquiring and forming them to the representation of that knowledge acquisition, including their role in every day spatial activity. The cognitive map represents an observer’s model of the world in which we live. Cognitive mapping's definitions are varied due to its multi-disciplinary nature. Kitchen (1994) noted that cognitive mapping has no one strong subject base and is essentially a research topic with inputs from most of the social sciences. This confusion concerning the meaning and context of the term has led to the use of alternative terms, such as cognitive configurations (Golledge, 1977), cognitive representations (Downs and Stea, 1973), topological representations (Shemyakin, 1962), and environmental images (Lynch, 1960).

O'Keefe and Nadel (1978) maintained that due to the role of the hippocampus in spatial memory, it should be called a cognitive mapping system, and the term cognitive map should define action derived from that system. Discourse regarding cognitive map use in animals has largely shifted from whether they are present to what form they take in specific species (Fagan et al., 2013).

### 1.3.7 Social organisations and home range overlap

Social organisation is made up of three aspects: social system, spacing system, and mating system (Sterling, 1993). Social systems are the patterns of intragroup relationships, mating systems describe reproductive interactions, and spacing systems describe the spatio-temporal distribution (Müeller, 1999b) (Table 1.1; Figure 1.3). Monogamy, polygyny, and promiscuity are the main patterns of social organisation observed in mammals (Clutton-Brock, 1989). Müeller (1999b) suggested several terms (gregarious, dispersed, spatial or promiscuous) to describe animals living within cohesive groups or solitary animals with social networks. The level of home range overlap, social interactions and sleeping associations are used to determine the social and spacing systems of the species. In 1978, Charles-Dominique already established the misconception of labelling nocturnal prosimians as 'solitary' since they do maintain social networks through vocal and olfactory communication and regularly meet at night even though they do not forage in groups.

**Table 1.1:** Definition of Social Organisations reprinted from Müeller (1999b; p 5).

| Distribution of Ranges | Cohesive Groups | Social Network | Solitary |
|---|---|---|---|
| Male range coincides with female range (A) | Gregarious family group or monogamy | Dispersed family group or monogamy | Spatial monogamy |
| Male range overlaps several female ranges and vice versa (B) | Gregarious multi-male group (polyandry) | Dispersed multi-male multi-female system | Promiscuity |
| Male range overlaps several female ranges (C) | Gregarious harem | Dispersed harem | Spatial harem |
| Female range overlaps several male ranges (D) | Gregarious polyandry | Dispersed polyandry | Spatial polyandry |

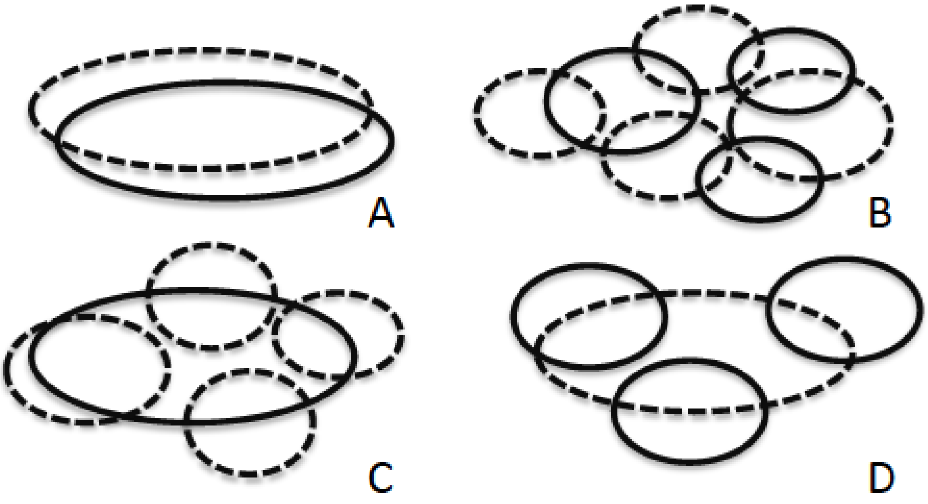


**Figure 1.3:** Visualisation the four social organisations described in Table 1.1, dotted lines represent female home ranges while solid line represents males home ranges.

## 1.4 Study taxa

### 1.4.1 Taxonomy

Slow lorises (*Nycticebus* spp.) are one of ten genera that make up three subfamilies of the Lorisiformes: Lorisinae (lorises), Galaginae (galagos) and Perodicticinae (pottos) (Sussman, 2003; Nekaris, 2013). Within the Order Primates the infraorders

Lorisiformes and Lemuriformes make up the suborder Strepsirrhini (Martin, 1990), representing some of the more basal primates within the Order. Regarding their taxonomy, the genus *Nycticebus* has undergone revisions multiple times since their first recorded sighting by Boddaert in 1784, with new discoveries and the elevation of subspecies following genetic testing and morphometric data. At the time of writing the thesis, nine species of slow lorises were recognized (Table 1.2).

**Table 1.2:** Summary of *Nycticebus* spp. recognition in publications from 1953-present.

| Osman Hill 1953 | Groves 1974 | Groves 2001 | Roos 2003 | Munds et al., 2013 | Rowe and Myer 2016 |
|---|---|---|---|---|---|
| *N. coucang* | *N. coucang* | *N. coucang* | *N. coucang* | *N. coucang* | *N. coucang* |
| | *N. pygmaeus* | *N. pygmaeus* | *N. pygmaeus* | *N. pygmaeus* | *N. pygmaeus* |
| | | *N. bengalensis* | *N. bengalensis* | *N. bengalensis* | *N. bengalensis* |
| | | | *N. menagensis* | *N. menagensis* | *N. menagensis* |
| | | | *N. javanicus* | *N. javanicus* | *N. javanicus* |
| | | | | *N. bancanus* | *N. bancanus* |
| | | | | *N. borneanus* | *N. borneanus* |
| | | | | *N. kayan* | *N. kayan* |
| | | | | | *N. hilleri* |

### 1.4.2 Geographical range

The nine species of slow loris are distributed throughout South and Southeast Asia (Figure 1.4). The Bengal slow loris (*N. bengalensis*) covers the largest area of Southeast Asia, with the second largest distribution belongs to the pygmy slow loris (*N. pygmaeus*), which is sometimes sympatric with the latter in Vietnam, Laos PDR and China (Streicher et al., 2008). The greater slow loris (*N. coucang*) occurs in Singapore, Malaysia, and Sumatra, Indonesia and may prove to be sympatric with the Sumatran slow loris (*N. hilleri*) or *N. bengalensis,* but field studies are needed to confirm this distribution. Further sympatry may be found between the Philippine slow loris (*N. menagensis*), the Bornean slow loris (*N. borneanus*), and the Kayan slow loris (*N. kayan*) in some parts of Borneo. The Javan slow loris (*N. javanicus*) and the Sody's slow loris (*N. bancanus*) are allopatric (Munds et al., 2013; Nekaris et al., 2013). Although slow lorises generally seem to rely on forested habitats they can also be found in disturbed forests, open savannah grasslands, forest plantations and rural agriculture areas (Wiens, 2002; Nekaris and Bearder, 2011; Rogers and Nekaris, 2011). Slow lorises occur at altitudes as high as at least 2000 m asl (Nekaris et al., 2014).

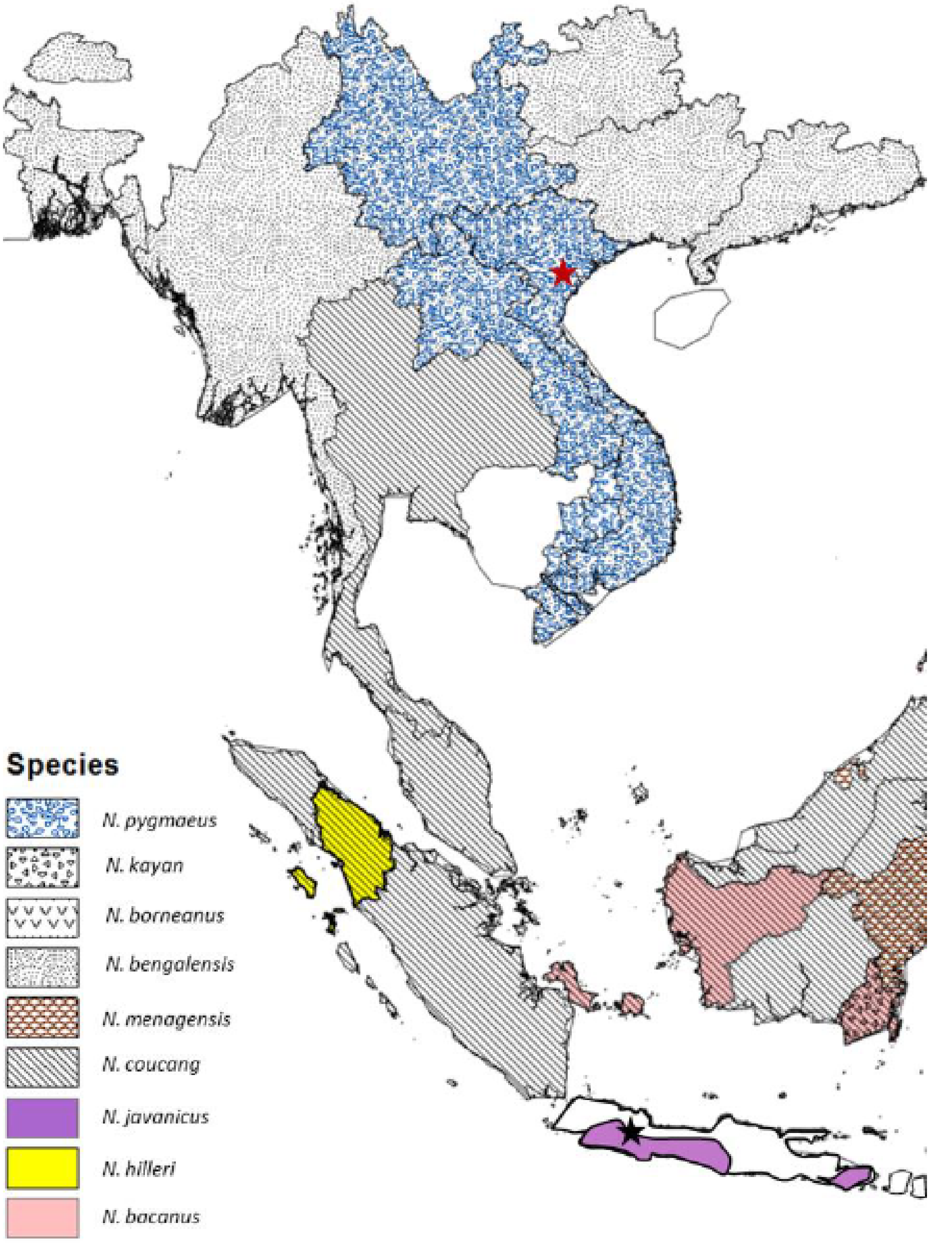


**Figure 1.4:** Map showing the geographical distribution of slow lorises (*Nycticebus* spp.) throughout Southeast Asia. The black star denotes the Little Fireface Project field site in Indonesia and the red star denotes the Endangered Primate Rescue Center in Vietnam.

### 1.4.3 General ecology

The slow loris is characterized by several unique morphological, behavioural, physiological, and ecological features. Slow lorises are visually identified by their varying facemasks and pelage coloration, which correlate with their geographical distribution (Nekaris and Munds, 2010). Slow lorises weigh between 300 g and 2 kg, have a short muzzle, large forward-facing eyes, a *tapetum lucidum*, small ears, and a short or absent tail (Martin, 1990, Nekaris and Bearder, 2011; Fleagle, 2013). They are considered more robust in comparison to the more gracile slender lorises (*Loris* spp.) of South Asia (Bearder and Nekaris, 2011). They possess a suite of hand, foot, and limb adaptations that facilitate their arboreal lifestyle; including a pincer-like grip between the hallux and the digits 3-5, a reduced second digit and specialized vascular bundles that allows blood flow during extended static postures, known as the *retia mirabilia* (Hill, 1953; O'Dea, 1990). Contrary to their common name, slow lorises are able to travel at fast speeds when needed; they cannot leap, but bridge canopy gaps by cantilevering, or terrestrial walk, though rare (Walker, 1969; Ishida et al., 1992; Sellers, 1996; Nekaris and Stevens, 2007). The geographic range of slow lorises includes regions that have low temperatures, especially in the dry season. Temperatures in Vietnam for instance, where the pygmy slow loris occurs, can be close to freezing (Streicher, 2004). Most *Nycticebus* spp. are obligatory exudate feeders (Starr et al., 2008; Das et al., 2014). The larger species (*N. bengalensis* and *N. coucang* consume the most, while the small species *N. pygmaeus* consume less (Swapna et al., 2010; Das et al., 2014).

### 1.4.4 Conservation status

*Nycticebus* species face various anthropogenic threats within their geographical range and internationally. These factors include, deforestation, hunting for traditional medicine and the illegal exotic pet trade, as well as, the photo prop trade (Osterberg and Nekaris, 2015; Starr and Nekaris, 2015). In 2007, all slow lorises were moved from Appendix II to Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). As an Appendix I species, international trade is prohibited in live animals, their parts, and any products derived from the animal (Nekaris and Nijman, 2007). Since 2009 slow lorises have become increasingly popular on websites such as, Youtube, Facebook and regional equivalent social media sites (Nekaris et al., 2013). Their exposure in this globalised market has increased their demand and created a more accessible marketplace (Nekaris et al., 2015), further threatening wild populations and increasing rescue centre populations. In 2016 the International Union of Conservation and Nature (IUCN) Red List evaluated all nine recognized species producing the following classifications, *N. coucang* (Endangered A2cd +4cd), *N. pygmaeus* (Endangered A2cd +4cd), *N. bengalensis* (Endangered A2cd+4cd), *N. menagensis* (Vulnerable A2cd+3cd), *N. javanicus* (Critically Endangered A2cd+4cd), *N. bancanus* (Critically Endangered C2ai), *N. borneanus* (Vulnerable A2cd), *N. kayan* (Vulnerable C1), *N. hilleri* (Endangered A2cd +4cd). Most *Nycticebus* species are protect by law within their geographical range as well as by CITES (Table 1.3).

In this thesis, I include novel data on the Javan slow loris and the pygmy slow loris, from Indonesia and Vietnam, respectively. The pygmy slow loris is one of 21 primate species in Vietnam listed as Critically Endangered, Endangered, Vulnerable, or Near Threatened (Roos et al., 2013), largely due to deforestation, hunting for the exotic pet trade and use in traditional medicine (Fooden, 1996; Ratajszczak, 1998; Groves, 2007; Nekaris and Starr, 2015). This species has been released throughout Vietnam, Thailand, and Cambodia, both monitored and unmonitored, often being unsuccessful (Streicher, 2004). New strategies for release have been developed, however, with the number of successful releases on the increase, a standardised best practice for release is beginning to be recognised (Kenyon et al., 2014). In Indonesia, many of the same threats affect the Javan slow loris. Indonesia has one of the fastest growing human populations, forested area is harder to find to release confiscated individual. It has become important to look at their response in fragmented areas to, anthropogenic disturbances, and the forest edges. While in rescue centres, they present several problems that need specialised attention (Gray et al., 2015; Moore et al., 2015).

**Table 1.3:** *Nycticebus* species and their legal protection in each range country, reproduced from Nekaris and Starr, 2015.

| **Species** | **Protected by Law** |
|---|---|
| ***Nycticebus javanicus*** | **Indonesia**; Protected by the Act of the Republic of Indonesia No. 5 of 1990 Concerning Conservation of Living Re- sources and Their Ecosystems which prohibits to catch, injure, kill, store, possess, nurture, transport and trade protected animals in live or dead condition. Exceptions from prohibition can only be made for the purpose of research, science, salvage of the animal species, or in cases when the animal endangers human life. |
| ***N. bengalensis*** | **Bangladesh;** Protected by the Bangladesh Wildlife (Prevention) Order of 1973 (Amendment 1974) in its Third Schedule of protected animals that shall not be hunted, killed, or captured.<br>Wildlife Protection Act (1981) states that slow lorises are protected species that cannot be hunted without a license. In Wildlife Sanctuaries shooting, hunting, killing, capturing, or taking any animal is completely prohibited.<br>**Bhutan;** Protected by the National Environment Protection Act (2007) that penalizes any direct or indirect harm to the environment involving removal, destruction of, or damage to indigenous animals.<br>**Cambodia;** Protected by Declaration 359 of the Ministry of Forestry and Fishery on Wildlife Species to be Prohibited for Hunting (1994).<br>**China;** Protected by the Law of the People's Republic of China on the Protection of Wildlife (1989) as First Class Protection. Catching of slow lorises can only be done for necessary scientific research, domestication and breeding, exhibition, or other special purposes with a license given by the Wildlife Administration of the State Council.<br>**India;** Protected by the Indian Wildlife Protection Act of 1972 (amended 2002) in its Schedule I, Part I, corresponding to the species of absolute protection.<br>**Laos;** Protected by the Wildlife and Aquatic Law (2007) that classifies slow lorises under the 'prohibition' category. Hunting wildlife from the 'prohibition category' is totally banned without previous authorisation from the Ministry of Agriculture and Forestry.<br>**Myanmar;** Protected by the Protection of Wild Life, Wild Plants and Conservation of Natural Areas Law that bans hunting without a license.<br>**Thailand;** Protected by the Wildlife Protection of 1992 that regulates hunting, propagating, possessing and trading wildlife or their carcasses.<br>**Vietnam;** Protected by the Decree 32 Group IB (2006) that prohibits their commercial exploitation and use. A permit is required for scientific and conservation purposes. |

| | |
|---|---|
| ***N. menegensis*** | **Indonesia;** Same as for Indonesia above.<br>**Malaysia;** Totally Protected Species as stated in the Wildlife Conservation Act (2010) Act 716. Zoos, commercial captive breeding, circus, wildlife exhibition, research and hunting of slow lorises of individuals or parts of them also needs a special permit.<br>**Philippines;** Protected by the Wildlife Resources Conservation and Protection Act (2001). Only accredited individuals can possess slow lorises for scientific, conservation, or breeding purposes. Commercial breeding may be allowed if minimum requirements are provided. Killing wildlife is prohibited unless it is for rituals of indigenous communities. Trading of wildlife is prohibited. Collecting, hunting, or possessing wildlife and derivatives is prohibited. |
| ***N. coucang*** | **Indonesia;** Same as for Indonesia above.<br>**Malaysia (Peninsular);** The primary wildlife legislation for Peninsular Malaysia is the Protection of Wild Life Act 1972 (Act No. 76), which is enforced by the Department of Wildlife and National Parks Peninsular Malaysia. Slow lorises are protected under Schedule 1 (Totally Protected Wild Animals) of the Protection of Wild Life Act 1972 (as revised 2007).<br>**Singapore;** Prohibited as pets by the Agri-food and Veterinary Authority of Singapore. Trading is illegal without a permit as stated in the Endangered Species (Import and Export) Act (2006). Hunting without a license is penalized as stated in the Wild Animals and Birds Act.<br>**Thailand;** Same as for Thailand above. |
| ***N. pygmaeus*** | **Cambodia;** Same as for Cambodia above.<br>**China;** Same as for China above.<br>**Laos;** Same as Laos above.<br>**Vietnam;** Same as for Vietnam above. |
| ***N. bancanus*** | **Indonesia;** Same as for Indonesia above. |
| ***N. kayan*** | **Indonesia;** Same as Indonesia above.<br>**Malaysia;** Same as Malaysia (Sabah) above |
| ***N. hilleri*** | **Indonesia;** Same as Indonesia above. |

# Chapter 2: General methods

**Figure 2.1:** The view from the front porch of the Little Fireface Project field house in the village of Cipaganti, West Java, Indonesia. Photo provided by author.

## 2.1 Introduction

This thesis was conceptualized by several parties based in the United Kingdom, Indonesia, and Vietnam requiring a high level of collaboration. From September 2014 –June 2017 I participated in research activities that directly and indirectly facilitated the completion of this thesis (Figure 2.2). To address my research questions, I worked at two field sites and focused on two species of slow lorises (*Nycticebus javanicus* and *N. pygmaeus*). In this chapter, I will describe in detail each of these sites, the study animals, the collection and analysis of data.

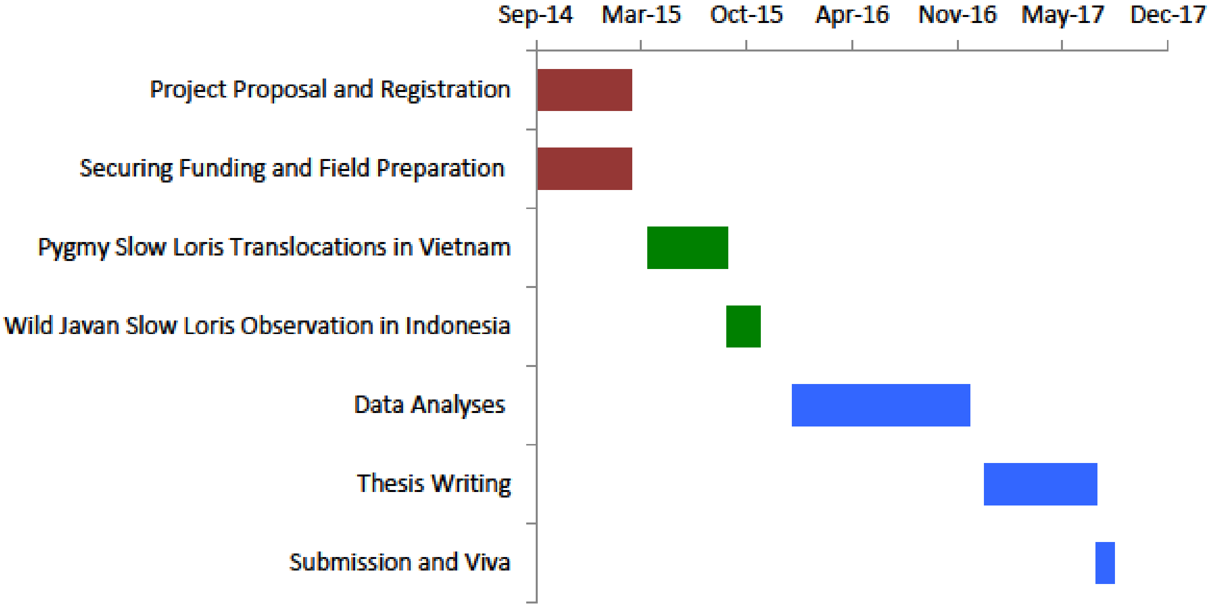


**Figure 2.2:** PhD programme at Oxford Brookes University, red represents preparatory activities; green represents fieldwork; blue represents desk-based work post-fieldwork.

## 2.2 Study sites

### 2.2.1 Little Fireface Project (LFP)

The Little Fireface Project (LFP) field station (S7°6’6” 7°7’ and E107°46’ 107°46’5”), is based in a small village at the foothills of Gunung Puntang, called Cipaganti (Figure 1.4). The nearest city to the village, Garut, is a one-and-a-half-hour drive from the field site in West Java, Indonesia. The area between the adjacent village and the protected forest is primarily patches of cultivated lands, bamboo, shrubs, and bordering trees that demarcate agricultural plots (Figure 2.3). The area where the LFP team conduct nightly observation encompasses a 50 ha range with elevations varying between 1254-2000 m asl (Nekaris, 2014; Reinhardt et al., 2016;). Cipaganti experiences a tropical climate, with continuous rainfall. The average temperature ranges between 17-21 °C and can be as low as 12°C or as high as 30 °C and the average annual rainfall is 2,843 mm (Reinhardt et al., 2016). In 2011, LFP established its field station representing the first long-term project dedicated to studying lorisines in the wild. The main goal of the project is to collect longitudinal data on the ecology of the Javan slow loris (*N. javanicus*), while contributing to the conservation and outreach of all *Nycticebus* species throughout their range countries. The Little Fireface Project works to address the conservation issues facing *Nycticebus* species and create conservation education programmes to bring their plight to light and ultimately improve the fate of both wild and captive slow lorises. In addition to the slow loris, the Little Fireface Project team also studies other nocturnal animals, including colugo (*Galeopterus*), pangolins

(Manidae), civets (Viverridae) small cats (*Prionailurus*), mustelids (*Herpestes*) and owls (Strigidae).

**Figure 2.3:** Photo from the Little Fireface field site in Cipaganti, West Java, Indonesia, showing an agricultural plot and the trees that line each plot. Photo provided by the Little Fireface Project.

### 2.2.2 Endangered Primate Rescue Center (EPRC)

The Endangered Primate Rescue Center (EPRC) (N20 19' 0" and E105 36' 30") is within the Cuc Phuong National Park located in the Ninh Bình Province, of Vietnam's Red River Delta. The nearest major city is Hanoi, a three-hour drive north of the national park. First established in 1993, through collaboration between Frankfurt Zoological Society and Cuc Phuong National Park, the centre is managed under the umbrella of the Vietnam Primate Conservation Program, jointly operated by Zoo Leipzig and Cuc Phuong National Park. They house 15 species of Vietnamese primates totalling approximately 180 individuals.

During the translocation project reported in this thesis, the main release site was characterised by tall continuous tree coverage, a dense variety of vegetation, and large limestone hills covered in sparse primary forest (Figure 2.4). As the area was a former plantation, many trees have remained in planted rows but much of it is overgrown. The average temperature in Cuc Phuong is 21 °C and high temperatures can reach above 30 °C and lows are just above freezing. On average, it rains more than 200 days a year and the average annual rainfall is 2,100 mm. The rainy season is from May to September and the dry season is from October to April (Vietnamese Admiration of Tourism, 2015). There was no formal faunal census prior to data collection for the translocation project, but during the five-month observation period in which I participated, I observed 15 flying squirrels (Sciuridae). The presence of flying squirrels at some study sites is negatively associated with the absence of slow lorises (Radhakrishna et al., 2006; Pliosungnoen et al., 2010).

**Figure 2.4:** Photo from the base of the pygmy slow loris (*Nycticebus pygmaeus*) release site in Cuc Phuong National Park, Vietnam, arrow denotes one of the hills where we observed release pygmy slow lorises. Photo provided by author.

## 2.3 Data collection

### 2.3.1 Collaring and release

At LFP, we follow a protocol approved by the Animal Ethics Subcommittee at Oxford Brookes University (OBU-AESC-EXC26). Experienced team members handled non-anesthetized individuals. The radio collars (BioTrack, UK) weighed 17 g, which is on average less than 2% of the body weight of an adult Javan slow loris and less than 4% of an immature Javan slow loris (Poindexter and Nekaris, 2017). At the EPRC, each translocated pygmy slow loris was fitted with a radio collar, which weighed 4 g (Holohil® transmitters model PD-2C) prior to being placed in the pre-release cage at the release site (Figure 2.5). This allowed us to track them on foot from the date of release until the lifespan of the collar elapsed, the collar fell off or we were unable to locate dispersing animals. Staff members from the EPRC were trained in radio-tracking methods using a two-pronged antenna and a handheld radio receiver (Icom Inc® receiver model ICOM IC-R10).

**Figure 2.5:** (A) Tilo Nadler and I examining a radio collar on one released pygmy slow loris (*Nycticebus pygmaeus*). (B) Pre-release cage placed at the release site in Cuc Phuong National Park, Vietnam. Photo provided by the Endangered Primate Rescue Center.

All pygmy slow lorises included in the translocation were residents at the EPRC confiscated from markets within Vietnam. Once deemed appropriate for release, staggered pair releases took place between October 2014-June 2015. Prior to release each pygmy slow loris spent two/three days in a medium sized in-situ pre-release cage. Following this period, each loris was released between 18:00 and 20:00.

### 2.3.2 Nightly observations

At LFP, a two-person team (observers and tracker) collected data through direct observation in two shifts throughout the night using a red-filter head torch (Clulite®)(Figure2.6). Shift one started at 18:00 at the initial sleep site of the focal animal and ended at 23:00, when a second team arrived to continue observations until 05:00 ending at the final sleep site. Individual Javan slow lorises were identified by a unique radio signal, emitted from the radio collar attached to each study animal. At a five-minute instantaneous sample point (Altman, 1974; Nekaris, 2001), team members collected information on the animal's behaviour (Table 2.1), the animal's locomotor mode or posture (Table 2.2 and Figure 2.7), the tree species occupied, proximity to conspecific, position in tree (central, crown, periphery, terrestrial, trunk, undergrowth), Diameter at breast height (DBH) (in cm), and a geographical position system (GPS) waypoint. During each shift, we followed one Javan slow loris (the focal animal), unless other animals were within the vicinity of the focal animal, in which case we used instantaneous scan sampling.

**Figure 2.6:** Photo trackers using antennas and receivers to locate pygmy lorises in the field (A) Cipaganti, (B) Cuc Phuong, Vietnam. Photos provided by author.

During the study at the EPRC, each night a two-person team located and observed each visible focal animal, between the hours of 18:00-03:00, for 1-2 hours (Figure 2.5B). When possible, prior to the night shift, a tracker and myself located the animals' sleep sites, this aided in forming trails and locating individuals at night (Streicher and Nadler, 2003). Due to the dense vegetation in which pygmy slow lorises regularly slept, we used triangulation to pinpoint the location of an individual when we could not make a reliable visual confirmation. I used a Garmin

64S to collect GPS points and my predecessors on this project used a Garmin eTrex 10 to collect GPS data.

**Table 2.1:** Names and definitions for the behaviours used to during observations of slow lorises in Cipaganti, West Java Indonesia and Cuc Phuong National Park, Vietnam.

| Behaviour | Definition |
|---|---|
| **Alert** | Remain stationary like in "rest" but active observation of environment/observer |
| **Feed** | Actual consumption of a food item |
| **Forage** | Movement associated with looking for food (often includes visual and olfactory searching) |
| **Freeze** | Interrupt locomotion to maintain motionless, rigid posture in standing or sitting position for at least three seconds |
| **Groom** | Autogroom, lick or use tooth comb on own fur |
| **Rest** | Remain stationary, often with body hunched, eyes open |
| **Sleep** | Remain stationary, head between the knees, eyes closed |
| **Social** | All interactions with conspecifics |
| **Travel** | Continuous, directed movement from one location to another |
| **Other** | Other behaviours not included above |

**Table 2.2:** Locomotor/postural modes (a-o) and definitions used during observations of slow lorises in Cipaganti, West Java Indonesia and Cuc Phuong National Park, Vietnam. Locomotor/postural modes defined here refer to those displayed in Figure 2.7.

| Locomotor and Postural Mode | Definition |
|---|---|
| **Sit (a)** | Remain stationary with body hunched and head erect |
| **Stand (b)** | Remain stationary in upright position using all four limbs |
| **Horizontal Suspension-2 (c)** | Hanging from two feet |
| **Horizontal Suspension-1 (d)** | Hanging from one foot (rare but can occur when playing) |
| **Horizontal Suspension-3 (f)** | Hanging from three feet |
| **Sleeping Ball (e)** | Remain stationary with body hunched and head erect, head between the knees |
| **Horizontal Suspension-4 (g)** | Hanging from four feet |
| **Vertical Suspension-2 (h)** | Hanging towards the side of a support, with 2 feet |
| **Vertical Suspension-3 Up** | Hanging towards the side of a support, with 3 feet, either facing upwards or downwards (not pictured in Figure 2.7) |
| **Vertical Suspension-3 Down** | |
| **Vertical Suspension-4 Up** | Hanging towards the side of a support, with 4 feet, either facing upwards or downwards |
| **Vertical Suspension-4 Down (i)** | |
| **Climb Horizontally (j)** | Moving horizontally through 90 or +/- 45 degree support |
| **Walk (k)** | Quadrupedal walking on support |
| **Suspensory Walk (l)** | Locomoting while hanging from 0 degree or +/- 45 degree support |
| **Climb Up (m)** | Moving upwards on support |
| **Climb Down (n)** | Moving downwards on support |
| **Bridge (o)** | Climbing from one support to the next, stretching over a gap of more than 15 cm |

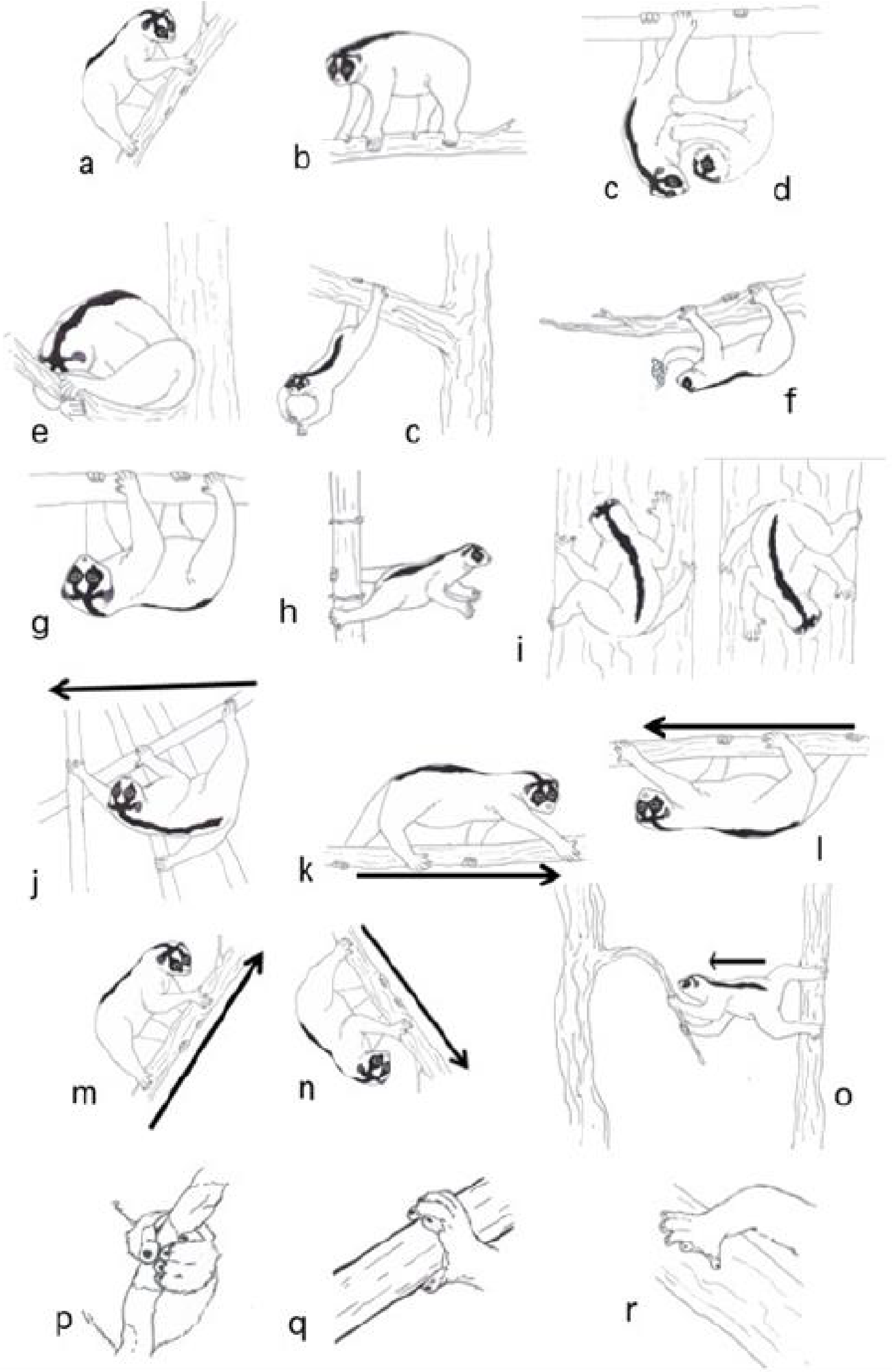


**Figure 2.7:** Locomotor behaviour and substrate size ethogram used at the Little Fireface Project in Cipaganti, West Javan, during nightly observations of Javan slow lorises (*Nycticebus Javanicus*).

### 2.3.4 Morphometric data

At LFP, we captured animals by hand and regularly monitored them over the course of the long-term observations, especially the immature animals, to ensure radio collars were not interfering with natural growth or causing discomfort. Using a 2.5 kg spring scale (Pesola, Canada) and a clean cloth bag, we weighed individuals either annually or every three months depending on collar life span and age. Using digital callipers and soft measuring tape, the total body length, hand and foot span, upper arm, lower arm, upper leg, and lower leg lengths, were measured for each captured individual (Figure 2.8- 2.10) (Nekaris and Jaffe, 2007).

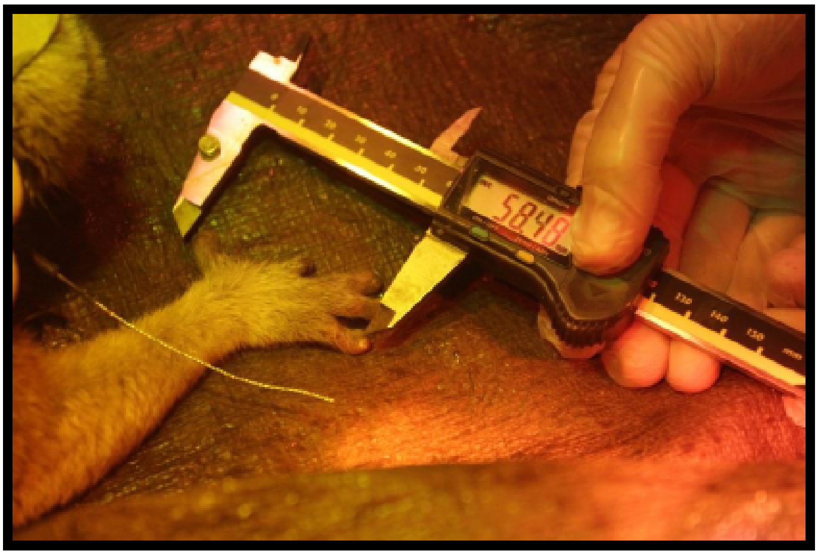
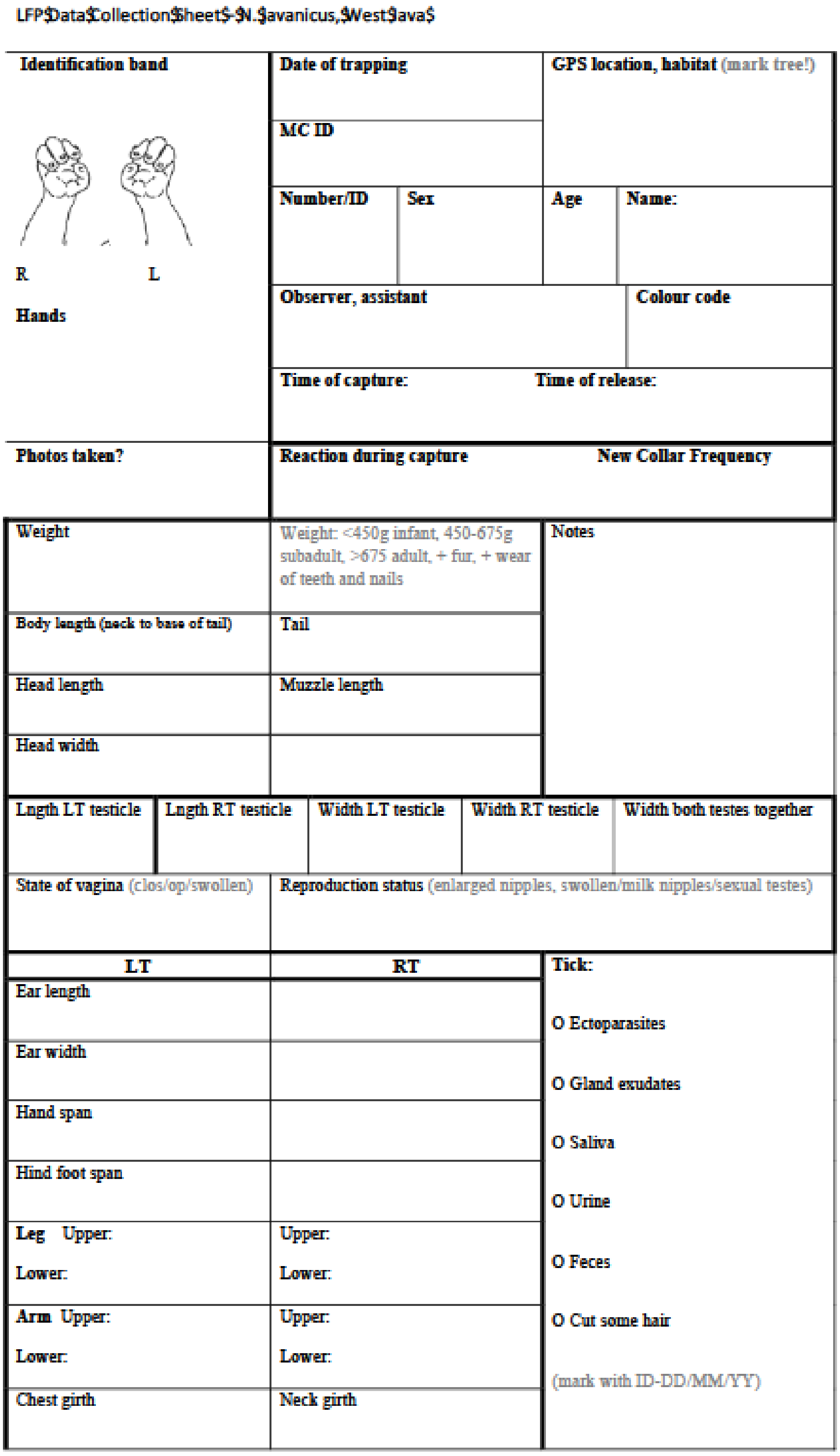


**Figure 2.8:** Photo of researchers at the Little Fireface Project measuring the handspan of a collared Javan slow loris (*Nycticebus javanicus*) in West Java, Indonesia, courtesy of the Little Fireface Project.



LFP$Data$Collection$heet$-$N.$avanicus,$West$ava$

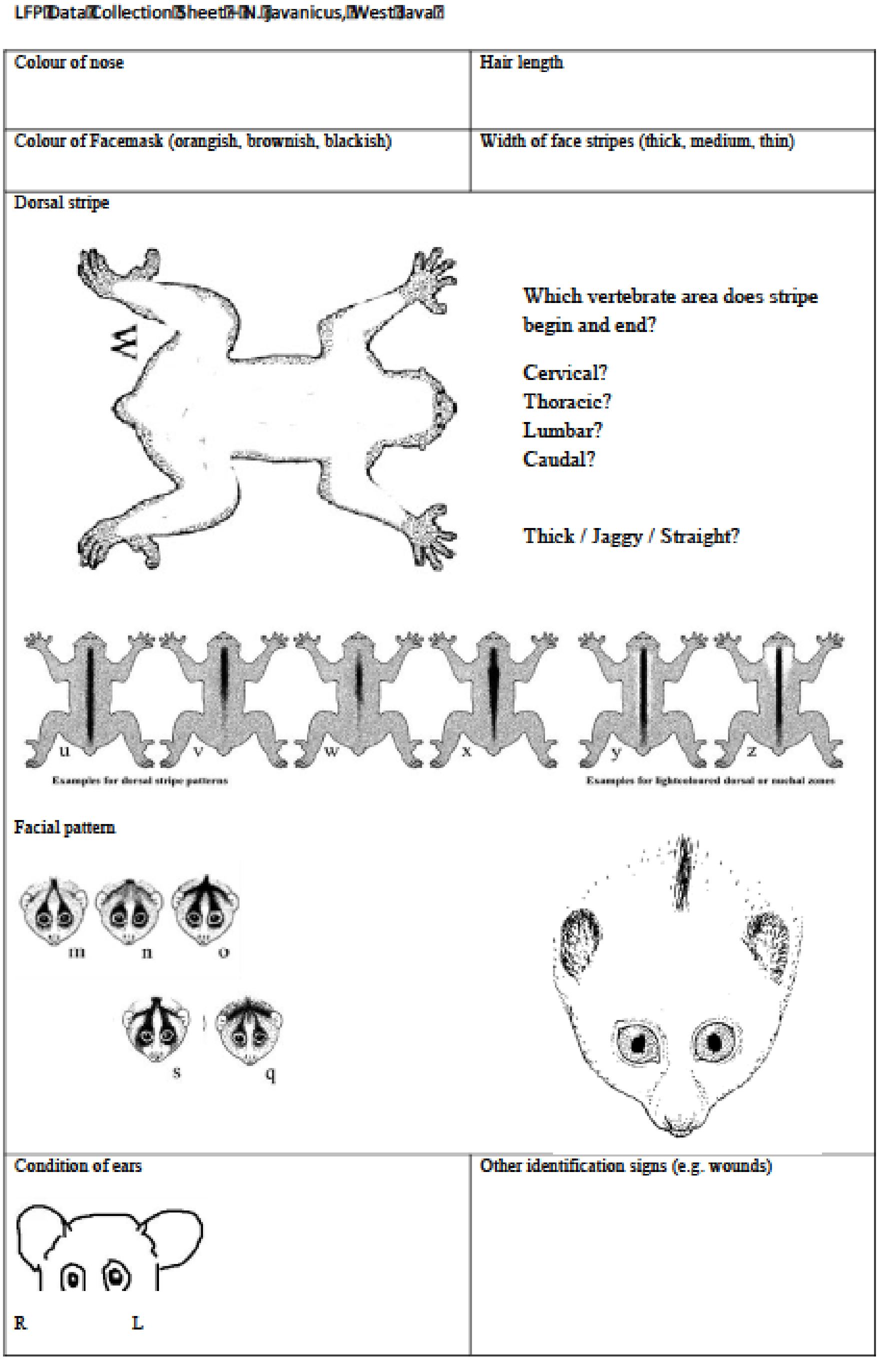
| | | | | |
|---|---|---|---|---|
| **Identification band**<br>R L<br>**Hands** | **Date of trapping** | | **GPS location, habitat** (mark tree!) | |
| | **MC ID** | | | |
| | **Number/ID** | **Sex** | **Age** | **Name:** |
| | **Observer, assistant** | | | **Colour code** |
| | **Time of capture:** | | **Time of release:** | |
| **Photos taken?** | **Reaction during capture** | | **New Collar Frequency** | |

| | | |
|---|---|---|
| Weight | Weight: <450g infant, 450-675g subadult, >675 adult, + fur, + wear of teeth and nails | Notes |
| Body length (neck to base of tail) | Tail | |
| Head length | Muzzle length | |
| Head width | | |

| | | | | |
|---|---|---|---|---|
| Lngth LT testicle | Lngth RT testicle | Width LT testicle | Width RT testicle | Width both testes together |
| State of vagina (clos/op/swollen) | Reproduction status (enlarged nipples, swollen/milk nipples/sexual testes) | | | |

| **LT** | **RT** | Tick: |
|---|---|---|
| Ear length | | ○ Ectoparasites |
| Ear width | | ○ Gland exudates |
| Hand span | | ○ Saliva |
| Hind foot span | | ○ Urine |
| Leg Upper:<br>Lower: | Upper:<br>Lower: | ○ Feces |
| Arm Upper:<br>Lower: | Upper:<br>Lower: | ○ Cut some hair |
| Chest girth | Neck girth | (mark with ID-DD/MM/YY) |

**Figure 2.9:** Page one of the slow loris (*Nycticebus* spp.) morphometric data collection sheet used at the Little Fireface Project in Cipaganti, West Java, Indonesia, courtesy of Little Fireface Project.



LFP Data Collection Sheet – N. javanicus, West Java

| | |
|---|---|
| Colour of nose | Hair length |
| Colour of Facemask (orangish, brownish, blackish) | Width of face stripes (thick, medium, thin) |

Dorsal stripe

Which vertebrate area does stripe begin and end?

Cervical?
Thoracic?
Lumbar?
Caudal?

Thick / Jaggy / Straight?

Examples for dorsal stripe patterns

Examples for lightcoloured dorsal or nuchal zones

Facial pattern

| | |
|---|---|
| Condition of ears | Other identification signs (e.g. wounds) |

**Figure 2.10:** Page two of the slow loris (*Nycticebus* spp.) morphometric data collection sheet used at the Little Fireface Project in Cipaganti, West Java, Indonesia, courtesy of the Little Fireface Project.

### 2.3.5 Study participants

The long-term dataset at LFP includes 57 Javan slow lorises (*N. javanicus*) (Figure 2.11), totalling 44814 data points across 2012-2016 (Table 2.3). Data collected at the Endangered Primate Rescue Center totalled 941 data points including six pygmy slow lorises (*N.pygmaeus*) (Table 2.4)

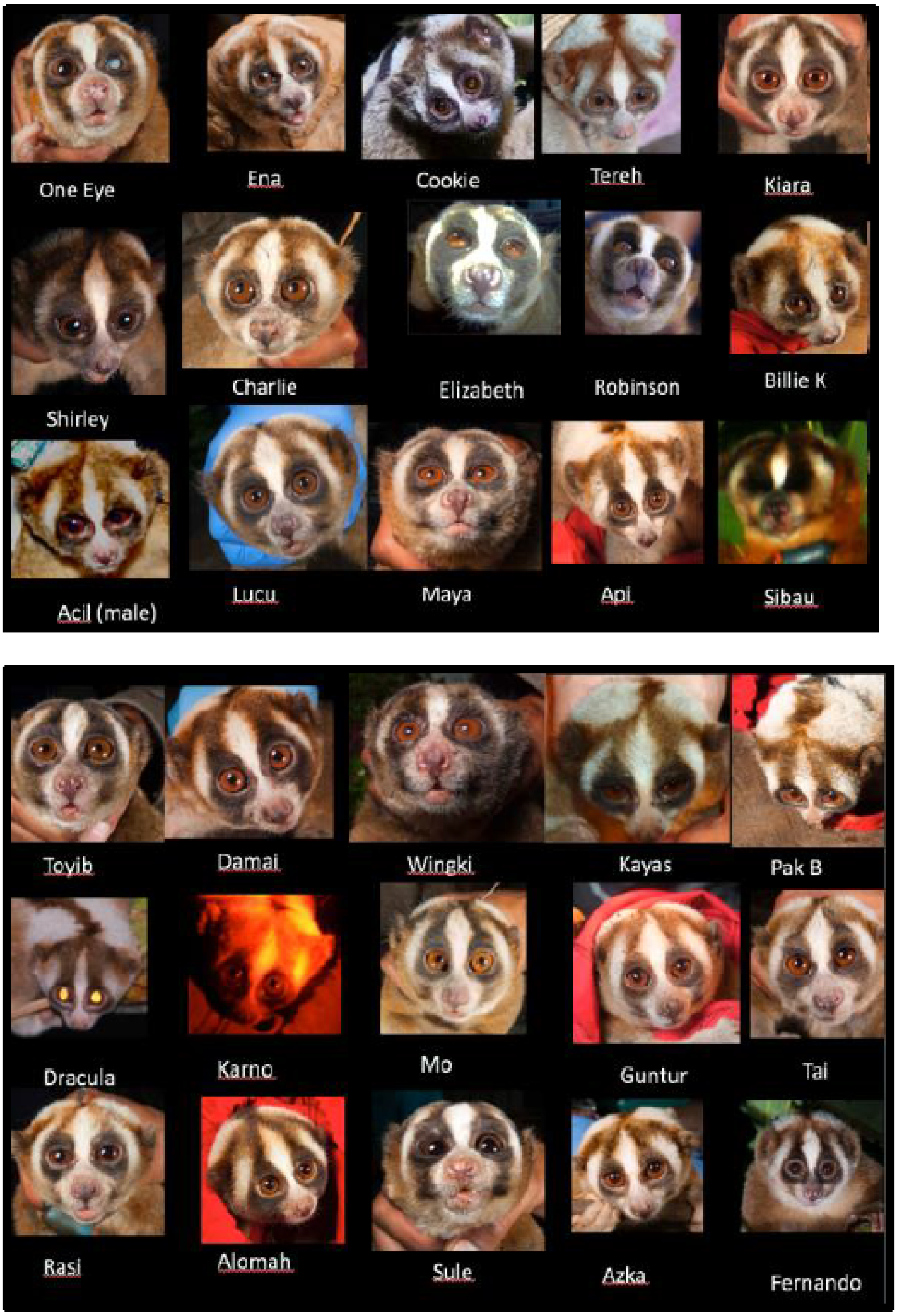


**Figure 2.11:** Facemask image showing the unique face markings of followed individual Javan slow lorises (*Nycticebus javanicus*) at the Little Fireface Project in West Java, Indonesia. Photos provided by the Little Fireface Project.

**Table 2.3:** The number of data points collected for the main Javan slow loris (*Nycticebus javanicus*) included in the analysed dataset from the Little Fireface Project field site in West Java, Indonesia. Individuals in blue are male and those in red are female; DOB= Date of birth; the data collected while the author was present at the field site are listed in the far right column.

| Individuals | DOB | 2012 | 2013 | 2014 | 2015 | 2016 | Total | Author Present |
|---|---|---|---|---|---|---|---|---|
| Acil (AC) | Pre-2014 | - | - | - | 349 | 488 | 837 | 106 |
| Alomah (AL) | Nov-13 | - | - | 252 | 719 | 2430 | 3401 | 270 |
| Azka (AZ) | Pre-2012 | 464 | 343 | 209 | 647 | 2004 | 3667 | 348 |
| Damai (DA) | Pre-2012 | - | - | 364 | 18 | - | 382 | |
| Dempak (DM) | Pre-2015 | - | - | - | - | 652 | 652 | |
| Endor (ED) | Feb-16 | - | - | - | - | 320 | 320 | |
| Fernando (FE) | 2013 | - | - | 247 | 557 | 1826 | 2630 | 241 |
| Guntur (GU) | Pre-2012 | 831 | 4 | - | - | - | 835 | |
| Hesketh (HK) | Nov-11 | 4 | 9 | - | - | - | 13 | |
| Mikio (MI) | Dec-14 | - | - | - | - | 575 | 575 | |
| Marvel (MR) | Oct-12 | 1 | 39 | - | - | - | 40 | |
| Mo (MO) | Pre-2012 | 634 | 232 | - | - | - | 866 | |
| Morris (MS) | N/A | 27 | - | - | - | - | 27 | |
| Mungkin (MU) | Jun-15 | - | - | - | - | 1072 | 1072 | |
| Rasi (RA) | Pre-2013 | - | - | 151 | 689 | 1131 | 1971 | 308 |
| Robinson (RB) | N/A | 162 | - | - | - | - | 162 | |
| Tombol (TB) | Aug-15 | - | - | - | - | 1374 | 1374 | |
| Toyib (TO) | Pre-2012 | 75 | 261 | 157 | 355 | 1708 | 2556 | 81 |
| Yogi (YO) | Nov-11 | 98 | 18 | - | - | - | 116 | |
| Charlie (CH) | Pre-2012 | 577 | 251 | 200 | 115 | - | 1143 | |
| Dali (DL) | Dec-13 | - | - | 286 | 25 | - | 311 | |
| Elizabeth (EL) | N/A | 313 | - | - | - | - | 313 | |
| Ena (EN) | Pre-2011 | 806 | 362 | 363 | 658 | 870 | 3059 | 282 |
| Galaksi (GA) | Sep-13 | - | 28 | 69 | - | - | 97 | |
| Honey (HO) | N/A | - | 69 | - | - | - | 69 | |
| Lucu (LU) | May-12 | 27 | 344 | 381 | 608 | 1894 | 3254 | 272 |
| Maya (MA) | Oct-13 | | | 287 | 419 | 1763 | 2469 | 160 |
| One Eye (OE) | Pre-2011 | 513 | 231 | 254 | 477 | 1228 | 2703 | 122 |
| Shirley (SH) | Pre-2012 | 100 | 160 | 216 | 682 | 1399 | 2557 | 181 |
| Sibau (SI) | Pre-2012 | 104 | 326 | 344 | 663 | 1351 | 2788 | 177 |
| Tahini (TA) | Mar-12 | 209 | 340 | - | - | - | 549 | |
| Tereh (TE) | Pre-2012 | 540 | 261 | 571 | 655 | 1868 | 3895 | 250 |
| Utari (UT) | Jun-12 | 29 | 82 | - | - | - | 111 | |
| **Grand Total** | | 5514 | 3360 | 4351 | 7636 | 23953 | 44814 | 2798 |

**Table 2.4:** The number of data points collected for each pygmy slow loris observed at the Endangered Primate Rescue Center in the Cuc Phuong National Park, Vietnam.

| **Individuals** | 2014 | | | 2015 | | | | | | | | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **10** | **11** | **12** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** | |
| F3 | - | - | 49 | 78 | - | - | - | - | - | - | - | **127** |
| F1 | - | - | - | - | - | - | - | 10 | 8 | 2 | - | **20** |
| F2 | - | - | - | - | - | - | - | - | - | 23 | 62 | **85** |
| M1 | 25 | 51 | 66 | 43 | 52 | 74 | 33 | 97 | 49 | 8 | - | **498** |
| M3 | - | - | - | 92 | 43 | 13 | - | - | - | - | - | **148** |
| M2 | - | - | - | - | - | - | 2 | 33 | 28 | - | - | **63** |
| Total | **25** | **51** | **115** | **213** | **95** | **87** | **35** | **140** | **85** | **33** | **62** | **941** |

### 2.3.5 Comparative data

Following the taxonomy presented in Rowe and Meyer (2017), I included available social organisations on 19 species, nine genera, and four families that all fall within the infraorder Lorisiformes. Lorises, galagos, and pottos make up the Infraorder Lorisiformes. In addition to the information, provided by Rowe and Meyer (2017), I also included available information on social organisation, group size, home range size, from the literature. In Chapter 7, I present data on lorisine home range size, we collated a dataset comprised 63 individuals, representing four Asian loris species (Javan slow, pygmy slow, red slender, and Mysore slender). Unpublished data included on the Javan slow loris were collected by KAIN and SP (See section 2.3.2 Nightly observations), unpublished data on the pygmy slow loris were collected from Carly Starr's (2010) PhD thesis, data on the red slender and Mysore slender lorises were collected from PhD thesis by Kaberi Kar Gupta (2007) and Lilia Bernede (2008).

## 2.4 Data analysis

### 2.4.1 Data management

Throughout my thesis, I used a variety of free and purchased software to manage large datasets from LFP and EPRC. Each software contributed to my ability to analyse data in varying ways. In Table 2.5 I detail each program and how I used it.

**Table 2.5:** Detailed descriptions of each program used to sort, transform, and analyse data and larger datasets throughout the course of the PhD.

| | |
|---|---|
| **R*** | In Chapter 5 and 6, I used R to create bivariate plots and apply the Change-Point test on collected spatial data. This software has the capabilities to analyse, organise and visualize large data sets. The open nature of the program allows users to create new packages and generate novel opportunities to analyse their data. |
| **Basecamp*** | This software is typically used in association with Garmin GPS products. All the included spatial data were collected using a Garmin GPS thus; it was the most efficient option for visualizing the GPS points using the same labels entered during collection. Once visualised and checked for significant errors, the data were exported from Basecamp. Unfortunately, Basecamp only exports waypoint in the Latitude and Longitude format and recodes the timestamp based on where you open the files, thus I needed to convert them in the following two programs. |
| **Ranges** | This software is a user interface program that analyses spatial data. I used this program to analyse the home range of each loris, their incremental area development, and overlap. The data must be in a text file prior to plotting it in Ranges, and coded so that each column is delimited. (ie. ID, Sex, Age, Easting, Northing, Hour, Minute, Second, Day, Month, Year). |

| | |
|---|---|
| **GPSBable*** | I used this software to import GPS waypoints as a GPX file (the raw data file type used in basecamp) then converted to UTM +7 (the universal coordinated universal time for Jakarta) then exported the waypoints as a CSV file. |
| **Hampster Map*** | This website, can convert 1,000s of listed spatial points from one format including UTM, Longitude/Latitude to another format, in a matter of seconds. It only deals with the GPS waypoints, thus if you need to correct the time, I recommend using GPSBable. |
| **ArcGIS** | I used this software to visualize spatial data. In Chapter 6 I emulated the heuristic search model used by Asensio 2011 and Joly and Zimmermann 2011 |
| **Mesquite*** | I used Mesquite to create phylogenetic trees based on character matrices in Chapter7. I entered collected data into a character matrix, which Mesquite converted into a phylogenetic tree. I then altered the tree to reflect the most recent genetic phylogeny for lorisiforms. Mesquite also has a function that calculated the likelihood of each character's presence at nodes, when presented as presence or absence. |

* Denotes free software

### 2.4.2 Home range estimation and range overlap analysis

Based on the techniques employed to analyse location data, the size and shape of a home range can appear differently (Lawson and Rogers, 1997). Here I used two types of estimation methods, Minimum Convex Polygons (MCP) and Kernel Contour (KC) to analyse the GPS waypoints in Ranges 8v2.16 (Anatrack LDT). We defined the home range as 95% of the area covered by the individual and the core area as 50% of the area covered (Pope et al., 2004; Sharpe and Goldingay, 2007). Each estimation method has positive and negative points (Table 2.6).

Historically MCPs have been the most common way of reporting an animal's home range especially in work on nocturnal prosimians (Bearder and Martin, 1980; Harris et al., 1990; Radespiel, 2000; Wiens, 2003; Nekaris, 2003). MCPs are calculated by creating a polygon around the outer perimeter of the collected GPS waypoints. This method is flawed in that it gives no indication of how frequently an animal utilizes any particular section encased by the convex polygon. In fact, MCPs will include area that the animal has never visited; MCPs are highly influenced by outliers and periphery waypoints, which may be the result of one foray or an abnormal observation point. Various methods are available to account for these shortcomings including the arithmetic mean peel, which looks at the generated MCP and excludes the points farthest form the arithmetic mean location. Secondly, the harmonic peel, excludes the locations farthest from the greatest harmonic mean density, by calculating the GPS location where the inverse reciprocal mean distance is lowest (Spencer and Barrett, 1984), another the recalculated arithmetic mean peel, looks at the adjusted MCP generated by the arithmetic centre peel, and recalculates the centre, to further remove the point farthest from the new mean (Kenward, 1987). In Ranges, I applied the arithmetic mean centre peel (Ac), when estimating MCP's.

Kernel contour estimation methods rely on non-parametric algorithms where the density at any location is an estimate of the probability of another point being recorded at the same location (Silverman, 1986; Seaman and Powell, 1996; Horne and Garton, 2006). A home range can then be defined as the smallest area of the utilisation distribution that accounts for a certain percentage of the animal's total space use where the boundary of the home range is delimited by a certain percentage from the utilisation distribution of the animals (Jenrich and Turner, 1969; Anderson, 1982; Gitzen et al., 2006). There are a number of kernel methods, which produce subtle differences in the shape of the contour. The normal "Gaussian" distribution weights all points in the study area, though proximate points are weighted more heavily than distal points in relation to highly used locations. The normal distribution can cause some edge effects, especially if there are several points adjacent to one of the study area boundaries use a restricted circle around the points, and weighs the uniform distribution weights all points within the circle equally. The quartic distribution adjustment gradually weights proximate points more than distal points. The triangular distribution weights proximate points more than distal points within the circle, but the drop off point happens sooner compared to a quadratic distribution. Each of the above-mentioned KC methods result in a relatively similar output, but one drawback of KC is its sensitivity to various smoothing methods. At present, there is no one universally applied or accepted smoothing factor.

**Table 2.6:** Detailed comparison of Minimum Convex Polygons and Kernel Contour as home range size calculation methods (Modified from a table printed by Kenward (2001).

| | **Contour Methods** | **Convex Polygons** |
|---|---|---|
| **Type** | Density | Linkage |
| **Number of density centres, size of linkage distances** | Many | Large |
| **Sensitivity of size and shape to distant outliers** | Some | High |
| **Home range outlines conform well to outer locations** | No | Yes |
| **Home range outlines conform well to multi-nuclear cores** | Yes | No |
| **Home range structure statistics (patchiness or dispersion)** | Yes | No |
| **A single home range centre is estimated** | Yes | Yes |
| **Number of locations needed for home range size to stabilise** | 10-30 | 30 |

### 2.4.3 Incremental area development (IAD)

To measure home range size growth in wild Javan slow lorises and translocated pygmy slow lorises I performed an incremental area development (IAD) analysis on both MCP and KC results in Ranges 8 v2.16. (Kenward et al., 2008). Incremental area analysis allowed me to examine how an animal's home range size changes as successive locations are added, starting with the first temporal GPS waypoint. I used the IAD graph to determine whether the number of locations for each loris reached an asymptote, data for MCP home ranges were examined using an incremental area analysis (Gese et al., 1990; Vernes and Pope, 2001; Moseby et al., 2009). The number of locations is plotted against home-range size, where I considered the home range stable or saturated when the plot reached an asymptote (Kernohan et al., 2001).

### 2.4.4 Path length, overlap, simulation and GPS visualization

Once I transformed the GPS data collected throughout nightly observations at LFP from Latitude and Longitude, to Universal Transverse Mercator (UTM) (Zone 48N) in GPSBabel I analysed the data in ArcGIS version 10.3, using the projected coordinate system datum WGS84. I visualized and turned individual waypoints into consecutive path lengths using the 'points to line' function in ArcGIS. I did not connect waypoints collected greater than 30 minutes apart, which represented an extended unknown period. Following a modified version of the methods used by Asensio et al. (2011), I determined path overlap using an index. I defined overlapping paths as those that fell within a 5 m buffer (to account for GPS error in Cipaganti), for 20 m (Asensio et al., 2011; Joly and Zimmermann, 2011). I calculated the index by dividing the total length of overlapping paths by the total length of all included paths for each slow loris. To test travel efficiency, I used a simulated heuristic travel model, where the first waypoint started at the being of a path and continued in a random direction until a visited goal location was encountered (Asensio et al., 2011; Joly and Zimmermann, 2011). To account for individual perceptional range, primarily vision; I added 5 m, 10 m, and 20 m buffers around each goal location, while running the heuristics model (Joly and Zimmermann, 2011). I defined the efficiency index, as (number of goal locations visited – number of goal locations found by the model)/ (total number of goal locations used within the home range). A negative value indicated that the model performed more efficiently than the study animal in encountering goal locations, and a positive value indicated that the study animal was more efficient than the model (Asensio et al., 2011).

### 2.4.5 The change point test (CPT)

I analysed paths that included at least 15 waypoints using the change-point test (CPT) created by Byrne et al. (2009) in R Programing 3.3. I applied the CPT to determine at which waypoint each path significantly changed direction, starting from the sleep site in the early evening to an assumed goal locations and/or the next sleep site. The CPT first calculates the length of vectors $\overline{R}_k$ (Equation 1), $\overline{R}_q$ (Equation 2) and the resultant vector $\overline{R}_{(k+q)}$ (Equation 3) (Fig 2.12). If $\overline{R}_k + \overline{R}_q - \overline{R}_{(k+q)}$ results in a large number, then the waypoint in question is more likely to be a change-point compared to when the resulting number being small.

**Equation 1:**

$$R_k = || V_k + \ldots + V_1 || = \sqrt{((V1x + \cdots + Vkx)^2 + (V1y + \cdots + Vky)^2}$$

**Equation 2:**

$$R_q = || V(_{k=q}) + \ldots + V1\ (_{k+1}) || =$$

$$\sqrt{((V1(k+1)x + \cdots + V(k+q)x)^2 + (V(k+1)y + \cdots + V(k+q)y)^2}$$

**Equation 3:**

$$R_{k+q} = || V(_{K+q}) + \ldots + V_1 ||$$

To assess the significance of $\bar{R}_k$ + $\bar{R}_q$ - $\bar{R}_{(k+q)}$, CPT applies a permutation test with a random set of N permutations. The values produced by the permutation of $\bar{R}_{k(\sigma)}$ + $\bar{R}_{q(\sigma)}$ - $\bar{R}_{(k+q)\,(\sigma)}$ are arranged in numerical order and if the observed value of $\bar{R}_k$ + $\bar{R}_q$ - $\bar{R}_{(k+q)}$ is the largest, the p value is equal to ($\bar{R}_{k(\sigma)}$ + $\bar{R}_{q(\sigma)}$ ≥ $\bar{R}_k$ + $\bar{R}_q$) / N). $\bar{R}_k$ + $\bar{R}_q$ - $\bar{R}_{(k+q)}$ and considered significant (a change-point) at $p \leq 0.05$. The test will be relatively insensitive to directional changes when using a low q value, whereas when q is larger, the segments will include conflicting directional changes and the ability to detect a significant difference using the test decreases. In addition, the larger q is, the further away from the starting point of the route are the points testable at all. Byrne et al. (2009) point out that there is a trade-off between statistical robustness of the results and the number of locations identified as change-points, therefore they recommend applying a sensitivity analysis to the CPT to determine the optimal value for q. Following this recommendation, I tested q-values; from 1 to 6 to determine which was the most appropriate to apply to this dataset. The greatest number of change-points was obtained with $q = 5$, $p < 0.05$

Image removed from electronic version

**Figure 2.12:** Visualisation of how the CPT evaluates routes, where $V_1$ –$V_6$ represent points along a route, and possible changes points are identified by comparing the distances $R_k$ and $R_q$ with the resultant $R_{k+p}$ (reprinted from Noser et al., 2009).

### 2.4.6 Phylogenetic tree

I used Mesquite 3.2 (Maddison and Maddison, 2007) to calculate the most likely ancestral social organisation at different nodes representing the last common ancestor of specific species and genera. I used the molecular phylogeny of Pozzi et al. (2015, 2016), to arrange the phylogenetic tree created in Mesquite. Not all species included in the molecular phylogeny were included in the social organisation reconstruction. Any lorisiform species that had available information about their social organisation, but was not listed in Pozzi et al. (2015, 2016), were excluded from the ancestral reconstruction. In Mesquite I created a character matrix were three social organisations (dispersed family group (monogamy), multi-female/multi-male (promiscuous), and multi-female/uni-male) were marked as either present (1) or absent (0). This resulted in a 19 x 3 presence-absence character matrix. I traced the character history using the maximum likelihood ancestral state reconstruction function, which uses a Markov k-state 1 parameter model (Mk1). This is a k-state generalization of the Jukes-Cantor model, and corresponds to Lewis's (2001) Mk model. The single parameter is the rate of change. Any particular change is equally probable (Felsenstein, 1981).

### 2.4.7 Statistical analysis

Using SPSS version 22 and R 3.3.3, I calculated the mean and standard deviation of observed data points in each of the collected variables. I tested each variable for normality using the Shapiro-Wilks or the Kolmogorov-Smirnov test in SPSS. If the p-value exceeded 0.05 then I considered the variables to be normally distributed. Both of the above-mentioned tests are used to compare two sets of continuous data to ascertain whether they come from the same distribution (Dytham, 2011). The one-way Kolmogorov-Smirnov test, which is the most commonly used normality test in this thesis, tests data against a hypothetical data set derived from the actual data. To test for significant differences across varying groupings (ie. Age-classes) (Table 2.7) I used the non-parametric Kruskal-Wallis, Mann-Whitney U, and/or Chi-square test with significance set at $p \leq 0.05$ for non-normal data. I applied the Bonferroni correction where there were multiple post-hoc comparisons changing the significance level according to the number of comparisons (0.05/# of combination = new p-value). The Kruskal-Wallis test is the non-parametric version of the one-way ANOVA. The null hypothesis is that all samples are from populations that have the same median. This test is preferable to the one-way ANOVA because it does not make assumptions about homogeneity of variance or normal distributions. It is less statistically robust than the one-way ANOVA, but is more conservative in instances where false positives are likely to occur, due to extreme data points. The Mann-Whitney U test also known as the Wilcoxon-Mann-Whitney test, is the non-parametric version of the independent sample t-test; this test can compare two groups. Like the Kruskal-Wallis test, it does not make assumptions about homogeneity of variance and normal distributions. The raw data are converted to ranks before the test is carried out, meaning that extreme data will have less of an effect on the outcome. The Chi-square test also referred to as the chi-squared goodness of fit, this test looks at the differences between observed and expected frequencies for categorical data (Dytham, 2011). Here I based the expected distributions on equal likelihood and the null hypothesis is that the expected and the observed do not differ. I used General Linear Models (GLM), to test the interaction between certain variables and the proportion of observed behaviours (Chapter 5). The GLM predicts one variable (the dependent or response variable) from one or more other variables (the independent or explanatory variables). First, I tested each variable for multicollinearity using Spearman's rho test, when the test did not produce any collinearity coefficients greater than 0.90 I defined the tested variables as not correlated (Field, 2013). Multicollinearity exists whenever two or more of the predictors in a regression model are correlated

Due to the non-normal nature of the many of the variables, they underwent a $\log_{10}$ transformation for normality. The log-transformation is widely used in to deal with skewed data (Feng et al., 2014). I used a canonical variate analysis (CVA) to identify the morphometric variables that are most varied between the age classes (Dytham, 2011). Canonical variate analysis follows the same principles as a principle components analysis, but each included individual is associated with a predetermined group prior to analysis. Next the test identifies what variable weightings best distinguish each group from the other (Dytham, 2011).

To look at the differential growth patterns of the reported morphometric measures in Chapter 5, I also calculated the allometry coefficient (slope) using a least-square (LS) regression for each log-transformed measure against the log-transformed body weight (Lawler, 2006). Least Squares methods are suitable for determining the best fit line using calculus and linear algebra (Miller, 2006). A least square regression produces a best-fit straight line (y = ax + b) under the assumption that for n ∈ {1. . . N}, the pairs (Xn, Yn) are observed.

**Table 2.7:** A summary of the tested variables and statistical tests applied in each chapter throughout the thesis.

| Chapter | Variables | Test |
|---|---|---|
| 3 | • Home range sizes | • Shapiro-Wilks<br>• Mann-Whitney *U* |
| 4 | • Home range size<br>• Dispersal Distances<br>• Dispersal Weight | • Shapiro-Wilks<br>• Mann-Whitney *U* |
| 5 | • Morphometric Measures<br>• Locomotor and Postural Modes<br>• Habitat use<br>• Allometry Coefficient | • Shapiro-Wilks<br>• Kruskal-Wallis<br>• Mann-Whitney *U*<br>• Least-square (LS) regression<br>• General Linear Model |
| 6 | • Efficiency Indices<br>• Change-point associations | • Shapiro-Wilks<br>• Mann-Whitney *U*<br>• Chi-square |
| 7 | • Home range size | • Mann-Whitney *U* |

# Chapter 3: Ranging patterns in translocated pygmy slow lorises (*Nycticebus pygmaeus*)

**Figure 3.1:** Translocated pygmy slow loris (*Nycticebus pygmaeus*) as he looks at his new environment just after being released from the in-situ cage at the Endangered Primate Rescue Centre in Cuc Phuong National Park, Vietnam. Photo provided by the author.

## 3.1 Introduction

Translocation is an important conservation tool used to reverse declining animal populations in the wild. Translocation is the overarching term used to define any form of population restoration and conservation introduction. Despite its frequent use and purported importance to conservation, historically translocations have a low success rate (Griffith et al., 1989). The causes of these failures are poorly understood due to the difficulty of post-release monitoring (Fisher and Lindenmayer, 2000) and the occasional reluctance by practitioners to publish negative results for fear of discouraging future funders (Moore et al., 2014. Furthermore, difficulties arise with the way we define success; is it the creation of a self-sustaining population or a pre-determined period of survival immediately following the release? The success or failure of translocations is dependent upon short- and long-term processes, including the immediate reaction of releasees to the novel area and the social dynamics of creating a new functional population (Armstrong et al., 1999). Intensive post-release monitoring allows us to determine whether a population that disappears following release has succumbed to stochastic demographic processes, increased post-release mortality, or post-release dispersal (Armstrong et al., 1999). Data on these various components of post-release are important, as they allow the identification of the mechanisms responsible for success or failure of translocation efforts (Griffith et al., 1989; Armstrong et al., 1999).

Few organisations use systematic slow loris translocation and post-release monitoring as a practical, yet expensive strategy to aid in replenishing wild populations, with an attempt at adherence to IUCN Reintroduction Specialist group policies (IUCN, 2013). Throughout their range, translocations of *Nycticebus* spp. occur that violate IUCN policies to the extent of introducing species outside of their endemic range. This practice may be due to government agencies requiring animals be returned to the wild immediately (Streicher, 2004), but it is also largely due to misconceptions regarding beneficial actions for individual welfare and conservation. Concerns regarding the welfare of translocated individuals have also risen with the increase in unsuccessful and unmonitored releases (Moore et al., 2014). To avoid arbitrary primate releases, it has become increasingly important for organisations to develop a conservation strategy that includes well-planned and well-monitored translocations to document and share their work, whether successful or unsuccessful (Kumar et al., 2015). Nekaris and Starr (2015) noted that the limited success of slow loris translocations was associated with scarce knowledge on social, behavioural, and ecological factors, including the variability across species, within this genus.

In Vietnam, pygmy slow loris translocations have been systematically carried out with published results by two rescue centres, the Endangered Primate Rescue Center (EPRC) in Cuc Phuong National Park, about 130 km south of Ha Noi, Vietnam, and the Endangered Asian Species Trust (EAST) in the Cat Tien National Park about 150 km north of Ho Chi Minh City, Vietnam. The EPRC was the first to report their translocation and post-release monitoring of pygmy slow lorises in 2000 releasing nine individuals into the Cuc Phuong National Park (Streicher and Nadler 2003, Streicher 2004). Streicher and Nadler (2003) observed a high intake of insects and exudates in the released individuals and their sensitivity to cooler temperatures, noting hypothermia as a possible cause of death. EAST has overseen more than 20 released pygmy slow lorises since 2009 (Kenyon et al., 2014). Kenyon et al (2014) noted that reintroduced pygmy slow lorises had a mean home range size of 20 ha, required at least two days in an *in-situ* release cage, and the ideal release season was between June and November (wet season). Following a wild study on this species in Cambodia, Starr (2011) noted that knowledge of the spacing and mating systems of the pygmy slow loris may lead to the development of useful *in-situ* and *ex-situ* conservation strategies, aiding in estimating population size and the carrying capacity of wild populations. She reported a mean home range size of 22 ha in males and 12 ha in females (Starr, 2011).

Home range formation and ranging patterns are essential aspects of long-term survival in all animal species (Schick et al., 2008). Ecological, behavioural, and social factors are known to influence ranging patterns in primate species; researchers have even associated the size and formation of home ranges with stress, specifically in translocated individuals (Nekaris, 2011). When trying to establish or re-establish a population, dispersal from a release area is a concern, since this will decrease the number of possible founders and will expose individuals to unknown factors outside of the release site (Allen et al., 1993; Clarke and Schedvin, 1997). Natal habitat preference induction (NHPI) can cause post-release dispersal as some animals show a preference for areas that resemble their natal range (Davis and Stamp, 2004). During the establishment phase of translocations, the mortality rates can be higher than seen in a normal population, due to stress and the inexperience of released individuals (Tweed et al., 2003).

In this chapter, I focus on the ranging patterns of six translocated pygmy lorises at Cuc Phuong National Park, Vietnam. My aim is to examine their home range formation and to discuss possible contributing factors to the fitness and potential survival of the individual pygmy slow lorises.

## 3.2 Methods

**See sections:**

2.2.2 Endangered Primate Rescue Center (EPRC)
2.3.1 Collaring and release
2.3.2 Nightly observations
2.4.2 Home range and overlap analysis
2.4.3 Incremental area development (IAD)
2.4.7 Statistical analysis

## 3.3 Results

### Home range size:

The average home range size for males was 81.5±SD105.5 (MCP); 25.3±31.2 (KC), while the average size for females was 9.7±1.6 (MCP); 8.8±5.5 (KC). The median home range size for males was 156.1 (MCP); 47.3 (KC) and 9.2 (MCP); 11.9 (KC) for females. Though males maintained a larger home range compared to females there was no statistically significant difference. Table 3.1 details the individual home range areas, including the number of fixes. It is important to note that some lorises were observed for a longer period, which is evident in the number of fixes collected for each pygmy slow loris

**Table 3.1:** The home range size in Minimum Convex Polygons and Kernel Contour for six pygmy slow loris (*Nycticebus pygmaeus*) three males and three females.

| **ID** | **# of fixes** | **MCP 50% (ha)** | **MCP 95% (ha)** | **Kernel Contour 50% (ha)** | **Kernel Contour 95% (ha)** |
|---|---|---|---|---|---|
| **$F_1$** | 20 | 4.87 | 8.48 | 4.66 | 11.98 |
| **$F_2$** | 85 | 7.61 | 11.58 | 4.63 | 12.14 |
| **$F_3$** | 125 | 8.84 | 9.26 | 0.58 | 2.49 |
| **Mean** | | **7.10±2.03** | **9.77±1.61** | **3.29±2.34** | **8.87±5.52** |
| **Median** | | **7.61** | **9.26** | **4.63** | **11.98** |
| **$M_1$** | 495 | 137.35 | 156.12 | 16.37 | 47.39 |
| **$M_2^*$** | 65 | 601.72 | 669.65 | 48.51 | 196.71 |
| **$M_3$** | 145 | 0.76 | 6.84 | 0.54 | 3.21 |
| **Mean** | | 69.0+96.5 | 81.5+105.5 | 8.4+11.2 | 25.3+31.2 |
| **Median** | | **137.35** | **156.12** | **16.37** | **47.39** |

**Overlap:**

Most pygmy slow loris home ranges and core areas overlapped, when considering the MCP home range calculation. Per cent overlap is reduced in the core for both calculation types, but overlap is absent in some cases for in the 95% KC home range calculation (Table 3.2). Figure 3.2 and 3.3 display the overlap in both MCP and KC home ranges at 95% and 50%, it is important to note that this project utilized staggered release thus there are temporal restrictions to how I can interpret these data. M1 was present during the entire observation period and overlapped with all subsequent pygmy slow lorises. F3 and M3 overlap for one month in January 2015, while F1 and M2 overlapped in May and June 2015. Considering the temporal variations, the level of overlap reported here can act as further evidence that released individuals of travelled outside the release sites, allowing for other individuals to safely occupy them.

**Table 3.2:** Individual overlap, reported as the per cent two individual's home ranges overlap at Cuc Phuong National Park, Vietnam. Home ranges were calculated using Minimum Convex Polygon and Kernel Contour for six pygmy slow loris (*Nycticebus pygmaeus*) three males and three females.

| 95% MCP | F1 | F2 | M2 | M3 | F2 | M1 |
|---|---|---|---|---|---|---|
| F1 | - | 33 | 97 | 28 | 59 | 100 |
| F2 | 24 | - | 100 | 53 | 38 | 100 |
| M2 | 1 | 2 | - | 1 | 1 | 20 |
| M3 | 35 | 90 | 100 | - | 62 | 100 |
| F2 | 54 | 48 | 93 | 46 | - | 100 |
| M1 | 5 | 7 | 86 | 4 | 6 | - |
| | | | | | | |
| **95% KC** | **F1** | **F2** | **M2** | **M3** | **F2** | **M1** |
| F1 | - | 30 | 100 | 6 | 9 | 100 |
| F2 | 30 | - | 100 | 23 | 0 | 88 |
| M2 | 6 | 6 | - | 2 | 1 | 24 |
| M3 | 23 | 87 | 100 | - | 0 | 69 |
| F2 | 43 | 2 | 100 | 0 | - | 100 |
| M1 | 25 | 22 | 100 | 5 | 5 | - |
| | | | | | | |
| **50% MCP** | **F1** | **F2** | **M2** | **M3** | **F2** | **M1** |
| F1 | - | 0 | 1 | 0 | 73 | 100 |
| F2 | 0 | - | 100 | 10 | 18 | 100 |
| M2 | 0 | 1 | - | 0 | 0 | 17 |
| M3 | 0 | 100 | 100 | - | 42 | 100 |
| F2 | 40 | 15 | 23 | 4 | - | 79 |
| M1 | 4 | 6 | 75 | 1 | 5 | - |
| | | | | | | |
| **50% KC** | **F1** | **F2** | **M2** | **M3** | **F2** | **M1** |
| F1 | - | 19 | 100 | 0 | 0 | 93 |
| F2 | 19 | - | 100 | 3 | 0 | 59 |
| M2 | 10 | 10 | - | 1 | 1 | 34 |
| M3 | 0 | 22 | 100 | - | 0 | 0 |
| F2 | 0 | 0 | 100 | 0 | - | 100 |
| M1 | 27 | 17 | 100 | 0 | 4 | - |

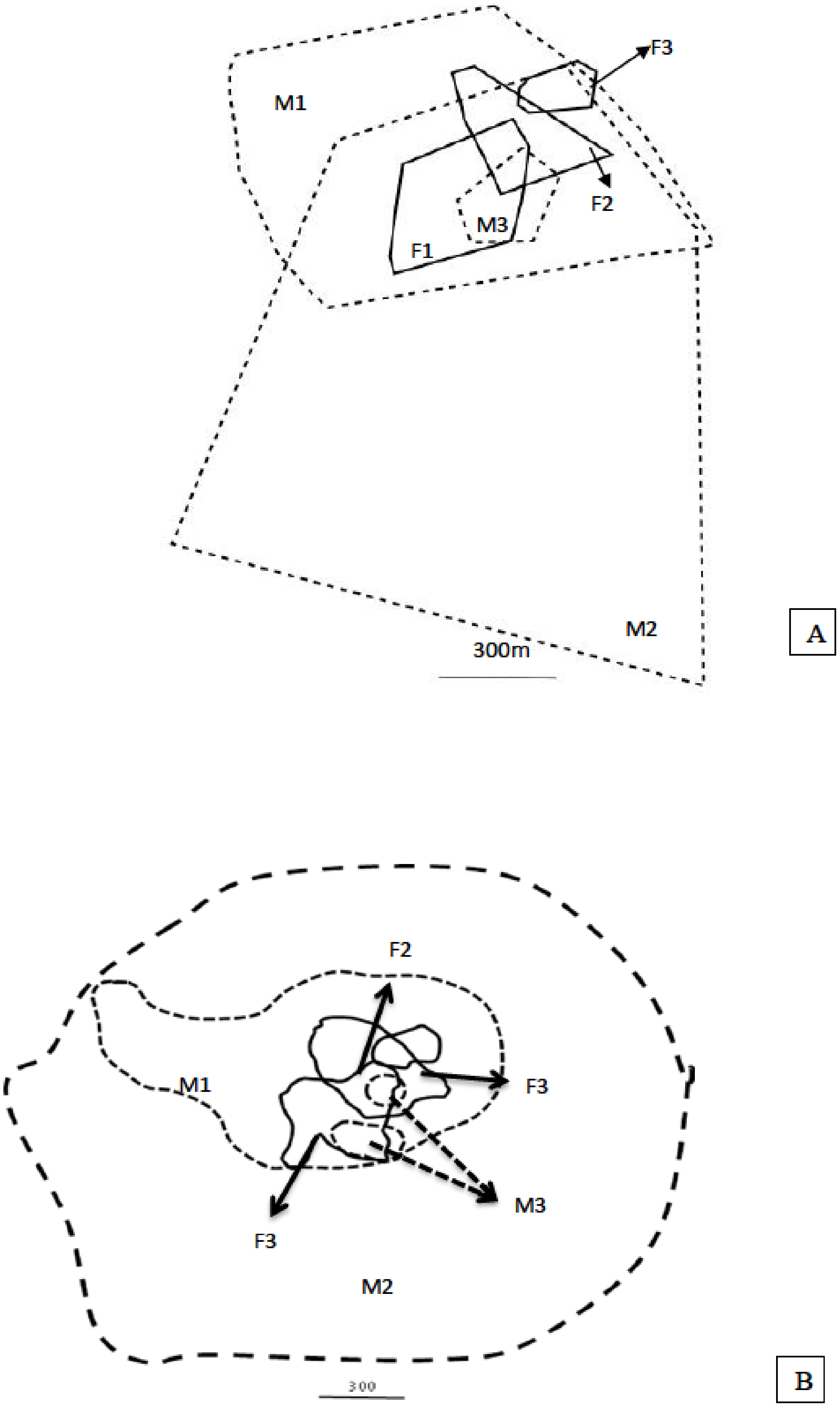


**Figure 3.2:** The 95% home range for the six pygmy slow lorises (*Nycticebus pygmaeus*) at Cuc Phuong National Park, Vietnam. Home ranges are presented as both Minimum convex polygons (A) and Kernel Contour (B)

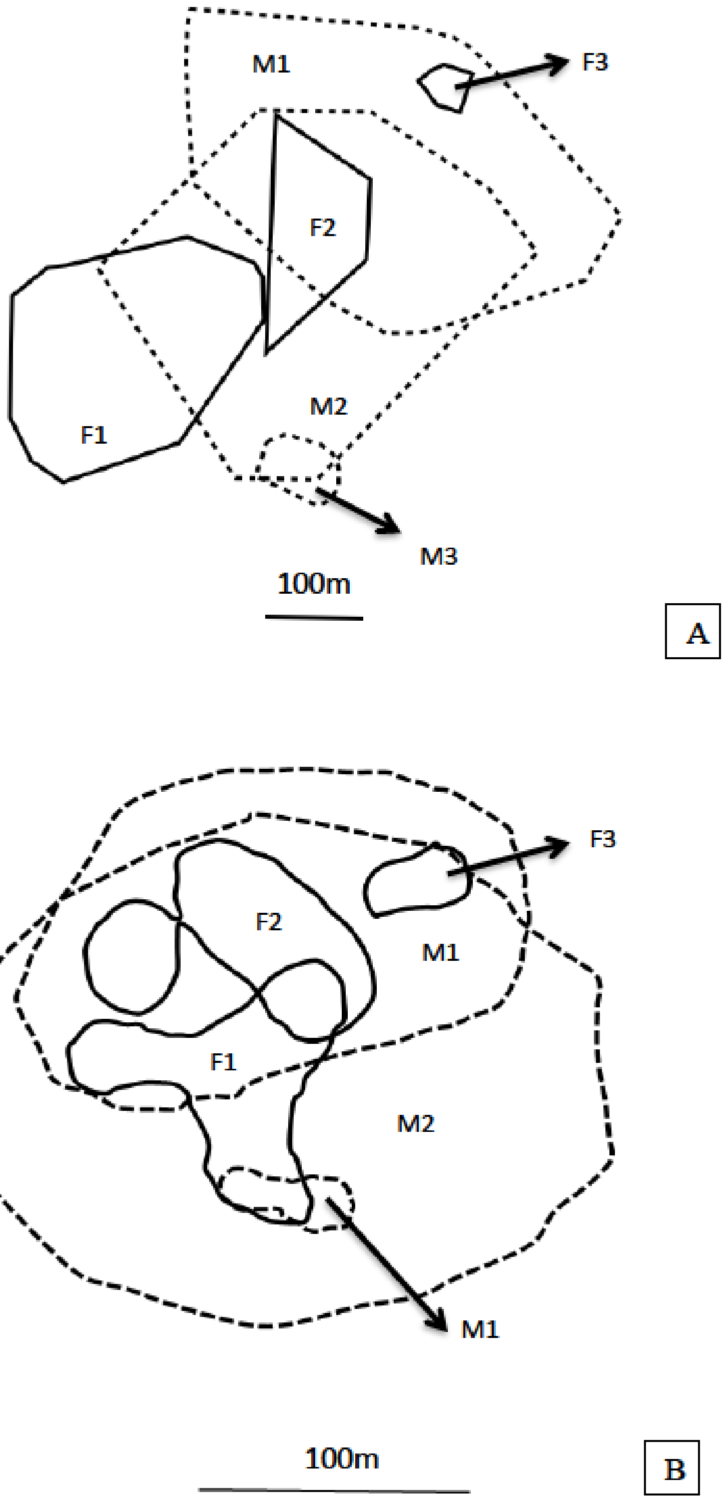


**Figure 3.3:** The 50% home range for the six pygmy slow lorises (*Nycticebus pygmaeus*) at Cuc Phuong National Park, Vietnam. Home ranges are presents as both Minimum convex polygons (A) and Kernel Contour (B)

**Incremental area development (IAD):**

The number of GPS waypoints it took before reaching a stable home range was variable and some individuals never reached a consistent home range size during the study period (Figure 3.4). M1 was the only individual who displayed a graph where he plateaued at ~280 GPS waypoints M3 continuously increased his area, never remaining consistent. The incremental areas differed between the method of analysis with MCP displaying more settlement and Kernel contours displaying a much less settled home range.

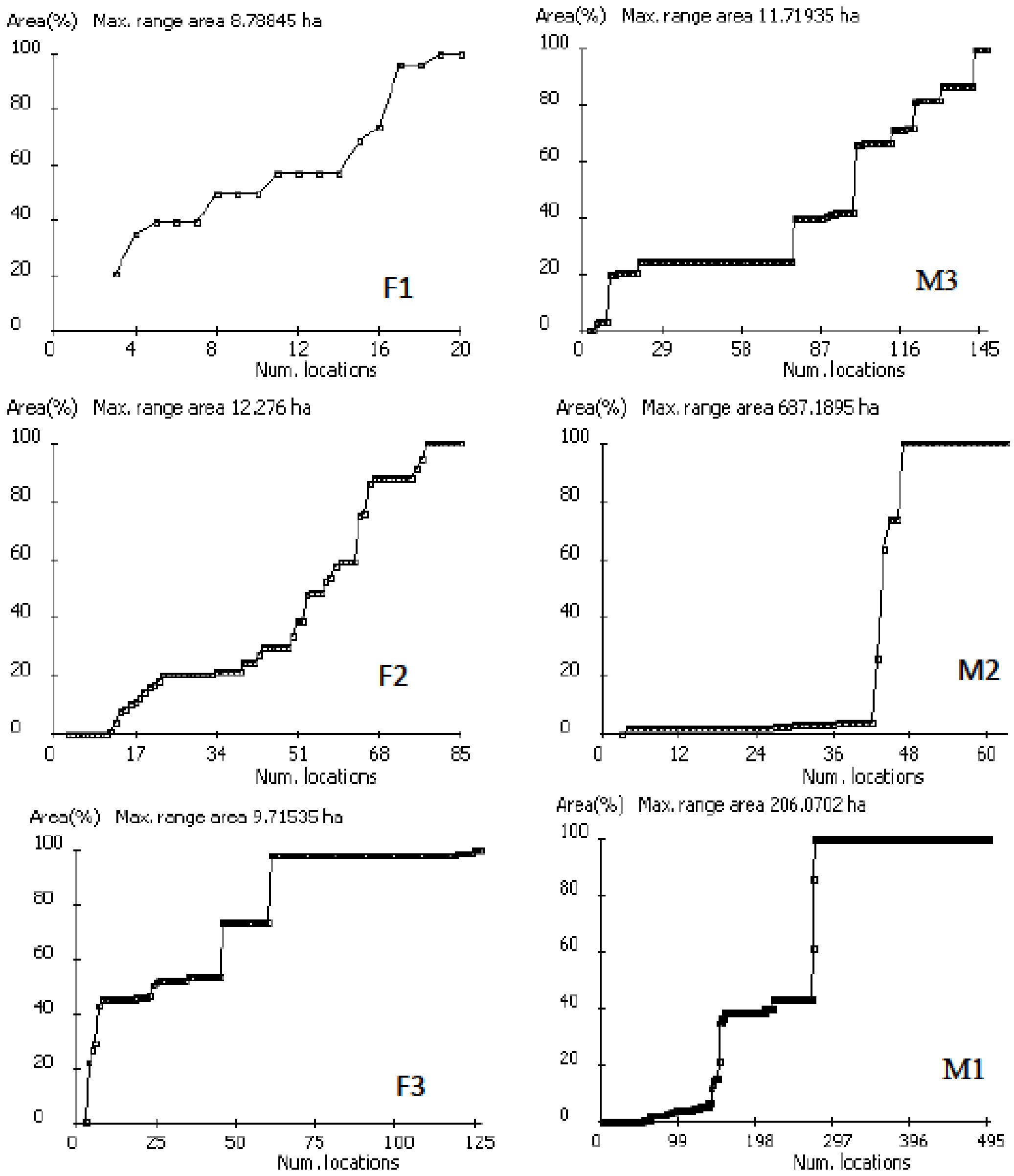


**Figure 3.4:** The incremental area development (IAD) graph using the Minimum convex polygon home range size of six released pygmy slow lorises (*Nycticebus pygmaeus*) in the Cuc Phuong National Park, Vietnam. The IAD graph shows how many Geographical position system waypoints represent increasing percentages of the total home range size.

### Post-release status:

Of the six released pygmy slow lorises reported in this study, we only know that M1 settled into the release site. We suspect that F3 remained in the area as well, following occasional sightings of a habituated female with the same unique pelage characteristics throughout the observation period. Two pygmy slow lorises (F2 and M3) died of unknown causes, but there was no evidence of wounds indicating an attack. We lost F1's signal very early into the study period and she was never seen again. Following dispersal out of the release site, we lost M2's signal, and we were unable to relocate him again.

## 3.4 Discussion

### Home range size and formation:

Home range sizes in the reintroduced males were larger than those reported in wild pygmy slow lorises in Cambodia (Starr, 2011) and those reported for translocated pygmy slow lorises in Dao Tien National Park (Kenyon et al., 2014). In this study, individuals were lost due to long-range dispersal and detached collars. Of the published slow loris translocations, individuals traveling long distances and disappearing soon after release is a common problem (Streicher and Nadler, 2003; Streicher, 2004; Keyon et al., 2014). The incremental area development of these six released pygmy slow lorises provides a unique view on their ability to acclimate to a new area. Measuring the development of pygmy slow loris home range can act as a proxy for adaptability in primates (Ossi and Kamilar, 2006), as it represents behavioural flexibility, showing how quickly an individual is able to settle into a new environment (Wright et al., 2010). In a study of wild and reintroduced Javan slow lorises in Indonesia, wild slow lorises displayed an incremental area development graph where 100% of their home range was identified in fewer fixes compared to the reintroduced slow lorises (Nekaris pers. comm). Once they were observed in 100% of their home range the graphs plateaued showing that they were settled in the observed area, while the translocated Javan slow lorises continued to expand their area, which never stabilized (Nekaris and Rodes, 2013). In other translocated animals, unusually large or small home ranges, and previously unobserved ranging patterns are commonly reported, but many of these individuals normalize their behaviour in a matter of weeks or months (Tweed et al., 2003; White et al., 2006; Molyneux et al., 2011). The current observation period for this study included ten months, and a similar level of normalization was not observed, suggesting that these pygmy slow lorises were not as behaviourally flexible as the individuals or species in the above studies.

Regarding home range fidelity, Starr (2011) observed a saturation point after a range of 100 to 300 fixes between wild males and females. Here the first released male (M1) was the only pygmy slow loris that reached a point comparable to a saturation point seen in settled wild animals. To uncover the maximum area covered by M1 required 297 fixes. Other individuals' areas continued to grow suggesting instability in their home range formation. M2 maintained a small part of his ultimate area, but at the 40th fix, he moved to a completely new area, significantly widening his calculated home range.

Based on previous field reports of home range size, it was believed that the National Park's former botanical garden (120 ha) would be large enough to support at least six pygmy slow lorises. The variation present not only between wild and translocated pygmy slow loris home ranges, but also between two translocated populations seems to be based on an unidentified factor, leading us to conclude that practitioners should increase the space needed for translocated pygmy slow lorises to establish a stable home range. During their release and in response to this novel environment, pygmy slow lorises will traverse large areas as they 'survey' the release site and eventually settle into an ideal location within it. Kelt et al. (2014) observed larger home ranges in the reintroduced Riparian brush rabbit (*Sylvilagus bachmani riparius*) compared to wild individuals, but hesitated to offer an explanation other than the effects of the varying topography. This may explain the differences seen between home range sizes reported at EAST and those observed at the EPRC.

Males tended to move outside of our discernible radio signal range, except for M1 who we could observe for the longest period. This individual was not only released first, but was released nearly two months before another male was reintroduced into an adjacent area. M2 and M3 spent the initial part of their post-release overlapping with M1, but eventually travelled far outside of his established territory. Partitioning territories is typical in wild slow and pygmy slow lorises as they are highly territorial (Fischer et al., 2003), but in this instance M1 maintained an unusually large home range of 156 ha (MCP)/47 ha (KC), accounting for all or half of the release site. The subsequent dispersal by M2 and M3 was no surprise, but the sheer size of M1's home range was surprising and may have caused M2 and M3 to move large distances to leave this claimed area. The home range reported for M2 is better described as a dispersal range, as he occupied very little of the area included in his calculated home range.

In contrast to the released males, the released females did not disperse to our knowledge out of the release site, and maintained smaller home ranges compared to those of the males. Reduced observation periods in females were largely due to lost and faulty collars; this loss also hindered our evaluation of their home range size. We did continue to see these individuals within the release site throughout the observation period and on a few occasions; we saw F2 and F3 interact with M1. The overlap seen in the male and female home ranges further supports the proposed promiscuous mating system in pygmy slow lorises (Starr, 2011), which is contrary to the monogamous mating system seen in other *Nycticebus* species (Nekaris, 2014). Wiens and Zitzmann (2003) observed spatial groupings in greater slow lorises (*N. coucang*) representative of a monogamous mating system and across slow loris species this is the accepted mating system. Female lorises are known to display aggression and territoriality, as they only share their wild territory with their offspring and one-three males (Nekaris et al., 2013). On the other end of the spectrum female tolerance has also been observed in captive Bengal slow lorises (*N. bengalensis*) housed together in groups of three to four adults, their offspring and one male (Poindexter and Nekaris, 2014). Here we saw evidence of both the territorial and the tolerant female pygmy slow loris as they overlapped with each other in areas included in their 95% home range, but no overlap was observed in areas included in their 50% core area.

**Stress:**

An animal's survival in a new environment depends on the individual’s ability to, secure resources, orientate themselves, decide how to respond to environmental stimuli and ascertain the location of conspecifics and predators (Teixeira et al., 2007). Mendl (1999) found that stress might influence animal survival by disrupting processes involved in decision-making. Hormones, such as epinephrine and vasopressin are released during stressful events, and can affect memory storage (Gold and Van Buskirk, 1978). In a chronically stressed animal, the short-term behavioural changes needed to alleviate acute stressors no longer aid survival, but become harmful to the animal, leading to pathological conditions (McEwen, 1998). Transfer of an animal from a known area to a novel environment stimulates both the glucocorticoid response, which is associated with learning and memory, and the fight-or-flight response (Hennessy et al., 1995; Roozendaal et al., 1997). Stress can contribute to translocation failure by increasing the animal's vulnerability to the effects of chronic stress (Dicken et al., 2010). The direct cause for failure is likely external factors, but vulnerability to these external factors is worsened by chronic stress among the reintroduced individual. Though we are unable to identify the exact cause of death in the deceased pygmy slow lorises in this study, there was no evidence of an attack from either a conspecific or a predator; leaving us to suspect that the cause was starvation, an illness, or poor acclimation to the environment. Starvation is often cited as a cause of mortality during the establishment phase of translocation (Work et al., 1999; Rosatte et al., 2002; Islam et al., 2008). The hypothalamic–pituitary–adrenal (HPA) axis plays a very important role in the regulation of food intake and metabolism (Dallman et al., 1993). A dysfunctional HPA axis, caused by chronic stress, will lead to both decreased feeding (Herzog et al., 2009) and an increased energy requirement (García-Díaz et al., 2007) putting animals into a negative energy balance. Regardless of the suitability of the release site, this negative relationship will put the stressed reintroduced individual in a vulnerable position and much more susceptible to starvation, or other external factors. Additionally, the pygmy slow lorises in this study travelled great distances throughout the observation period, causing them to exert extra energy.

**Natal habitat preference induction (NHPI):**

The post release dispersal seen in these pygmy slow lorises may be the result of NHPI. Even in cases where there is no question about the suitability of the release site, NHPI can lead released individuals to leave the release site seeking familiar environmental cues. Marbry and Stamps (2008) showed that brush mice (*Peromyscus boylii*) will settle in a habitat type similar to their natal habitat more than expected by chance. Hanghland and Larsen (2004) reported similar behaviour in red squirrels (*Tamiasciurus hudsonicus*) where given the choice between logged or intact conifers forest individuals selected the option that reflected their natal habitat. One major component of NHPI is associative learning; this speaks to the complex cognitive processes present in these species. Natal Habitat Preference Induction has three effects on habitat selection that are particularly relevant to the study of ecology and evolution. First, it is a predictable source of individual differences in habitat preferences. Second, NHPI provides a mechanism by which individuals are more likely to select habitats to which they are best suited, thus encouraging the maintenance of genetic variation in heterogeneous landscapes. Finally, NHPI acts as a mechanism for the inheritance of phenotypically plastic traits in which expression depends on the natal environment. Environmental heterogeneity play an important role in maintaining genetic variation, as different genotypes are likely to be favoured in different environment (Kassen, 2002). Natal habitat preference induction is a behavioural mechanism that elicits adaptively non-random dispersal: individuals are more likely to select habitats in which they (or their offspring) are likely to perform well after arrival. In species with NHPI, environmental heterogeneity might maintain genetic variation despite high rates of dispersal. Natal Habitat Preference Induction can encourage the inheritance of phenotypically plastic traits by providing a comparable natal environment for parents and their offspring. Further study of the pygmy and slow loris cognitive capacity may shed light on the extent to which NHPI influences *Nycticebus* translocation successes. Unlike wild studies looking at NHPI the pygmy lorises in this study did not have the option to decide between habitat types. Our limited knowledge of their individual origin, especially their natal habitat type, limited the opportunity to include their characteristics as a criterion for release site selection.

### 3.5 Chapter summary

Territoriality, chronic stress and the negative effects that stress can have on physiological process, as well as, NHPI are all possible explanations for the unusual ranging patterns and deaths seen in this translocation study. In this chapter, I found that translocated pygmy slow lorises ranged over much larger areas compared to wild individuals. Their overlap patterns are congruent with reports of a promiscuous mating system in this species. Finally, the observed patterns of area size development supports theories that translocated animals have difficulty settling into unfamiliar areas, as most of the pygmy lorises here never created a stable area. Following the results in this chapter, I concluded that more work is needed to uncover how varying ecological, social, and psychological factors influence ranging behaviours not only in translocated slow lorises, but in wild slow lorises as well. In this chapter I looked directly at translocations for conservation and discussed aspects of the physical, social, and cognitive factors that affect nightly movement and spacing (Figure 3.5). To uncover how slow lorises establish home ranges in new areas in the next chapter, I looked to natal dispersal as a proxy for translocations. In a wild setting, I can assess the natural process of reestablishment.

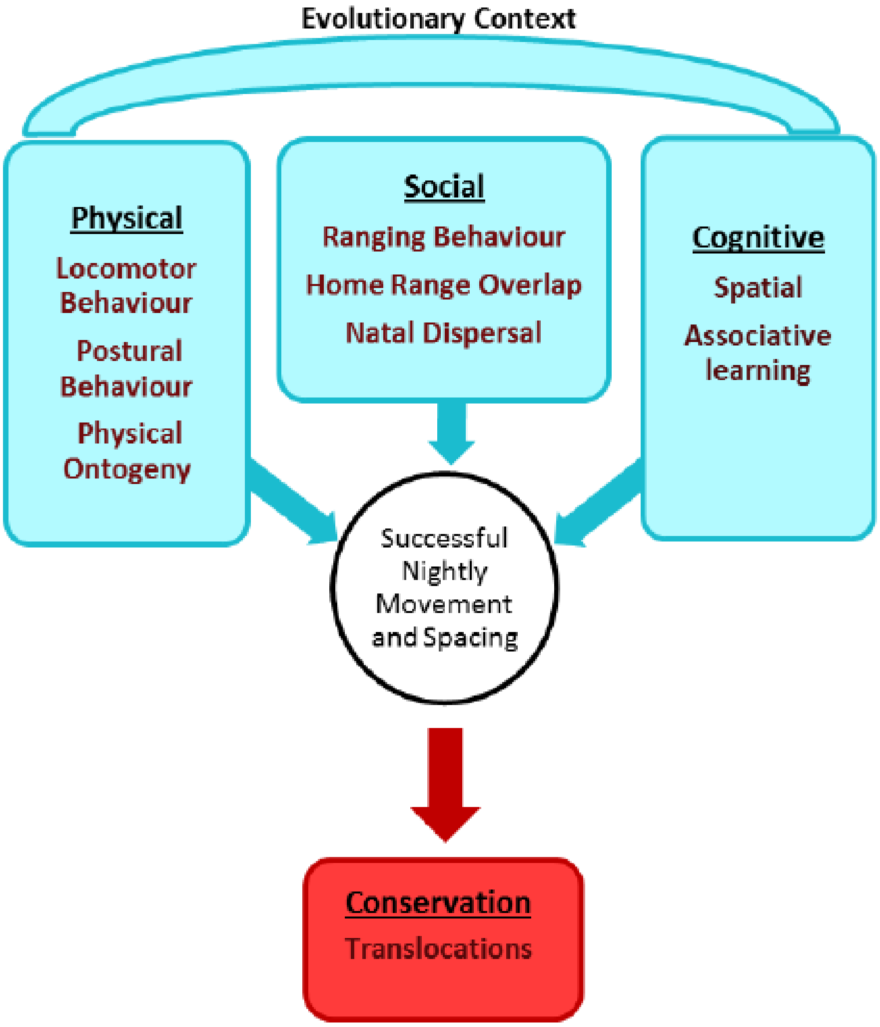


**Figure 3.5:** Visualisation of the framework of the thesis highlighting how the data and conclusions presented in Chapter 3, fit into the context of the entire thesis. Topics in red are the focus of the chapter; topics in blue are related though not explicitly discussed.

# Chapter 4: Behaviour within and dispersal from the natal group in the Javan slow loris (*Nycticebus javanicus*)

**Figure 4.1:** Young Javan slow loris (*Nycticebus javanicus*) holding on to a thin branch at the Little Fireface Project in West Java, Indonesia. Photo provided by the Little Fireface Project.

## 4.1 Introduction

Natal dispersal affects the demography and structure of a population, genetically and socially (Bowler and Benton, 2005). Generally, natal dispersal is regarded as a three-stage process; characterized by the departure from the natal area, search for a new area, and settlement within that new area, otherwise referred to as departure, vagrancy, and settlement (Baguette and Van Dyck, 2007; Clobert et al., 2009). Dispersal reduces inbreeding and kin competition, but also the potential for kin cooperation, depending on the dispersal distance. Ultimately, individuals disperse to avoid inbreeding with relatives (Wolff, 1994; Gundersen and Andreassen, 1998), to minimize competition for mates (Dobson, 1982), or to gain access to environmental resources, such as food (Greenwood, 1980). Despite these benefits, dispersal is costly both energetically and physiologically (Waser et al., 1994; Plissner and Gowaty, 1996). These potential constraints can lead to individual, age, size and sex based differences regarding dispersal time and distances.

Natal dispersal distances and the mechanism of dispersal vary considerably among species (Swingland, 1982). The most clear-cut distinction is between active and passive dispersal (Clobert, 2012). Active dispersal is when the individual has control over their own movement during the dispersal process, including decision-making based on available environmental and social cues (Clobert, 2012). The capacity to move can heavily effect dispersal in that dispersers must possess certain levels of physical, mental, and physiological competence to successfully complete the three-stage process (Bernard and McCauley, 2008). Passive dispersal is largely out of the individual's control and initiated by factors ranging from wind to interference from other organisms (Van de Stocken et al., 2015). Though passive dispersal is typically seen in species with limited mobility, plants, and small invertebrates there are occasion where larger species are separated from their group or interfering organisms displace them (Clobert, 2012). Considering the varying forms of displacement, we should remember that dispersal is a spatial process thus, factors affecting spacing systems within the existing population can also effect dispersal (Clobert et al., 2009).

Most active dispersers have long dispersal distances and display a strong age and sex based bias (Johnson, 1986). All influential factors are assumed to incur costs to survival and reproductive success (Bengtsson, 1978), but these costs may increase with the distance travelled outside of the natal home range. Numerous studies have investigated the probability of dispersal in mammals (Swilling and Wooten, 2002; Le Galliard et al., 2006; Zedrosser et al., 2007; Armitage et al., 2011), but few studies focus on the timing of dispersal (Lens and Dhondt, 1994; Nunes and Holekamp, 1996). Each stage of dispersal is a precarious time for the dispersing animal (Lucas et al., 1994), and can lead to an increased probability of mortality (Bonnet et al., 1999), thus timing is crucial to ensuring survival and sexual reproduction within a new home range.

One possible scenario affecting dispersal timing and distance is group size. Younger siblings might be forced to disperse earlier as older siblings are larger and more experienced; or older siblings might disperse earlier because they have achieved the needed competencies, thus are fit for the dispersal process (Nunes and

Holekamp, 1996; Bowler and Benton, 2005). Researchers often present these social factors as a common theme affecting immigration and emigration in larger more social species, like chimpanzees (Sugiyama, 2004; Langergraber et al., 2009). In solitary foraging species, such as *Nycticebus* species, few researchers have discussed social network, including their dispersal pattern.

Wiens (2002) noted four possible dispersal events in the greater slow loris (*N. coucang)* during his year-long study, involving two males and two females, who travelled between 500 and 3000 m outside of their natal range. He described these events as forays, as he observed instances of the dispersers returning to their natal range, while occupying their new range. Given Wiens's (2002) observations from a wild population of greater slow lorises (*N. coucang*) and personal observations of the Javan slow loris (*N. javanicus*), we know that both male and females disperse, they are aged between 16-27 months, but the proximate factors influencing these dispersal events is still unknown. Here I investigate (1) family group size and behaviour in the natal home range (2) immature offspring home range size (3) family group overlap, (4) status of all LFP offspring at the field site (5) and the distance travelled outside of the family group home range.

## 4.2 Methods

**See sections:**

2.2.1 Little Fireface Project (LFP)
2.3.1 Collaring and release
2.3.2 Nightly observations
2.3.4 Morphometric data
2.4.2 Home range and overlap analysis
2.4.3 Incremental area development (IAD)
2.4.7 Statistical analysis

## 4.3 Results

### Annual family group size:

From 2011-2016 LFP identified 30 infants (F: 6, M: 9, UK: 15) confidently (Figure 4.2). Each known adult female had between zero and two offspring per year, SI was the only female that had two offspring born within a single year. Annually groups were comprised of two (one adult male and one adult female), three (one adult male, one adult female, and one offspring), or four (one adult male, one adult female, one older offspring and one younger offspring). One-Eye (OE) consistently had a baby each year since LFP began observing her; she also had the highest number of offspring at the field site. Lucu (LU) was born and became sexually mature over the course of the five-year study period, thus she has only one recorded baby at the time this was written, born at the end of 2015, and consequently she has the least number of offspring at the field site (Table 4.1).

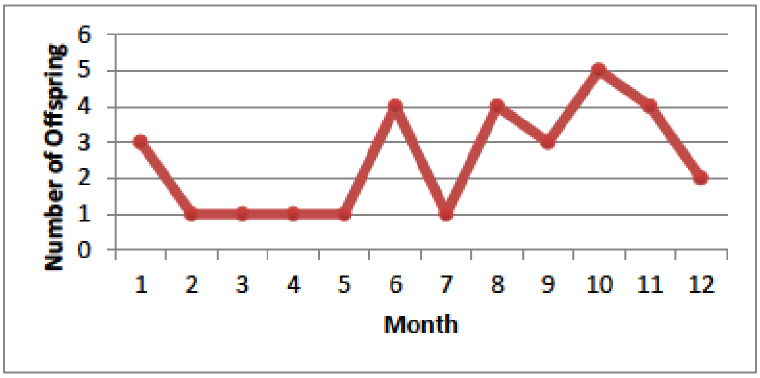


**Table 4.1:** The eight known mothers and their annual offspring born at the Little Fireface Project between 2011 and 2016. The individual total is provided on the far right and the year total is in the last row of the table.

| | **2011** | **2012** | **2013** | **2014** | **2015** | **2016** | **Individual Total** |
|---|---|---|---|---|---|---|---|
| **Charlie (CH)** | - | 1 | 1 | - | 1 | - | **3** |
| **Ena (EN)** | - | - | 1 | - | - | 1 | **2** |
| **Lucu (LU)** | - | - | - | - | 1 | - | **2** |
| **Maya (MA)** | - | - | - | 1 | 1 | 1 | **3** |
| **One-Eye (OE)** | 1 | 1 | 1 | 1 | 1 | 1 | **6** |
| **Shirley (SH)** | - | 1 | 1 | 1 | 1 | - | **4** |
| **Sibau (SI)** | - | - | 1 | - | 2 | 1 | **4** |
| **Tereh (TE)** | - | 1 | 1 | 1 | 1 | - | **4** |
| **Year Total** | **1** | **4** | **6** | **4** | **8** | **4** | |

**Behaviour in the family group:**

Between 2011 and 2016 the LFP team recorded 184 data points of social interactions between mothers, fathers, and their offspring. Play (43.5), groom (23.5), proximity (12.4) and lead (10.6) were the most frequently recorded behaviours. In addition to the behaviours and interactions that fall on a scheduled sample point, the LFP team report several *ad libitum* behaviours and anecdotes, which supplement the quantified data.

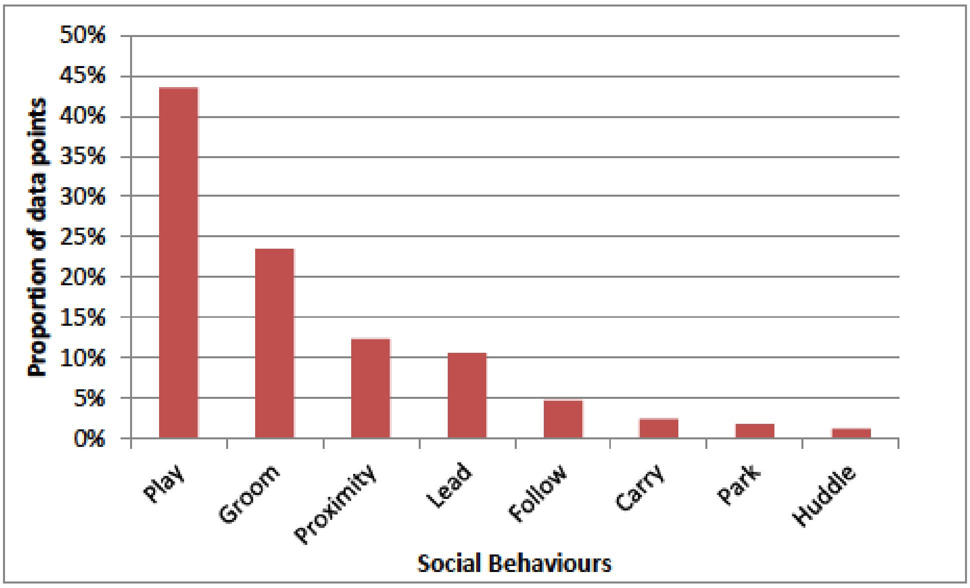


**Figure 4.3:** Proportion of observed social behaviour between Javan slow loris (*Nycticebus javanicus*) family group members at the Little Fireface Project in West Java, Indonesia.

During one observation, both the mother and the social father engaged in play-hanging with their juvenile offspring for several hours. During this play bout, the mother periodically left then returned, while the father continued to play with the juvenile. Another time, a pair of siblings travelled together through bamboo (Figure 4.3). The elder sibling (sub-adult) led the travel bout while the younger sibling followed. Towards the end of that observation, the elder sibling left the younger sibling very close to the initial location where their mother left the younger sibling, then departed and used a different sleep site than both the mother and the younger sibling (Figure 4.4). In 2015 TE spent a large portion of one observation with DA, one of her offspring from Dec-2013 and just before she settled into her sleep site, she returned to a small parked baby (TM). One-eye, AL and a juvenile were seen huddled at the beginning of an observation then OE left the group for the duration of her active hours, and then later returned to AL and the juvenile. Another LFP team member described how two unrelated adult females with juvenile offspring, one collared (OE) and another uncollared engaged in social play during an observation. The two juveniles were play-hanging with each other, while the two adult females also engaged in play-hanging. The two mother-offspring dyads remained in close proximity for a few hours before departing in different directions.

**Figure 4.4:** Photo of two young Javan slow lorises (*Nycticebus javanicus*) in the wild following one another at the Little Fireface Project field site in West Java, Indonesia.

**Family group home range size:**

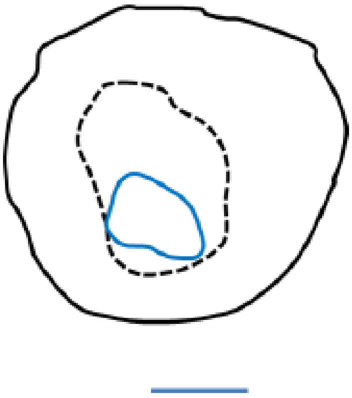
Of the 30 identified offspring in the area, there were sufficient data available for eight family groups. The following analyses focuses on those family groups unless otherwise noted. Home range size in immature offspring, mothers, and fathers ranged between 0.21- 7.1 ha, 1.7-12.7 ha, and 3.5-19.9 ha, respectively. Immature offspring displayed a mean home range size of 2.3 ±2.4 ha, mothers 5.4 ± 3.1 ha, and fathers 11.1 ± 6.5 ha. Due to the high standard deviations, I also included the medians, which in immature offspring was 1.5 ha, in mothers 4.5 ha, and fathers 11.3 ha (Table 4.2).

**Table 4.2:** Home range size in eight Javan slow loris (*Nycticebus javanicus*) family groups, including the immature offspring (ages: infants-sub-adult), mother, and father. Abbreviated names refer to the individuals in Table 2.3.

| **Family group** | Home range size (ha.) | | |
|---|---|---|---|
| | **Immature offspring** | **Mother** | **Father** |
| **LU /CH / TO** | 0.77 | 2.85 | 11.3 |
| **AL / OE / AZ** | 5.7 | 7.5 | 11.9 |
| **MU / MA / FE** | 0.68 | 4.24 | 11.1 |
| **TA / TE / GU** | 3.1 | 4.5 | - |
| **DA / TE /?** | 1.6 | 4.5 | - |
| **TM / TE / AL** | 1.5 | 4.9 | 8.3 |
| **ED / EN / RA** | 0.21 | 5.9 | 12.1 |
| **GA/ SI / DA** | 7.1 | 12.7 | 19.9 |
| Mean | **2.3+2.4** | **5.4 + 3.1** | **11.1+6.5** |
| Median | **1.5** | **4.5** | **11.3** |
| Min | **0.21** | **1.7** | **3.5** |
| Max | **7.1** | **12.7** | **19.9** |

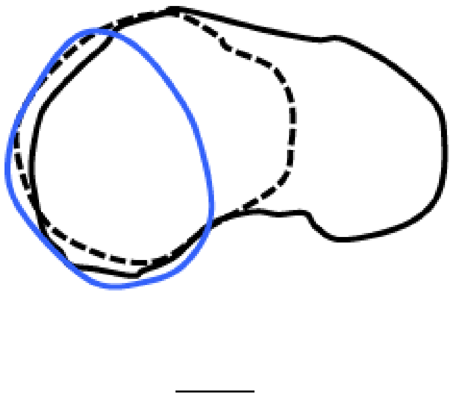
### Family group overlap:

The maximum overlap between mothers and immature offspring was 100%, and the minimum was 0%, the mean overlap was 77.3±37.6% and the median was 100%. Immature offspring and fathers overlap ranged between 61.2% and 100%, the mean overlap was 87.7±16.4%, and the median was 99.9%. Mother-Father overlap ranged between 75.8% and 100%, the mean was 93.4±9.57%, and the median was 99.5% (Figure 4.5 and Table 4.3).



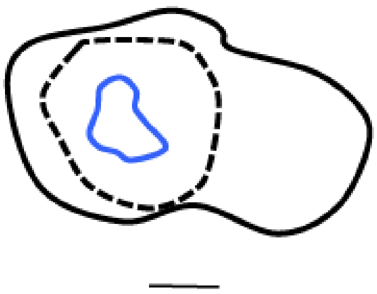
| | LU | CH | TO |
|---|---|---|---|
| LU | 100.0 | 99.9 | 99.9 |
| CH | 27.0 | 100.0 | 100.0 |
| TO | 6.8 | 25.3 | 100.0 |

A



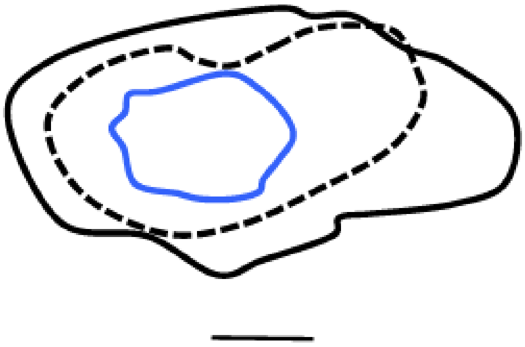
| | AZ | OE | AL |
|---|---|---|---|
| AZ | 100.0 | 59.4 | 39.9 |
| OE | 94.2 | 100.0 | 64.4 |
| AL | 83.3 | 84.8 | 100.0 |

B



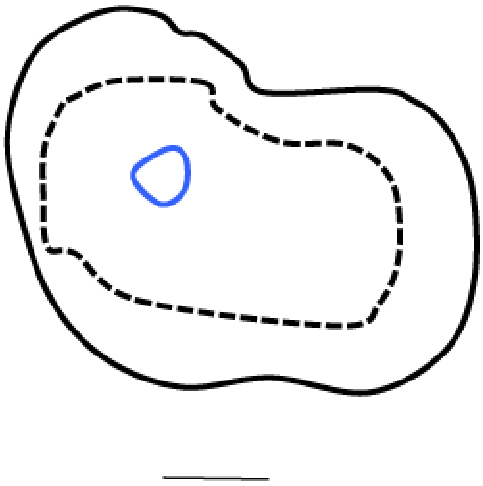
| | MA | FE | MU |
|---|---|---|---|
| MA | 100.0 | 99.9 | 15.9 |
| FE | 38.2 | 100.0 | 6.1 |
| MU | 99.9 | 99.9 | 100.0 |

C



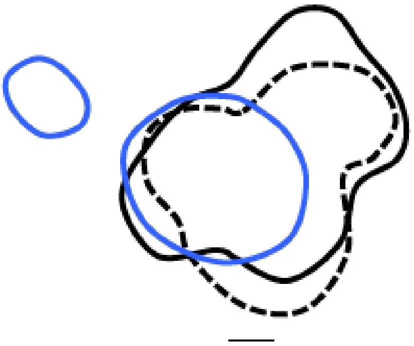
| | TE | AL | TM |
|---|---|---|---|
| TE | 99.9 | 99.5 | 30.9 |
| AL | 58.5 | 99.9 | 18.1 |
| TM | 99.9 | 99.9 | 99.9 |

D



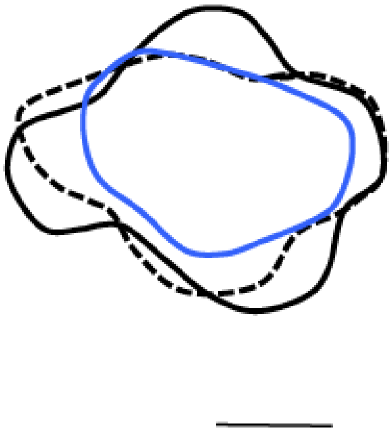
| | RA | EN | ED |
|---|---|---|---|
| RA | 99.9 | 48.5 | 1.7 |
| EN | 99.9 | 99.9 | 3.6 |
| ED | 99.9 | 99.9 | 99.9 |

E



| | SI | GA | DA |
|---|---|---|---|
| SI | 100.0 | 50.8 | 84.8 |
| GA | 57.0 | 100.0 | 61.2 |
| DA | 77.1 | 49.6 | 100.0 |

F



| | GU | TA | TE |
|---|---|---|---|
| GU | 99.9 | 57.1 | 77.7 |
| TA | 99.5 | 100.0 | 98.8 |
| TE | 92.9 | 67.8 | 100.0 |

G

**Figure 4.5 A-G:** and **Table 4.3 A-G:** Home range overlap between males (black line), female (dotted line), and young offspring (blue line) family groups in the Javan slow loris (*Nycticebus javanicus*) at the Little Fireface Project (LFP) in West Java Indonesia. The black line represents 100 m in each home range overlap. Accompanied by the percentage of home range overlap in seven Javan slow loris (*Nycticebus javanicus*) family groups observed at the Little Fireface Project field site in West java, Indonesia.

**Offspring status and natal dispersal:**

Of the 30 offspring initially identified at the LFP field site, six are collared and included in current observations, two are known to be dead (one drowned while trying to cross the river (TA), the other was killed after being tied to a kite by members of the village (MU)), eight are present at the field site, but are not included in focal observations, and 15 have unknown whereabouts. Some are presumed dead, others are believed to have dispersed. The last month and year where the LFP team saw an offspring show that the mean age that an immature slow loris was no longer seen in the area was 15±5 months, ranging between 6 months and 24 months, the median was also 15 months (Table 4.4). Of the 27 offspring where the team could identify the mothers, I identified dispersal events, forays and/or the beginning stages of vagrancy in eight offspring (LU, AL, MU, TA, DL, ED, GA, UT). Considering both males and females, the mean distance travelled outside of the natal home range was 857.0±255.0 m, ranging between 599.7 m and 1,368.0 m, and the median distance was 837.1 m (Table 4.5).

**Table 4.4:** List of the offspring at the Little Fireface Project field site in West Java Indonesia, including their mothers, dates of birth (DOB), status at the time this thesis was written, date last seen, and their age when last seen.

| Offspring | Mother | DOB (M-YY) | Status | Date Last Seen | ~Age Last Seen (Mo) |
|---|---|---|---|---|---|
| **Hesketh** | One-eye | Nov-11 | Unknown | Jan-13 | 14 |
| **Yogi** | Unknown | Nov-11 | Unknown | Nov-13 | 24 |
| **Tahini** | Tereh | Mar-12 | Died | Oct-13 | 19 |
| **Lucu** | Charlie | May-12 | Collared-present | - | |
| **Utari** | Shirley | Jun-12 | Unknown | Nov-13 | 17 |
| **Marvel** | One-eye | Oct-12 | Unknown | Apr-13 | 6 |
| **Wingki** | Ena | Jan-13 | Unknown | Apr-14 | 15 |
| **Sri** | Shirley | Apr-13 | Unknown | Dec-13 | 8 |
| **Galaksi** | Sibau | Sep-13 | Unknown | Nov-14 | 14 |
| **Kacang** | Charlie | Oct-13 | Unknown | May-2015 | 19 |
| **Maya** | Unknown | Oct-13 | Collared-present | - | - |
| **Alomah** | One-eye | Nov-13 | Collared-present | - | - |
| **Dali** | Tereh | Dec-13 | Unknown | Jun-15 | 18 |
| **Luna** | Unknown | Jun-14 | Unknown | ? | - |
| **Oniks** | One-eye | Jun-14 | Unknown | ? | - |
| **Timone** | Shirley | Aug-14 | Unknown | ? | - |
| **Bunga** | Tereh | Sep-14 | Unknown | ? | - |
| **Mikio** | Maya | Oct-14 | Collared-present | - | - |
| **Click** | Charlie | Jan-15 | Uncollared-present | - | - |
| **Gjahe** | Sibau | Jan-15 | Uncollared-present | - | - |
| **Mungkin** | Maya | Jun-15 | Died | Aug-2017 | 26 |
| **Sempurna** | Shirley | Jul-15 | Uncollared-present | - | - |
| **Ghost** | Sibau | Aug-15 | Uncollared-present | - | - |
| **Tombol** | Tereh | Aug-15 | Collared-present | - | - |
| **Lily** | Lucu | Sep-15 | Uncollared-present | - | - |
| **Opal** | One-eye | Nov-15 | Unknown | - | - |
| **Maaf** | Maya | Jan-16 | Uncollared-present | - | - |
| **Endor** | Ena | Feb-16 | Collared-present | Sept-2016 | 8 |
| **Gula** | Sibau | Aug-16 | Uncollared-present | - | - |
| **Oxygen** | One-eye | Oct-16 | Uncollared-present | - | - |

**Table 4.5:** Distance travelled out of the natal home range in eight Javan slow lorises (*Nycticebus javanicus*) born at the Little Fireface Project in West Java, Indonesia

| Offspring | Distance travelled (m) |
|---|---|
| LU | 953.0 |
| AL | 628.2 |
| MU | 599.7 |
| TA | 1368.0 |
| DA | 668.0 |
| ED | 933.4 |
| GA | 741.3 |
| UT | 959.0 |

Two offspring (MU and TM) aged 26 and 22 months travelled 599.7 m and 0 m outside of their natal home range, but have not established their own independent home ranges (Figure 4.6).

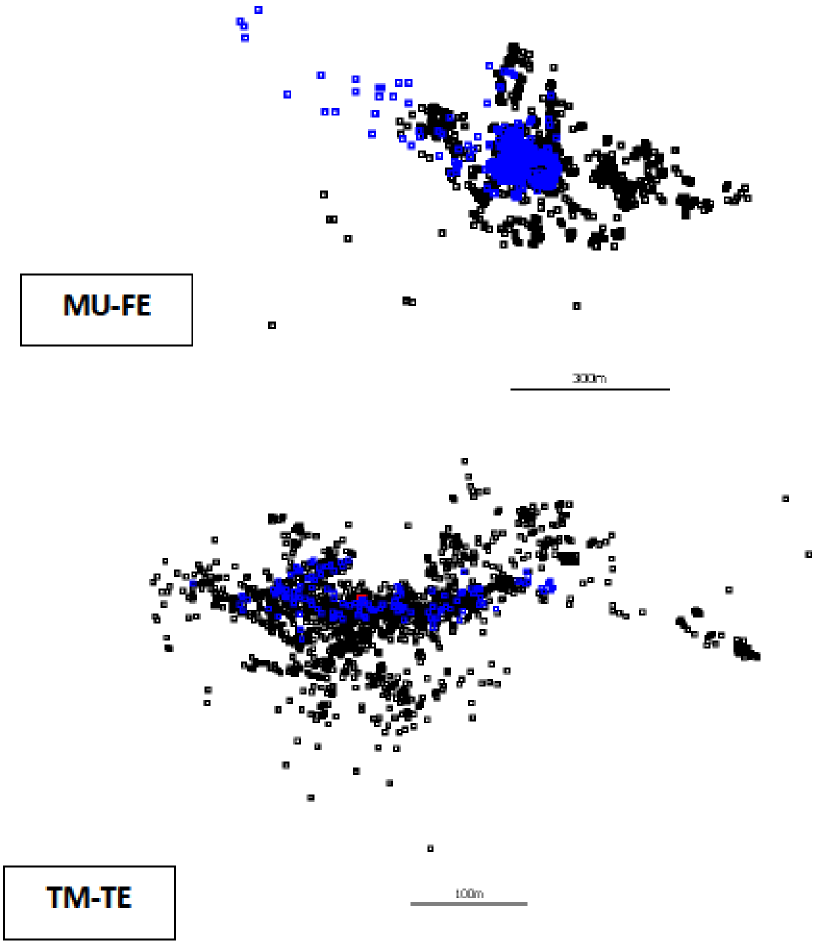


**Figure 4.6:** GPS Data for two Javan slow loris (*Nycticebus javanicus*) offspring at the Little Fireface Project in West Javan, Indonesia.

**Case studies:**

Highlighting two case studies, where one male (AL) and one female (LU) were observed from infancy to adulthood, LU and AL settled into adult home ranges, ~1000 m and ~600 m away from their mother and father, respectively.

Lucu's home range displayed minimal overlap with her mother CH (Figure 4.7A), though these overlapping points likely represent one of her final forays between the natal ranges to her new home range. Her incremental area graph, which included GPS points from Sept-2013 to Dec-2016 showed that LU quickly arrived, and settled into another area. After ~ 150 points, the graph plateaued and the following ~1380 GPS points were all within the established home range (Figure 4.8A). Alomah continues to overlap with his natal range 0.6% of the time (Figure 4.7B). Alomah's incremental area development graph comprised 1530 points over 20 months between April 2015 and Dec-2016.  He took a stepwise approach to finding and settling into his 'Adult' home range, which plateaus at 1224 (Figure 4.8B)

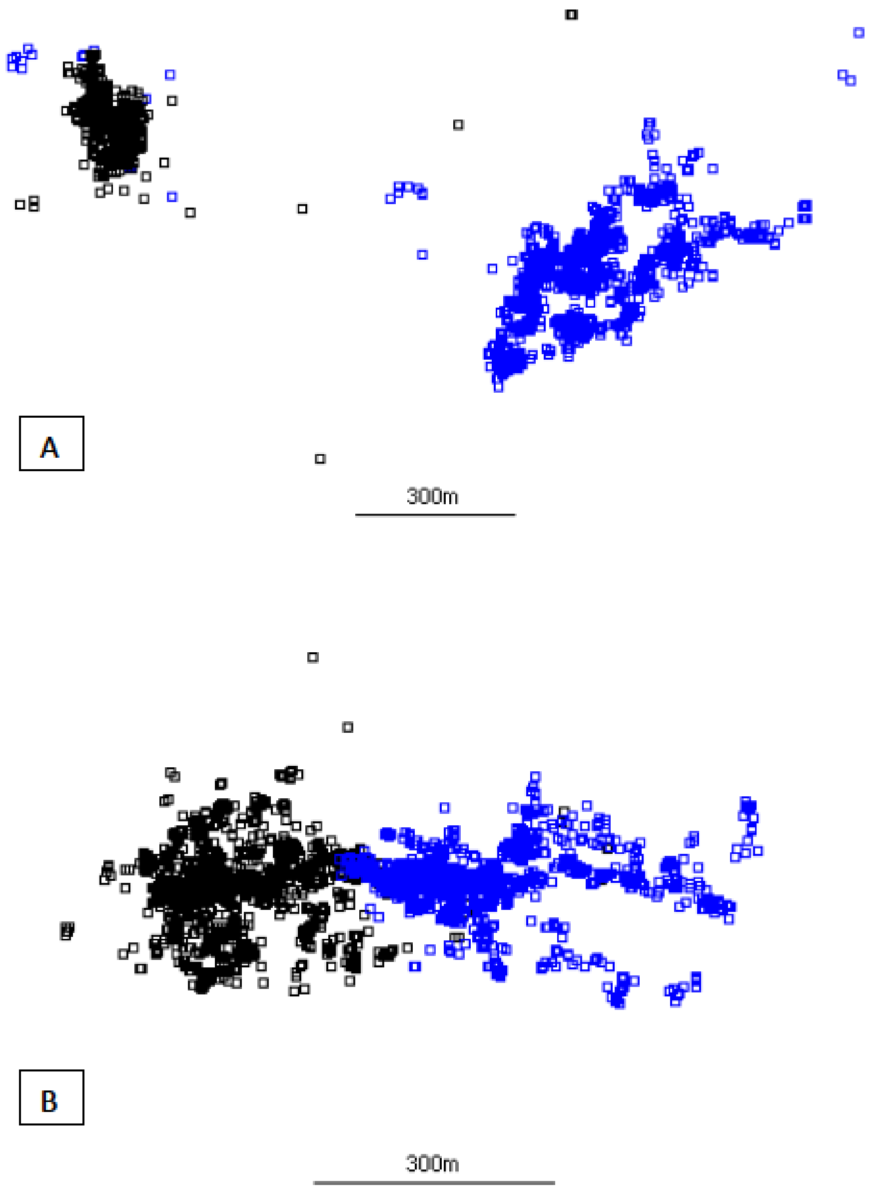


**Figure 4.7:** (A) The 'adult' home ranges for two female Javan slow lorises (*Nycticebus javanicus*) (LU: blue dots and CH: black dots) LU is the adult offspring of CH. (B) The 'adult' home range of one male and one female Javan slow lorises (*N. javanicus*) (AL: blue dots and one female OE: black dots) AL is the adult offspring of OE. Lucu does not overlap with CH's home range consistently, though AL's home range overlaps 0.6% of the data points consistently.

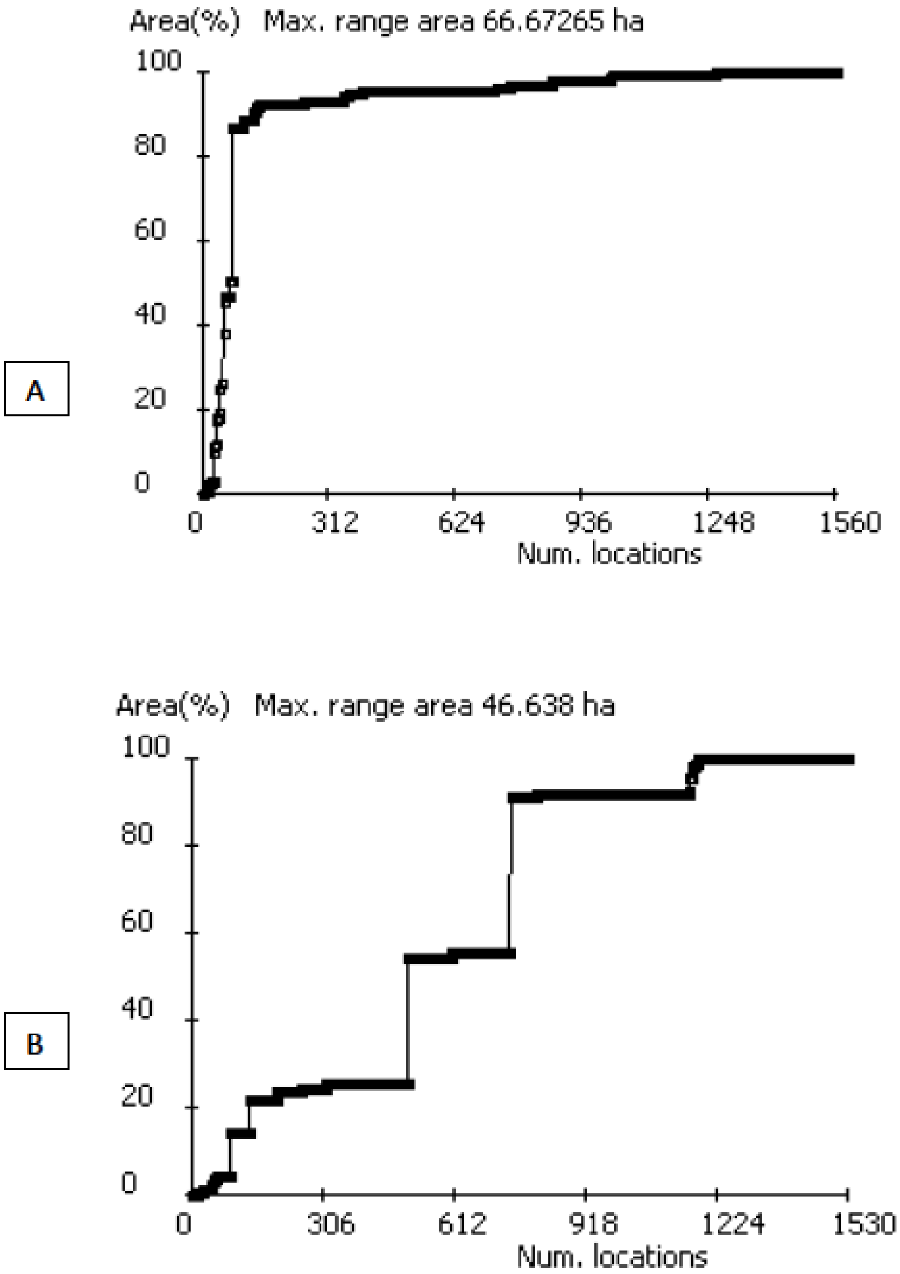


**Figure 4.8:** The incremental area development graph for two Javan slow lorises (*Nycticebus javanicus*) observed at the Little Fireface Project in West Java, Indonesia. This graph represents the ‘adult’ home range development of Lucu (A) and Alomah (B) between 2013-2016 and 2015-2016 respectively. On the x-axis ‘Num. locations’ are the number of GPS points collected and how it relates to the percentage of the home range those points represent (y-axis).

### 4.4 Discussion

The Javan slow loris (*N. javanicus*) displays variable family group sizes ranging between two and four members. Female slow lorises at the LFP field site typically had one offspring per year, with one exception (SI). Family group members consistently overlap with one another, where the father's home range largely enveloped the mother's home range, and her home range enveloped the offspring's home range. Many of the identified offspring are still present at the field site both as focal animals and as uncollared residents. Eight have displayed clear evidence of forays and dispersal, where they travelled as far as 1,368 m outside of the natal range. There were no significant sex differences in meters travelled offering no support for any sex biases in dispersal. In the case of LU and AL two Javan slow lorises intensively observed from infancy to adulthood, LU (f) settled into her new adult home range quickly after dispersal. While AL (m) took a more step-wise approach to establishing a new adult home range, which continued to overlap with his natal home range. These findings support previous work that both male and female offspring disperse in *Nycticebus* spp., while family groups overlap. Dispersal time and distance highlight the potential importance of the kinship associations established during offspring development within their natal home range. These data also show that the presumed age of sexual maturity derived from captive studies may not hold true in the wild.

Differences in the individual dispersal strategies can be explained by examining the varying costs and benefits of dispersing for each immature individual (Bowler and Benton, 2005). Animals have varying sensitivities to environmental cues, which can illuminate which evolutionary pressures are most influential to dispersal, such as a reliance on a depleting resource or conflict within the family group (Lawrence, 1987; Kuussaari et al., 1996; Aars and Ims, 2000; Byers, 2000; Albrectsen and Nachman, 2001). Naturally, wild populations are heterogeneously distributed across an area (Bowler and Benton, 2005), such is the case in this population of Javan slow lorises, which is further described in Chapter 6. The spatial layout of an environment can be defined on a spectrum from highly connective to minimally connective (Thomas and Kunin, 1999). Along this spectrum, the effect dispersal events will have on local population dynamics is variable (Hanski and Gilpin, 1997; Thomas and Kunin, 1999). During movement, the use of cues, identifying the direction and proximity of suitable habitat may reduce search time and potentially increase dispersal success. In addition to increasing patch detectability, the ability to recognize ecological cues provides information about the suitability of a new environment prior to dispersal (Lima and Zollner, 1996; Danchin et al., 2001). The ability to detect these cues, through various sensory systems, like olfaction (Schooley and Wiens, 2003) or vision (Compton, 2002) vary among species, this is also known as, their perceptual range, which is unknown for most taxa, including *Nycticebus* species (Lima and Zollner, 1996). The perceptual range of an animal will determine the importance of such cues for nightly and dispersal movement. Though it is noted that when the costs of movement are high, or when suitable habitats are well spaced, there may be little opportunity to explore different patches so environmental cues may be used only to detect suitable habitat, and not for patch discrimination (Kareiva, 1982; Mayhew, 1997).

It is difficult to identify the differing cost and benefits of dispersal based on size and age constraints in vagile species (Bowler and Benton, 2005), as resource competition affects age classes differently and to varying extents. Younger animals are not competitive threats for older more established individuals within the population. In the Javan slow loris immature individuals display a comparable level of feeding and foraging competence as juveniles both behaviourally and in their physical proportions resemble adults (Poindexter and Nekaris, 2017; Chapter 4). A key feeding resource in *Nycticebus* species are exudates, which are considered stable year-round resources, and are unevenly distributed throughout their environment (Cabana et al., 2017b). Additionally, they feed on insects, which are abundant in most areas where *Nycticebus* species occur (Wiens et al., 2006; Rode-Margono, 2014). This along with the relative stability of their key feeding resource lead me to believe that food related competition is not a defining factor in initiating dispersal in this population of Javan slow lorises, and likely any *Nycticebus* spp. in a comparable environment.

When considering all dispersal events presented here, there were no consistent sex difference in the distance travelled, overlap, home range size, or age at dispersal. If we only consider the comparative case studies between LU and AL, LU not only settled faster, but she travelled farther, stayed within her natal range longer, and created a larger adult home range, compared to her mother (CH) and to AL. Sex-based dispersal is commonly seen in mammals, where males typically disperse. Female migration does occur and has been reported in the greater white tooth shrew (*Crocidura russula*), and the yellow-bellied marmots (*Marmota flaviventris*), as well as, other primate species including langurs (*Presbytis thomasi*), lowland gorillas (*Gorilla gorilla gorilla*) and chimpanzees (*Pan troglodytes*) (Favre et al., 1997; Sterck et al., 1997; Nishida et al., 2003; Stokes et al., 2003; Armitage et al., 2011). Sex differences in life history traits are likely the reason for sex-biased differences in dispersal. Both inbreeding avoidance and asymmetries in intersexual competition have been implicated in determining sex-biased dispersal strategies for mammals (Greenwood, 1980), which is more important remains a contentious topic (Johnson and Gaines, 1990; Perrin and Mazalov, 2000). We expected to see both sexes disperse as observed, given the level of territoriality in the Javan slow loris, males and females fight over resources, largely believed to be social resources (Nekaris et al., 2013), explaining a lack in sex-biased differences in presumed dispersal events. Radespiel et al. (2002) found in the grey mouse lemur (*Microcebus murinus*), a comparable primate species, that they display a male-biased dispersal. Based on genetic and spatial analysis, they discovered that daughters disperse only short distances away from their mothers and males disperse over a larger distance away from their fathers. The grey mouse lemur is regularly used as a point of comparison with slow lorises, but in this scenario, there is a key difference between the two; the grey mouse lemur will participate in the first mating season following their birth (Wrogemann et al., 2001). The Javan slow loris does not reach this maturity level until at least 18-24 months. Male ring-tailed lemurs (*Lemur catta*) reportedly disperse at 24 months and seeming do so to avoid male competition, by moving to groups with fewer non-natal males and inbreeding by never returning to their own natal group (Parga and Lessnau, 2008)

Female slow lorises park their infants within their home range while they forage throughout the night, periodically returning to the parked infant. Other members of the familial unit may also engage with the infant, including older siblings and the social father (Wiens, 2002). Both behaviours were observed in this population of Javan slow lorises. All juvenile home ranges should fall 100% within the mother's home range; I observed three instances where the overlap was less than 100%. It is possible that juveniles were observed on the periphery on their mother's home range and potential under sampling of the mother's area led to a misrepresentation of the overlap. Regarding unit size and the possible influence of older siblings in inducing dispersal, the mother (SI) that had two offspring born in the same year, one born in Jan-2015, the other in Aug-2015, but this did not seem to display any indication of strain because of having two offspring at shorter birth interval than other females. As a counter point, the pygmy slow loris (*N. pygmaeus*) regularly has twin (Jurke et al., 1998). This species is ecologically and physically very similar to the Javan slow loris, and twinning is not considered detrimental to their successful dispersal and settlement.

The sociality of primates may have led to an increase in cooperative care of infants (Hardy, 2009). Lucas and Dunbar (2013) suggest that social monogamy evolves in mammals when females occupy small and discrete ranges such that males cannot monopolize more than one female. Primates species have flexible behavioural systems and with this comes high variability in social systems and in father-offspring parenting styles both between and within species. Bi-parental care allows the energetic demands to be shared between both parents, which can improve the number of surviving offspring a male produces (Saltzman and Ziegler, 2014). Infant care by fathers and non-breeding males is also currently associated with a range of mating systems including monogamy, polyandry, and cooperative breeding. The ways in which a father interacts with his offspring are usually classified as direct or indirect care and there is considerable variation in what behaviours fathers display towards offspring. Besides the Javan slow loris, only a few species of lemurs (such as the red-bellied lemur (*Eulemur rubriventer*), Overdorff and Tecot, 2006), marmosets and tamarins (Callitrichidae), titi monkeys (*Plecturocebus*), and owl monkeys (*Aotus*) show direct care of their offspring (Fernandez-Duque et al., 2009).

In captivity, females reportedly copulate for the first time between 18-24 months and males will sire their first offspring at 17 months (Izard et al., 1988). In this study, young Javan slow lorises, both male and females, started ranging outside of their mother's home range at about 15 months. The only instance of an offspring being born to a known mother with a known age is LU who had her first offspring at 40 months. I also note two instances where males older than 17 months have not fully dispersed (TM; 22 months) or were just beginning their vagrancy period (MU; 26 months). Difference in the age that captive and wild animals of the same species reach sexual maturity is attributed to various factors. In yellow baboons (*Papio cynocephalus*), Onyango et al. (2013) found difference between captive and wild individuals as well as higher ranking mothers and lower ranking mothers.

### 4.5 Chapter summary

Spatial process including natal dispersal are important for maintaining wild populations, especially as the natural world faces climatic and environmental changes (Hanski and Thomas, 1994; Dunning et al., 1995; Swinton et al., 1997; Clutton-Brock et al., 2002). Most population models in put a basic assumption regarding dispersal events, following a static strategy, but natal dispersal is not a simple fixed stagey event. In this chapter, I found that the Javan slow loris maintain family units comprised of two adults and 1-2 offspring. It was previously unknown just how much older sibling interacts with younger siblings, based on reports from the LFP field site there is a high level of cooperative care. When they do disperse both male and female can travel long distances to create a new home range or continue to overlap with their natal group. Natal dispersal is dependent on the presence of kin, the perceptual range, individual cognitive ability, which may also indicative of plasticity in response to the predicted level of inbreeding. Offspring development and dispersal is seemingly rooted in the social interactions between family group members. Here I focused on the social aspects of nightly movements and spacing in the Javan slow loris (Figure 4.9). The skills they acquire during this time help them to find and establish suitable home ranges.

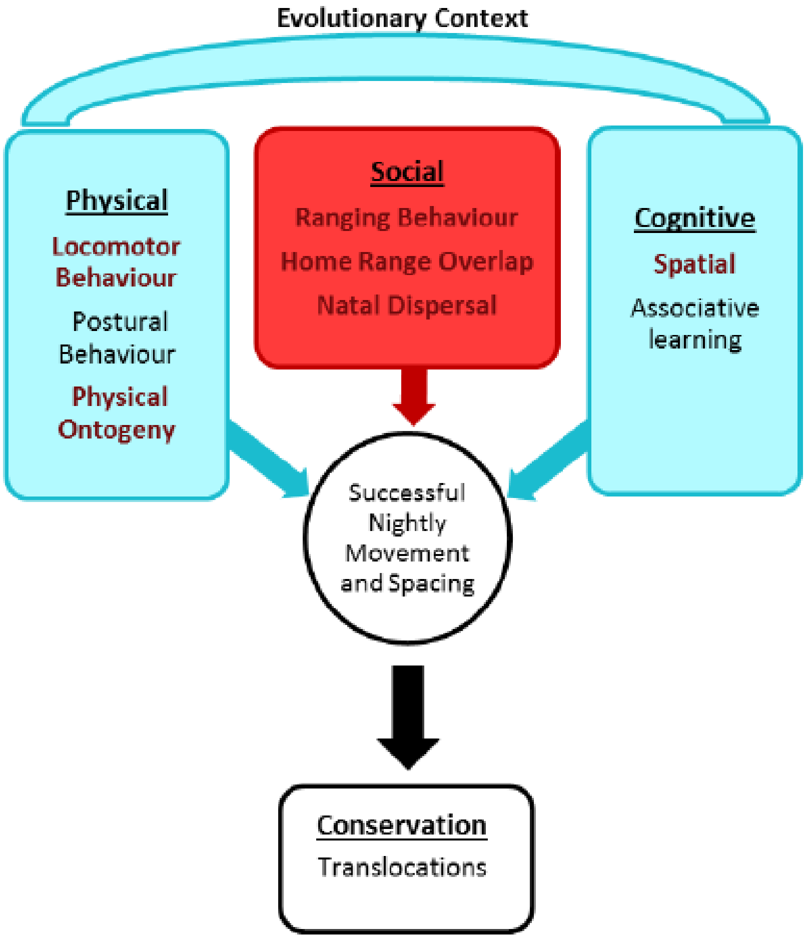


**Figure 4.9:** Visualisation of the framework of the thesis highlighting how the data and conclusions presented in Chapter 4, fit into the context of the entire thesis. Topics in red are the focus of the chapter, topics in blue are related though not explicitily discussed.

# Chapter 5: Rapid acquisition of adult limb proportions facilitates feeding behaviours in young Javan slow lorises (*Nycticebus javanicus*).

**Figure 5.1:** Javan slow loris (*Nycticebus javanicus*) feeding on gum at the Little Fireface Project field sit in West Java, Indonesia. Photo provided by the Little Fireface Project.

## 5.1 Introduction

Mammals that rely on specific food resources must also possess a suite of adaptations to facilitate the access and digestion of these food items. Behavioural and morphological specialisations associated with feeding ecology are notable among mammal species (Dierenfeld et al., 1982; De Muizon and Lange-Badré, 1997; Ercoli and Youlatos, 2016; Naples, 1999; Tan, 1999; Ley et al., 2008; Koyabu et al., 2009; Ravosa et al., 2010). Mammals typically acquire needed feeding skills long before sexual maturity, allowing them to access vital resources before adulthood (Schuppli et al., 2016). One developmental strategy, rapid growth in infants, is a known adaptation to aid in reducing infant vulnerability and to help them surpass the juvenile bottleneck, (Williams, 1966; Case, 1978; Young and Heard-Booth, 2016).

Specialised gummivory is only seen in a small number of Australian marsupials and primates (Irlbeck and Hume, 2003; Viguier, 2004). These animals have evolved morphological traits and behavioural specializations to access and digest gums (Nash, 1986; Smith, 2010; Cabana et al., 2017a). P-linked polysaccharides, such as gums, require specific microbes for fermentation (Monke, 1941; Booth and Henderson, 1963; Power and Myers, 2009). Mammals that eat gums enable fermentation through having a longer cecum and large intestine (Chivers and Hladik, 1980; Smith, 1982; Power and Myers, 2009). In addition to digestive specializations, gummivory is often consistent with postcranial adaptations, including keeled nails or claws, which allow animals to climb and cling to large tree trunks and branches for extended periods, reducing the amounts of energy necessary during gouging (Kubota and Iwamoto, 1966). Across gouging mammals, mandibular variation is associated with the percentage of gum in a species' diet (Viguier, 2004). Gougers use specialized dentition to damage a tree's bark to elicit gum production and flow (Petter, 1978). In strepsirrhine primates, this adaptation takes the form of a specialised toothcomb used to elicit flow of or to scrape gum.

Charles-Dominique (1977a) proposed that gums were inaccessible to mammals that lacked claws or modified nails. A number of primates consume gum and lack these features, including lesser galagos (*Galago senegalensis*) mouse lemurs (*Microcebus* spp.), and the slow lorises of Asia (*Nycticebus* spp.). Despite lacking claws or modified nails, Nekaris (2014) noted that *Nycticebus* spp. are true gougers characterised by stout mandibles, U-shaped hind limbs, and camouflaged fur that allow them to specialize on exudates up to 97.5% their feeding time (c.f. Swapna et al., 2010; Das et al., 2014). *Nycticebus* spp. possess a specialised toothcomb and a reduced last lower molar compared to *Loris* spp. further supporting their distinction as obligatory gougers (Burrows et al., 2015). In order to cling to trees in the absence of specialized nails or claws, they possess a host of characteristics, including a firm grip, reduced second digit, and a vascular artery bundle that lowers the temperature of their limbs called the *retia mirabilia*, enabling them to maintain long- duration static postures necessary for gouging gum (Ishida et al., 1992; Kingston et al., 2010; Nekaris, 2014).

Despite a general lack of research regarding *Nycticebus* ontogeny in the wild, the consensus is that for an animal of its size, *Nycticebus* has a long gestation period (6 months) (Izard et al., 1988; Zimmermann, 1989; Nekaris, 2014). The period between these developmental milestones is poorly understood and previous reports on this topic offer varying results on the emergence of key behaviours (Rasmussen, 1986; Ehrlich and Macbride, 1989; Zimmermann, 1989; Fitch-Snyder and Ehrlich, 2003). This variation is attributed to variable captive conditions and small sample sizes. In captivity, infants were first observed consuming solid foods at ~40 days (Zimmermann, 1989) and in the wild Wiens and Zitzmann (2003) observed the solid feeding behaviour of an eight-week old infant. In regards to exudates, individuals as young as three months elicit gums from tree trunks (Nekaris, 2014).

Juvenile primates are generally regarded as being less successful at foraging than older individuals (Altman, 1980, Janson and van Schaik, 2002). Juvenile primates may require more time to process foods than adults (Post et al, 1980), and may also be restricted in their abilities to process and consume certain food items leading to differences in the time spent feeding on different items (Harrison, 1983). Where food items are difficult to process, juvenile primates may acquire knowledge through the observation of adult group members, although there is wide variation in such social tactics of food acquisition during ontogeny in Primates (Rapaport and Brown 2008). The evidence in support of juveniles' feeding efficiency or processing abilities being lesser than adults is inconclusive, and varies across species and dietary items. Juvenile primates may be restricted in the food items they can process not only from a lack of experience, but also from a lack of physical strength, particularly in the case of extracting hard to access food sources such as hard-shelled fruits, embedded vertebrates, and subterranean grass corms (Fragaszy and

Boinski, 1995; Altmann, 1998; MacKinnon, 2005). It is likely that the majority of primates' learning about food items may have already taken place during their infancy (Joffe, 1997), and indeed the diet of primates near the point of weaning has been found to act as a predictor for adult fitness (Altmann, 1998). Even if juveniles are not limited in their foraging or food processing abilities, their small body sizes may affect their access to foods inaccessible to larger, heavier adults (Menard, 1985; Menard and Vallet, 1986).

Until now, there has been no exploration of either the behavioural repertoire used to access tree gums or the ontogenetic development of these behaviours. Here, we aim to explore the mechanisms used by the Javan slow loris to access gum from the juvenile period to adulthood. I address three research questions: (1) What physical adaptations facilitate the prolonged vertical postures needed to access tree trunks? (2) Do Javan slow lorises display any ontogenetic variation in their locomotor behaviour and habitat use during feeding? (3) What, if any, are the morphometric differences across age classes and do they influence locomotor behaviour or habitat use? Following these questions, I hypothesise that young Javan slow lorises will quickly attain the necessary physical and behavioural competence to gouge trees, as gum is a key component of their wild diet (Cabana et al., 2017b). In accordance with this hypothesis, I also predict that there will be little to no difference in habitat utilization, as defined by their position in tree, and the diameter at breast height (DBH) of feeding trees.

## 5.2 Methods

**See sections:**

2.2.1 Little Fireface Project (LFP)
2.3.1 Collaring and release
2.3.2 Nightly observations
2.3.3 Locomotor and postural behaviour definitions
2.3.4 Morphometric data
2.4.7 Statistical analysis

## 5.3 Results

### Vertical gouging posture:

While feeding and foraging specifically on tree trunks, Javan slow lorises of all age classes used either an upward or a downward facing vertical posture. Animals had either three or four limbs in contact with the substrate, while feeding but I never observed them on tree trunks with only two limbs in contact with the substrate. When gripping the substrate, slow lorises pressed their distal phalanges into the surface of the substrate; the joint between the midline and proximal phalanges was bent. The pollex was perpendicular to the other digits and is similarly pressed into the surface. Both feet were used in a reversed position, where the hallux was adducted along the substrate, while the other four digits were parallel to one another. On larger substrates, arms were fully extended, but on smaller trunks, arms may be flexed at the elbow. The hind limbs were flexed and depending on the size of the substrate, we observed varying degrees of abduction, as they wrapped around the substrate. Together with the reversed foot position, the flexed and abducted hind limb created a U-shaped appearance (Figure 5.2).

**Figure 5.2:** Images of two Javan slow lorises in vertical postures on large-medium sized substrates. Photos taken at the LFP field station.

**Locomotor behaviour during feeding:**

During all feeding bouts including those involving non-gum items, Javan slow lorises displayed a wide range of locomotor and postural modes in equal measure across all three-age classes (Table 2). Vertical suspension 2 ($H$ = 14.1, df = 2, p = 0.001) and horizontal suspension 3 ($H$ = 11.31, df = 2, p = 0.003) were the only postures that statistically differed, where juveniles and sub-adults displayed these postures less than adults or not at all. In juveniles three postures made up 57.6% of their repertoire, stand (20.7%), vertical suspension 4 up (15.6%), and vertical suspension 4 down (15.8%) The most used postural modes used in sub-adults were both vertical suspension 4 up (24.8 ± 4.2%) and down (16.8 ± 13.7%). Vertical suspension 3 up and down was rarely observed in adults and sub-adults (adults: 1.3 ± 1.0% sub-adults: 3.9 ± 0.8%) and was absent in juveniles. The locomotor modes employed across all behaviours showed statistically significant differences in more modes compared to the locomotor behaviours during feeding alone (Table 5.1). These differences appear in walk (*H*=9.09, df=2, p=0.011), bridge (*H*=19.83, df=2, p=0.001), vertical suspension 2 (*H* = 17.34, df = 2, p < 0.0001), and horizontal suspension 3 (*H* = 26.05, df = 2, p< 0.0001)

**Table 5.1:** Proportion of locomotor and postural modes used while feeding and across all behaviours in wild Javan slow lorises. Proportions are presented as the mean and standard deviation (SD), with the number of included individuals listed at the top (N).

| **Locomotor/Postural Modes** | | | | | | |
|---|---|---|---|---|---|---|
| **Feeding** | **Adult (22)** | | **Sub-adult (5)** | | **Juvenile (9)** | |
| | Mean | SD | Mean | SD | Mean | SD |
| **Stand** | 20.3 | 11.9 | 10.2 | 7.3 | 20.7 | 17.7 |
| **Vertical Suspension 4 Up** | 14.4 | 9.6 | 24.8 | 4.2 | 15.7 | 22.5 |
| **Vertical Suspension 4 Down** | 11.0 | 6.5 | 16.8 | 13.7 | 21.3 | 19.4 |
| **Vertical Suspension 2**** | 9.2 | 10.4 | 6.8 | 4.0 | 0.2 | 0.7 |
| **Sit** | 8.6 | 9.8 | 6.4 | 2.9 | 6.2 | 11.5 |
| **Horizontal suspension 4** | 8.2 | 5.5 | 8.8 | 6.0 | 6.0 | 10.4 |
| **Horizontal Suspension 2** | 6.5 | 6.2 | 7.8 | 11.8 | 1.2 | 3.3 |
| **Climb Down** | 3.9 | 3.5 | 2.8 | 3.7 | 9.0 | 22.0 |
| **Bridge** | 3.5 | 3.8 | 2.4 | 3.6 | 4.4 | 13.3 |
| **Climb Up** | 2.9 | 2.6 | 5.0 | 4.0 | 1.6 | 3.1 |
| **Horizontal Suspension 1** | 2.8 | 4.8 | 0.2 | 0.4 | 0.8 | 2.0 |
| **Horizontal Suspension 3*** | 2.4 | 2.6 | 0.4 | 0.9 | - | - |
| **Suspensory Walk** | 1.5 | 2.2 | 1.6 | 3.6 | 0.1 | 0.3 |
| **Vertical Suspension 3 Up** | 1.4 | 2.1 | 3.2 | 4.4 | 5.6 | 16.7 |
| **Walk** | 1.3 | 2.0 | 1.4 | 1.9 | 0.2 | 0.7 |
| **Vertical Suspension 3 Down** | 1.1 | 3.0 | 0.6 | 1.3 | - | - |
| **Climb Horizontal** | 1.0 | 1.9 | - | - | 0.8 | 2.0 |
| **Horizontal Position** | 1.0 | 3.1 | 0.8 | 1.8 | 6.7 | 20.0 |
| | | | | | | |
| **All Behaviours** | **Adult (24)** | | **Sub-adult (7)** | | **Juvenile (23)** | |
| **Sit** | 20.7 | 6.9 | 14.0 | 16.6 | 16.2 | 15.7 |
| **Climb Down** | 15.5 | 5.7 | 12.0 | 8.4 | 20.7 | 23.5 |
| **Climb Up** | 11.5 | 5.7 | 11.2 | 8.7 | 15.8 | 13.6 |
| **Stand** | 9.2 | 9.6 | 3.2 | 2.3 | 12.6 | 22.2 |
| **Walk*** | 8.3 | 4.7 | 18.9 | 36.0 | 8.1 | 20.7 |

| | | | | | | |
|---|---|---|---|---|---|---|
| **Sleeping Ball*** | 6.8 | 5.7 | 0.8 | 1.0 | 1.2 | 3.1 |
| **Climb Horizontal** | 4.6 | 2.3 | 4.5 | 3.6 | 5.0 | 5.9 |
| **Vertical Suspension 4 up** | 4.3 | 2.4 | 4.7 | 4.4 | 3.8 | 5.4 |
| **Horizontal suspension 4** | 3.8 | 2.2 | 2.9 | 2.3 | 2.5 | 4.4 |
| **Bridge**** | 3.1 | 1.4 | 2.0 | 2.1 | 1.3 | 2.4 |
| **Suspensory Walk** | 2.8 | 1.8 | 2.2 | 2.8 | 1.2 | 4.2 |
| **Vertical suspension 4 down** | 2.6 | 1.5 | 17.7 | 36.4 | 3.1 | 4.8 |
| **Horizontal suspension 2** | 1.5 | 1.3 | 2.5 | 3.7 | 1.5 | 3.3 |
| **Vertical suspension 2***** | 1.3 | 1.9 | 0.8 | 1.2 | 0.5 | 2.1 |
| **Horizontal suspension 1*** | 1.0 | 1.3 | 0.9 | 2.3 | 0.5 | 1.0 |
| **Horizontal suspension 3***** | 0.7 | 0.6 | 0.4 | 0.6 | 0.1 | 0.4 |
| **Race walk** | 0.5 | 0.7 | 0.5 | 0.6 | 4.5 | 20.8 |
| **Play-hang** | 0.2 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| **Vertical suspension 3 up** | 0.2 | 0.2 | 0.6 | 0.9 | 0.7 | 2.5 |
| **Vertical suspension 3 down** | 0.1 | 0.2 | 0.2 | 0.3 | 0.4 | 1.5 |

Significant p-values are denoted with a (*),*≤ 0.01, ** ≤ 0.001, *** ≤ 0.0001.

### Habitat utilization during feeding:

Table 3 presents the mean and standard deviation for each tree position variable between adults, sub-adults, and juvenile Javan slow lorises. None of the measured variables while feeding provided any significant differences. I observed the following trends in the age specific distribution of tree and environment locations during feeding; in adults feeding took place at the centre of the tree canopy (30.7 ± 17.5%), the crown (17.9 ± 20.9), trunk (17.4 ± 11.4%), and periphery (17.1 ± 9.7%), with the remaining locations used less that 1% of the time. Juveniles spent most of their time in the periphery (32.5 ± 22.1%), then the centre (32.0 ± 16.7%) and the trunk (21.7 ± 14.1%) (Table 5.2). We found no significant difference in the mean DBH of the trees used by adults (38.0 ± 16.9 cm), sub-adults (34.9 ± 14.0 cm), and juveniles (37.6 ± 16.7 cm).

**Table 5.2:** Mean, N and standard deviation (SD) of wild Javan slow lorises (*Nycticebus javanicus*) habitat use variable described as Position in Tree.

| **Position in Tree** | **Adult (16)** | | **Juvenile (6)** | |
|---|---|---|---|---|
| | Mean | SD | Mean | SD |
| **Central** | 30.6 | 17.6 | 32.0 | 16.7 |
| **Crown** | 18.0 | 21.0 | 13.0 | 6.9 |
| **Trunk** | 17.4 | 11.4 | 21.7 | 14.1 |
| **Periphery** | 17.1 | 9.8 | 32.5 | 22.1 |
| **Undergrowth** | 0.8 | 1.0 | 1.0 | 2.4 |
| **Terrestrial** | 0.1 | 0.3 | - | - |

### Morphometric measures:

We observed significant differences in five measures, body mass ($H$ = 38.3, df = 2, p< 0.0001), total body length ($H$ = 9.2, df = 2, p = 0.010), head length ($H$ = 8.8, df = 2, p = 0.012), upper arm length ($H$=8.6, df=2, p=0.013), and lower arm length ($H$=11.0, df=2, p < 0.0001). Table 5.3 displays the mean, N number of measurements, and standard deviation for each morphometric measure for each age class. The juveniles had the smallest mean body mass (609.7±121.4 g), followed by the sub-adults (819.4±38.5g), then adults (907.2 ± 72.0 g). In contrast to the upper and lower arm lengths, which were lower in juveniles, the upper and lower leg lengths showed very little difference across and within age classes. Head length, head width, hand span, foot span, the proportional indices, both arm/body length and hindlimb/body length (Figure 5.3) showed no substantial variations. The two canonical axes identified by the Canonical variate analysis (CVA) accounted for 89.2% and 10.8% of age class variation (Wilk's λ = 0.235, p < 0.0001) (Figure 5.4). Body weight contributed the main discrimination along the first axis and total body length was the main discriminant along the second axis. Overall, age classes were correctly classified 90% of the time, 95.6% for Adults, 50% for Sub-adults, 100% for Juveniles. The results of the GLMs showed that none of the morphometric measures had predictive power for the response variables; proportion of time spent in vertical suspension 4 up/down or vertical suspension 3 up/down. The growth allometries provided by LS regression for head length, head width, hand span, foot span, upper arm, lower arm, upper leg and lower leg are presented in Figure 5.5 and Table 5.4. Footspan (0.03), handspan (0.07), and upper leg (0.06) had the lowest coefficients; upper arm (0.23), lower leg (0.18), and head length (0.17) were the highest.

**Table 5.3:** Morphometric measures of wild Javan slow lorises, results include the mean weight in grams (g) and length in millimetres, the number of individuals measured (N) and the standard deviation (SD).

| | Adult | | | Sub-adult | | | Juvenile | | |
|---|---|---|---|---|---|---|---|---|---|
| | Mean | SD | N | Mean | SD | N | Mean | SD | N |
| **Body Weight ***** | 907.2 | 72.0 | 32 | 819.3 | 38.5 | 12 | 609.7 | 121.4 | 14 |
| **Total Body Length*** | 266.2 | 14.4 | 30 | 250.8 | 11.2 | 10 | 244.4 | 32.1 | 10 |
| **Head Width** | 51.5 | 9.2 | 30 | 47.8 | 5.2 | 12 | 45.6 | 15.8 | 12 |
| **Head length*** | 54.7 | 11.2 | 29 | 50.7 | 5.5 | 12 | 38.5 | 20.4 | 12 |
| **Foot Span** | 73.3 | 6.0 | 28 | 72.9 | 7.3 | 11 | 71.4 | 9.8 | 10 |
| **Hand Span** | 59.0 | 6.7 | 29 | 57.8 | 5.3 | 10 | 57.4 | 5.1 | 10 |
| **Lower Leg Length** | 87.9 | 10.9 | 29 | 84.5 | 5.8 | 12 | 81.3 | 8.0 | 11 |
| **Upper Leg Length** | 83.7 | 9.6 | 28 | 81.7 | 5.4 | 12 | 79.4 | 9.4 | 11 |
| **Lower Arm Length*** | 75.0 | 4.2 | 30 | 73.1 | 5.0 | 12 | 64.4 | 16.0 | 12 |
| **Upper Arm Length*** | 79.4 | 5.9 | 30 | 74.6 | 6.8 | 12 | 72.3 | 9.1 | 11 |

Significant p-values are denoted with a (*),*$\leq$ 0.01, ** $\leq$ 0.001, *** $\leq$ 0.0001.

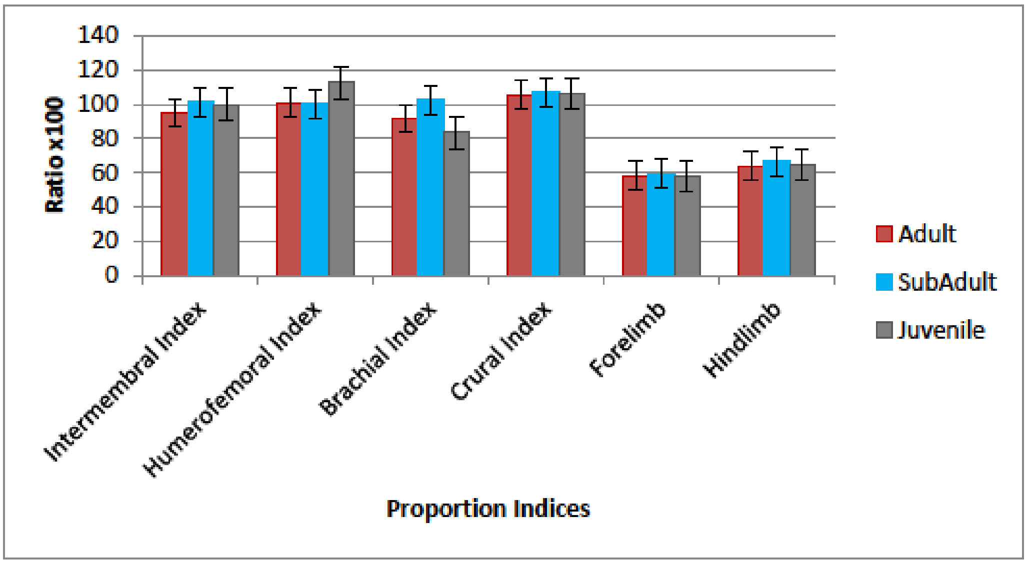


**Figure 5.3:** Proportion indices, forelimb/total body length and hindlimb/ total body length calculated from the limb measurements taken from $N_A = 30$, $N_{SA} = 11$, $N_J = 8$. Error bars represent standard error.

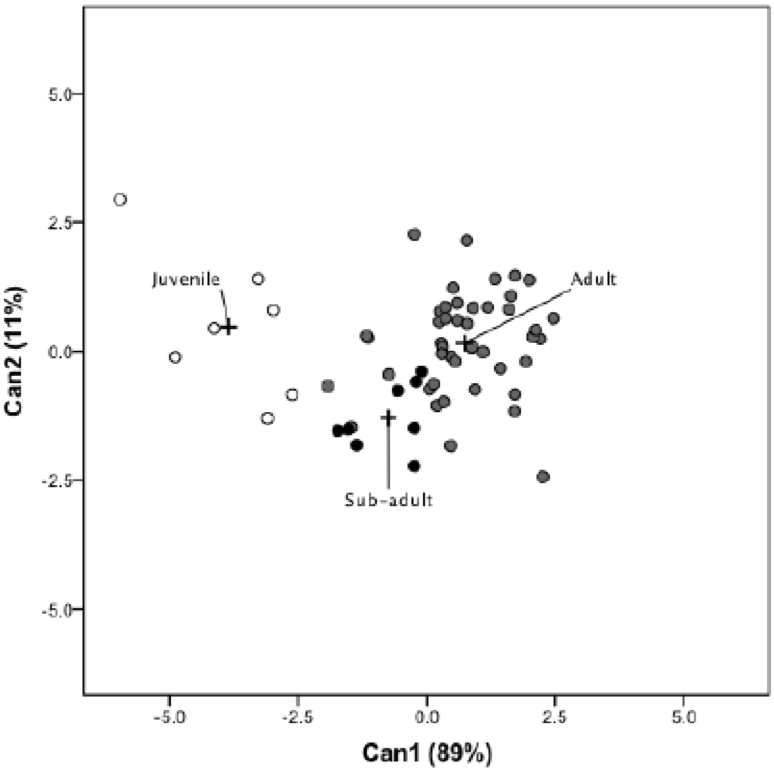
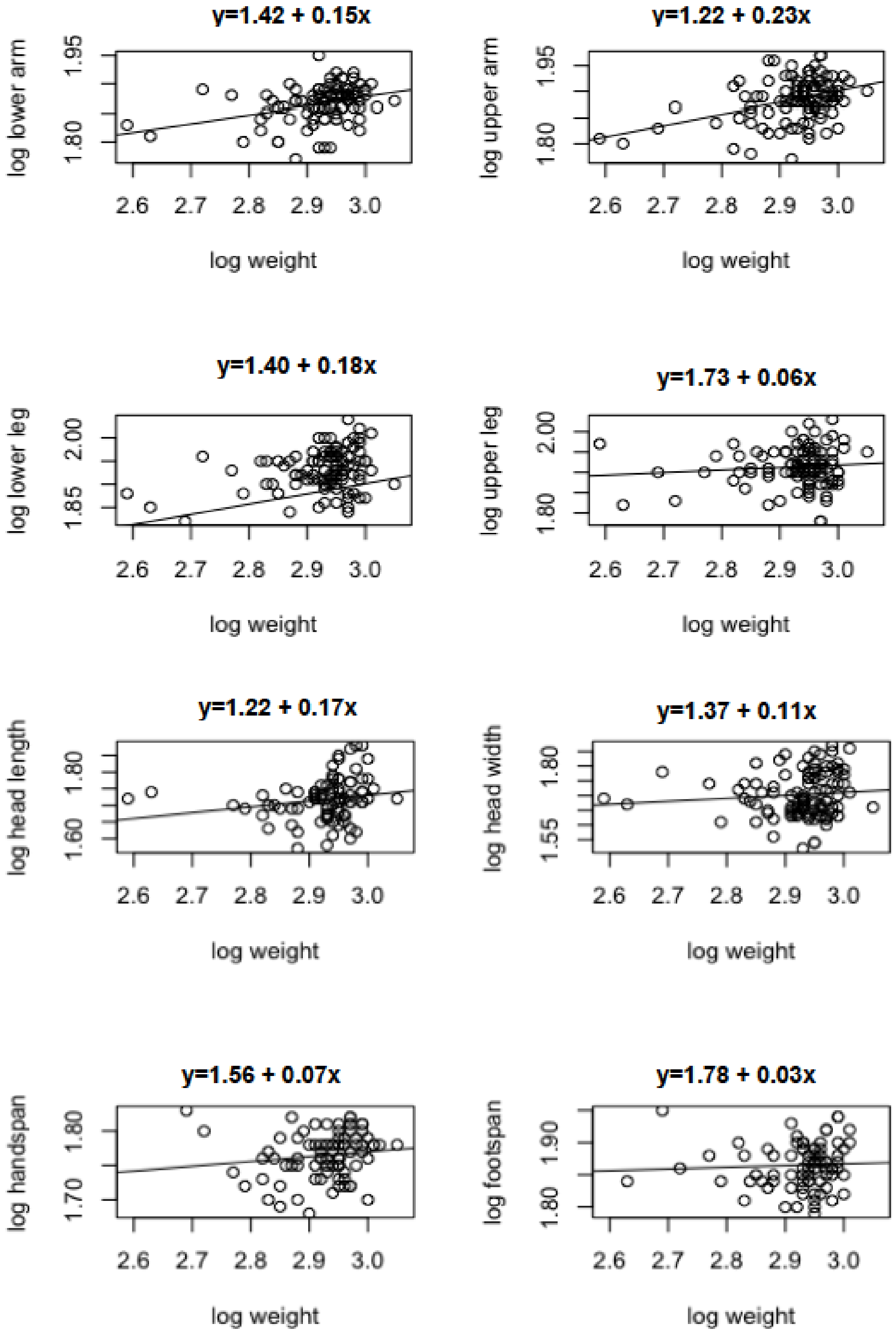


**Figure 5.4:** Canonical variate analysis (CVA) calculated with eight morphometric measures and three age class identifiers (Adult, Sub-adult, and Juvenile) (Wilk's $\lambda = 0.235$, $p < 0.0001$). Crosses indicate the centroid of each group that defined the canonical component axes for Can1 and Can2, percentage represents the influence of the two functions in identifying group differences.



$y=1.42 + 0.15x$

$y=1.22 + 0.23x$

$y=1.40 + 0.18x$

$y=1.73 + 0.06x$

$y=1.22 + 0.17x$

$y=1.37 + 0.11x$

$y=1.56 + 0.07x$

$y=1.78 + 0.03x$

**Figure 5.5:** Bivariate plots of morphometric measures and body weight in Javan slow lorises (*Nycticebus javanicus*). The generated least square regression formula is presented above each plot.

**Table 5.4:** Regression statistics for allometric bivariate plots presented in Figure 5.5

| Trait | $R^2$ | LS-intercept | p-value |
|---|---|---|---|
| **Lower arm** | 0.12 | 0.15 | <0.0001 |
| **Upper arm** | 0.15 | 0.23 | <0.0001 |
| **Lower leg** | 0.09 | 0.18 | 0.004 |
| **Upper leg** | 0.01 | 0.06 | 0.332 |
| **Head length** | 0.04 | 0.17 | 0.072 |
| **Head width** | 0.01 | 0.11 | 0.346 |
| **Handspan** | 0.02 | 0.07 | 0.210 |
| **Footspan** | 0.03 | 0.03 | 0.644 |

## 5.4 Discussion

I observed that Javan slow lorises rely on their hand, foot, and limb morphology in place of specialized nails or claws to maintain vertical postures on large tree trunks. In relation to this important feeding adaptation, young animals obtain adult body proportions and gain locomotor and postural competence by three months of age. Some variables such as arm measures scaled isometrically, while leg, hand, and feet measures scaled allometrically and thus were relatively larger in juveniles. The age classes showed little difference in habitat utilization, and the general morphometric measures were not determinants of the proportion of vertical postural modes. Feeding on gums and exudates in slow lorises is reflected to some extent in their pelage, life history, mandible morphology, and social behaviour (Nekaris et al., 2010). In conjunction with all the physiological, morphological, and behavioural adaptations that facilitate gouging and exudate consumption in Javan slow lorises, data presented here suggest an ontogenetic adaptation as well.

### Vertical gouging posture:

Javan slow lorises across all age classes used their hands, feet, and limbs to maintain vertical postures on large tree trunks. Mammals that lack specializations like claws or suction cups such as Javan slow lorises can only grasp large vertical substrates if they can exert enough force on the surface through adducting limbs inwards (Cartmill, 1979). To thwart gravity these animals must rely on a static friction grip, which is maintained through the interaction of their volar pads, the substrate surface, and the normal component of frictional force created from pressing against the substrate (Johnson et al., 2015). Considered unique among primates for their locomotor and physical characteristics (Ishida et al., 1992; Sellers, 1996), Javan slow lorises may also use aspects of these features to create the needed force to uphold vertical postures on tree trunks; to confirm this notion further studies on the force of the *Nycticebus* grip in a controlled setting are required.

Although I did not record specific grasping behaviours in this study, it is clear during our live observations and through photos that, as stated by Gebo (1985), *Nycticebus* spp. use a I–V grasp, while engaging with substrates, which uses the flexing force of the hallux to oppose the flexing force of the four laterally placed digits. Gebo (2011) later revisited vertical clinging and leaping, detailing the morphological features present in strepsirrhines that inherently facilitate access to vertical substrates, noting that strepsirrhines evolved modified upper ankle joints to improve foot abduction and lateral rotation, which ultimately improves their ability to utilize vertical substrates. Though Gebo (2011) stated that only indriids, lepilemurids, galagids, and to some extent gentle lemurs, could be considered vertical clingers, Javan slow lorises, generally regarded only as a slow climber, possess many of the same morphological modifications as vertical clingers. Our data showed that vertically clinging is one of their most common postures in the wild.

**Locomotor behaviour and habitat utilization during feeding:**

While feeding, Javan slow lorises display adult-like locomotor and postural competence during development, only displaying two significantly different locomotor modes among adults, sub-adults, and juveniles. The increased number of significant differences seen across all behaviours contrasts the low level of differences seen during feeding, highlighting the importance of locomotor and postural competence to access certain food resources. Knowing that gums elicited from trees can make up as much as 97.5% of the *Nycticebus* feeding time (Swapna et al., 2010; Das et al., 2014), it is not surprising that juveniles and adults use tree trunks in equal measure during feeding bouts. Typically used on smaller sized trunks and branches while individuals begin to bridge from one substrate to the next, Vertical Suspension 2 is virtually unobserved in juveniles. Bridging, which is associated with Vertical Suspension 2 requires individuals to maintain their balance and quickly re-establish stability once they cross a gap (Ishida et al., 1992). Horizontal Suspension 3 again is a rarely seen mode, but is associated with grabbing insects during Suspensory Walk and is typically classified as Suspensory Walk instead of Horizontal Suspension 3, because it can be difficult to see the fast moving hand of slow lorises while they grasp insects in the wild (Streicher et al., 2012).

In contrast, the ontogenetic differences seen in locomotor modes across all behaviours suggest that indeed there are some physical or behavioural differences that prevent juvenile Javan slow lorises from fully mirroring adults within the same environment. Researchers working on ontogeny and positional behaviour, cite exploratory behaviour, changing musculoskeletal systems and varying environmental pressures as explanations for significant differences in locomotor behaviour between juveniles and adults (Workman and Covert, 2005; Bezanson, 2009; Dunham, 2015). The morphometric scaling reported in this study highlights how vertical clinging and gum feeding are essential aspects of Javan slow loris survival and allows juveniles to access tree trunks the way adults do.

**Morphometric measures:**

The basic morphometric differences among adult, sub-adult, and juvenile Javan slow lorises were limited to their body mass, total body length, arm length, and head length. The mean body mass in juveniles was almost two-thirds of the mean in adults, with sub-adults nearly 100 g less than the adults. Within juveniles we found a wide range of variation, evident in the high standard deviation. The ontogenetic difference in body mass, which is a proposed influential factor for locomotion and substrate selection (Fleagle and Mittermeier, 1980; Hurov, 1991), did not influence the observed individuals' ability to secure necessary resources successfully. These data further support the assertion by Preuschoft et al. (1998) that strepsirrhines and tarsiers show no apparent correlation between body size and preferred locomotor mode, due to their limited absolute body size variation.

Similar to previous studies on young primate individuals compared to adult conspecifics, young Javan slow lorises had a hand and foot span comparable to both adults and sub-adults, while maintaining a relatively smaller body size. This relationship is a mechanism to improve stability in arboreal environments (Jungers and Fleagle, 1980; Lammers and German, 2002; Young, 2009); I also note that both hands and feet are key proponents in vertical clinging. As I predicted, young Javan slow lorises quickly attain the necessary physical and behavioural competence to vertically cling and gouge trees. These findings are supported by the fact that Javan slow lorises possess what Martin (1975) believed to be a vital gouging tool, their toothcomb, at a young age. Reports on slow loris dental eruption vary, where some report that they are either born with a full set of teeth (Pournelle, 1955), complete their adult dentition as early as six months (Smith et al., 1994), or no later than nine months (Hill, 1937). Martin (1975) thought that access to gums was the main evolutionary purpose of the toothcomb and that grooming developed secondarily. To reinforce these findings we would need to look at the ontogenetic trajectory in a broader phylogenetic context, comparing various primate species.

Focused on the results presented here we suggest that more primates could be adapted to utilize rapid growth to reduce infant vulnerability. This notion is supported by the rapid physical competence during feeding observed in this study, and suggestion from other researchers of dissociation among life history traits, including body mass, brain size, age of maturation, and ontogenetic positional patterns (Godfrey et al., 2001; Pereira and Leigh, 2003; Leigh, 2004; Bezanson, 2009). Acquiring adult-like physical features and behaviours is present in other animals that share the same behavioural and physiological traits as Javan slow lorises, including nocturnality (*Aotus*), low basal metabolic rate (*Tarsius*), slow quadrupedal climbing (*Choloepus*) and neonate parking (*Varecia*) (Veselousky, 1966; Dixson and Fleming, 1981; Pereira et al., 1987; Roberts, 1994). Leigh (1994) found that compared to frugivorous anthropoids, folivorous anthropoids attained adult body size at an earlier age. She suggested a number of factors that would lead to this difference, focusing on diet type and the varying risks each group faces to retrieve food resources. Like foliage, exudates are considered to be a more stable food resource compared to fruits, which may account for the ontogenetic similarity between folivorous anthropoids, pilosans and Javan slow lorises. In primates, the influence of ontogeny on locomotor behaviour and habitat utilization varies from species to species. Despite differences in body size and age, several primate species employ various locomotor and postural modes in equal measure (Doran, 1992, 1997; Wells and Turnquist, 2001; Lawler, 2006; Thrope and Crompton, 2006; Bezanson, 2009; Zhu et al., 2015;).

I have yet to understand the origin and potential impact that tree gouging and gum feeding may have had on the development and evolution of *Nycticebus* species. Burrows et al. (2015) noted that it is unlikely that tree gouging existed in the last common ancestor of lorisiforms, but that it evolved multiple times following the split of Lorisidae and Galagidae. If exudativory evolved independently multiple times, the varying adaptations seen in how species elicit gums or access tree trunks is representative of their individual lineages and the specific environmental pressures at the time exudativory emerged. As a non-leaping primate, Javan slow lorises have seemingly modified their limb, hand, and foot morphologies to facilitate access to vertical substrates. Having highlighted the importance of physical competence to access gums, Javan slow lorises may limit the period of time where these specializations are out of reach, to increase the likelihood that offspring reach sexual maturity, surpassing the juvenile bottleneck.

In the present study, I focused on the gum feeding diet of Javan slow lorises and the potential ontogenetic adaptations used to facilitate it, but this case only exemplifies the complex relationship between feeding ecology and the specialized adaptations that evolved to enable it. Across all mammal species, unique adaptations emerge to increase the likelihood of survival, including reducing predation risks or maternal energetic expenditure. Gaining adult- like body proportions is yet another of many strategies used to achieve this goal.

## 5.5 Chapter summary

In this chapter, I highlight the important role gum producing trees play in the diet and locomotor behaviour of *N. javanicus*. Their reliance of gum producing trees is reflected in their physical ontogeny. The rapid acquisition of adult limb proportions and the indistinguishable proportion of employed locomotor behaviours observed during feeding speak to their physical specialization for vertical clinging. In this chapter I focused on the physical aspects of nightly movement and spacing in the Javan slow loris (Figure 5.6). Now that I have established their physical capacity to access and consume gum even at a young age, I explore the way individuals locate and return to this spatially dispersed resource. Understanding how an animal perceives their environment will facilitate a better understanding of what they need to settle within a new area successfully.

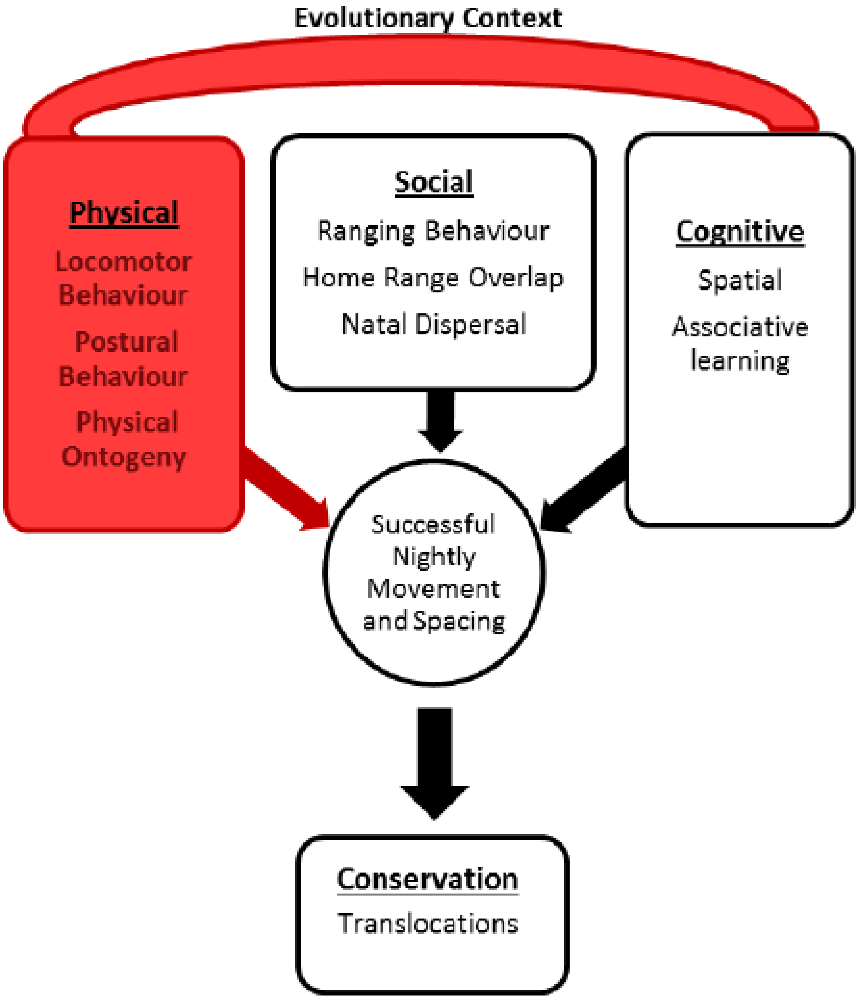


**Figure 5.6:** Visualisation of the framework of the thesis highlighting how the data and conclusions presented in chapter 5, fit into the context of the entire thesis. Topics in red are the focus of the chapter, topics in blue are related though not explicitly discussed.

# Chapter 6: Cognitive map use in the javan slow loris (*Nycticebus javanicus*)

**Figure 6.1:** Aerial image of the Little Fireface Project field site in West Java, Indonesia, taken by Andrew Walmsley 2017 using an unmanned aerial vehicle.

## 6.1 Introduction

In the wild, an animal's ability to navigate its home range in search of essential resources is a key aspect of its ecology (Di Fiore and Suarez, 2007; Müeller and Fagan, 2008). The demand on individuals to forage and locate resources may act as an important selection pressure on the evolution of spatial cognition (Hopkins, 2016). Animals must integrate spatial, temporal, and ecological inputs to meet the demands of searching and foraging for resources (Lurhs et al., 2009). Many taxa maintain large home ranges that contain many potential feeding locales, many of which are not within sight of one another (Di Fiore and Suarez, 2007). Travelling from one locale to another requires an understanding of the spatial relationship between the two locales and the spatial relationship between the animal itself and these locales (Gallistel, 1989). Additionally, primates have the ability to locate and monitor large quantities of feeding resources, as a result of selection pressures in the evolution of their brain sizes (Milton, 1981).

Historically, researchers have been interested in cognitive map use and spatial cognition (Tolman, 1948; Blodgett et al., 1949; Kendler et al., 1949), first they focused on humans and rodents (Tolman, 1948), then expanded to include bees (Gould, 1986), followed by other insects, and birds (Wehner and Menzel, 1990; Poucet, 1993; Bennett, 1996; Foo et al., 2005). Those focussing on the evolution of primate cognition and foraging strategies, explore how each primate taxon stores, represents, and utilizes spatial, temporal and resource availability information to locate feeding sites (Garber and Dollins, 2014).

Byrne (2000) and Garber (2000) identified two navigational mechanisms used by primates during foraging. Topological or network maps are based on the spatial relation between objects (Byrne, 2000; Piaget and Inhelder, 1956). This type of map implies that individuals have a representation of space, in which they are not able to visualize distance and direction to a desired locale directly, but instead they must use landmarks along a route (Normand and Boesch, 2009). The Euclidean or vector map (Normand and Boesch, 2009; Bryne, 2000) allows the animal to perceive distance and direction from any point in the environment, and is comparable to a Euclidean representation of space (Piaget and Inhelder, 1956). A third spatial mechanism animals may use is path integration, where mental representations are regularly updated based on small directional changes as individuals move towards their goal. As with a Euclidean map, path integration enables animals to use novel paths to out-of-site locales within their environment if some form of landmark is always within sight. The inherently complex nature of identifying the mental state of animals makes it difficult to attribute any one navigational mechanism to observed movements. We can infer what mechanism is likely to be used, under the assumption that it will be the most efficient option available.

Studies on navigational mechanisms, spatial memory and foraging include Apes, Old World monkeys, New World monkeys, and prosimians. These studies showed that route-based maps are the most commonly used form of cognitive map, and Euclidean maps have thus far only been seen in chimpanzees (Normand et al., 2009; Normand and Boesch, 2009) and bonobos (Menzal et al., 2002). Beyond just the navigational mechanism there is ample evidence of efficient travel, between resources, including the closest or the most productive (Menzel, 1973; Garber, 1988; Janson, 1998). Furthermore, potential food sources are bypassed in favour of more preferred ones (Garber 1989; Janson 1998; Noser 2004; Noser and Byrne, 2007b; Janmaat, 2006; Cunningham and Janson, 2007; Valero and Byrne, 2007; Normand et al., 2009). The routes primates use when travelling are reportedly goal-directed and in most cases, the routes used between known resources are highly linear (Janson, 1998; Pochron, 2001; Cunningham and Janson, 2007; Valero and Byrne, 2007) or a series of linear segments (Di Fiore and Suarez, 2007; Noser and Byrne, 2007b, 2010). Some animals rely on topographic or environmental features within their environment to orient or travel (Di Fiore and Suarez, 2007; Valero and Byrne, 2007). The need of some animals to monitor their home range on a regular basis may also require relatively long and rapid movements, which may result in straight-line travel (Terborgh and Stern, 1987), to quickly access those resources.

Despite this widespread interest in primate spatial ecology and cognition, only a few studies have yet focused on nocturnal primates, such as the grey mouse lemur (Joly and Zimmermann, 2007; 2011). Grey mouse lemurs reportedly return to specific feeding locations and used characteristics of a route-based cognitive map while traveling throughout their environment. As another small-bodied, nocturnal, solitary forager, it is plausible that the Javan slow loris would share similar navigational skills to this lemur species.

Determining when and where travel decisions are made is essential for studying decision-making and spatial cognition (Noser and Byrne, 2007a, 2007b; Byrne et al., 2009, Normand and Boesch, 2009). Locations where travel decisions are made have been suggested to be those at which a travelling animal or group of animals significantly changes travel direction and as such, starts orienting towards the next goal (Byrne et al., 2009). The change-point test (CPT) is a robust statistical method for determining such locations, referred to as change-points, independent of the possible reasons for the change of direction, including behaviour, or resources abundance (Byrne et al., 2009).

The Javan slow loris, provides an opportunity to examine navigational mechanism use in a species thought to closely resemble the ancestral condition in primates (Clutton-Brock, 1974). As a specialized exudate feeder, they rely heavily on immobile food resources (Nekaris, 2014). Thus, it would be advantageous for this species to possess some form of spatial memory and the ability to efficiently navigate between specific locales. Unlike other group-living primates, the Javan slow loris utilizes a uni-male/uni-female social system, where two adults and their immature offspring keep close association (Nekaris, 2014; Chapter 4 and Chapter 7). The Javan slow loris ranges over areas comparable to larger animals, with home range sizes ranging between 5-10 ha. (Nekaris and Nijman, 2015). Given that, the Javan slow loris travels long distances throughout the night and is likely unable to see all aspects of their environment from any one vantage point, the ability to create a mental representation of their environment would aid in their survival and fitness. This is not yet proven formally and the specific mechanism used to navigate between locales is still unknown.

Other strepsirrhine primates display characteristics that suggest a degree of spatial cognition and directed travel. Traveling and foraging make up as much as 50% of nightly activity in *Loris* species, where traveling is defined as directed movement (Nekaris, 2001). Males were observed traveling in a direct line for more than 50 meters to reach female conspecifics (Nekaris 2001, 2003). Lemur species reportedly do not randomly move within their environment, which is a preliminary indicator of higher navigational skills. The Milne-Edward's sifaka, Northern red-fronted lemur, red-bellied lemur, grey mouse lemur, red-fronted lemur, and Southern ruffed lemur, all display non-random use of their environment, leading researchers to conclude that they utilized distinct routes when traveling between locales (Everhart and Overdorff, 2008; Lührs et al., 2009; Razafindratsima et al., 2014; Joly and Zimmerman, 2011; Schliehe-Diecks et al., 2012). The Milne-Edward's sifaka and Northern red-fronted lemur used 'travel' routes to get from one food patch to the next. Using these routes, animals are able to check the status of various resources along the way as they move from one important food source to another (Milton, 2000), particularly resources that are out of sight from their current position. The grey mouse lemur, red-bellied lemur, and Southern ruffed lemur all reused particular routes to travel between feeding resources (Lührs et al., 2009; Razafindratsima et al., 2014), and the red-fronted lemur displayed frequent backtracking behaviour.

In this chapter, I examine the travel patterns of the Javan slow loris in a wild montane agroforest. To determine if the Javan slow loris uses some form of cognitive map and spatial memory while navigating their environment, I addressed the following research questions: does the Javan slow loris display directedness when navigating their montane agroforest? If so, which type of navigational mechanism best characterizes their spatial representation of this environment? I predict that the Javan slow loris will display directed travel between resources, where their nightly routes overlap towards revisited feeding trees, specifically immobile gum producing trees and the use of change–points during nightly travel. Bryne et al. (2009) noted that nodes, represented here through change-points, may indicate locales where individuals make travel decisions. Another indicator of directed travel is a decreasing circuity index, as individuals get closer to their goal locale (Menzel et al., 2002). Furthermore, I predict that the Javan slow loris will display directedness best categorized as a route-based cognitive map or topological cognitive map. This species may represent the only other report of a solitary nocturnal forager, along with the grey mouse lemur that presents characteristics of planning to travel to distant out-of-sight resources (Joly and Zimmermann, 2007; 2011).

## 6.2 Methods

**See sections:**

2.2.1 Little Fireface Project (LFP)
2.3.1 Collaring and release
2.3.2 Nightly observations
2.3.3 Locomotor and postural behaviour definitions
2.3.4 Morphometric data
2.4.4 Path length, overlap, simulation and GPS Visualization
2.4.5 The change point test (CPT)
2.4.7 Statistical analysis

## 6.3 Results

In 2016, the top four tree species used by 13 Javan slow lorises made up 78.5% of their feeding time. Thirty-four per cent in green wattle (*Acacia decurrens*), a gum producing tree, 21% in weeping paperbark (*Melaleuca leucadendra*), another gum-producing tree, 12.5% were non gum producing feeding sites calliandra (*Calliandra spp.)* and 11% were bamboo temen (*Gigantochloa atter*) (insect feeding and sleep sites).

I identified 140 change-points used during nightly travel (Table 6.1). Most change-points were associated with feeding (87%), sleeping (7%), and social (4%) events. For two change-points we were unable to identify any biologically meaningful associations. Of the 122 change-points associated with feeding behaviours, 104 were at immobile gum producing tree species and 18 were associated with nectar producing calliandra trees (Figure 6.2).

Figure 6.1 displays a sample nightly route for one male and one female Javan slow loris included in this study. Across all 13 individuals, the mean full night path length (NPL) was 541 m and the mean half night NPL was 239 m (Table 6.2).

Route overlap averaged 29% per individual and ranged from 16% in TO to 44% in TE (Table 6.1). Finally, we determined that the efficiency index significantly varied across the detection radii ($H$ = 569.5, df = 2, $p < 0.0001$). Here efficiency is defined as taking routes that lead to highest number of visits to preferred trees. Javan slow lorises were more efficient than the model at the five-meter detection radius, performed similarly at 10-meters, but were less efficient at the 20-meter detection radius (Figure 6.3 and 6.4).

**Table 6.1:** The number of change-points and per cent of route overlap for each included Javan slow loris (*Nycticebus javanicus*) in Cipaganti. Two letter codes refer to the observed Javan slow lorises reported in Table 2.3.

| **Sex** | **ID** | **Number of CP** | **Route Overlap** |
|---|---|---|---|
| **Female** | EN | 10 | 30 |
| | LU | 14 | 35 |
| | MA | 11 | 32 |
| | OE | 8 | 39 |
| | SH | 5 | 22 |
| | SI | 9 | 25 |
| | TE | 13 | 44 |
| **Male** | AC | 6 | 32 |
| | AL | 18 | 37 |
| | AZ | 8 | 28 |
| | FE | 15 | 19 |
| | RA | 12 | 18 |
| | TO | 11 | 16 |

**Table 6.2:** Full and half night path lengths including the, number of routes analysed (count), mean path length (mean), and maximum and minimum path lengths (maximum and minimum) in the Javan slow loris (*Nycticebus javanicus*) in Cipaganti. Two letter codes refer to the observed Javan slow lorises reported in Table 2.3.

| | | **Full Night** | | | | **Half Night** | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Sex** | | NPL Count | Mean | Maximum | Minimum | NPL Count | Mean | Maximum | Minimum |
| **Male** | AC | - | - | - | - | 6 | 250.6 | 686.1 | 107.9 |
| | AL | 5 | 733.2 | 1121.7 | 485.5 | 25 | 275.8 | 1582.6 | 73.2 |
| | AZ | 6 | 417.8 | 684.6 | 133.6 | 12 | 190.4 | 307.1 | 96.3 |
| | FE | 3 | 668.1 | 811.4 | 414.6 | 20 | 257.5 | 627.7 | 93.7 |
| | RA | 1 | 516.5 | 516.5 | 516.5 | 17 | 192.5 | 317.9 | 61 |
| | TO | 4 | 317.9 | 377 | 289 | 13 | 189.9 | 355.3 | 63.1 |
| **Female** | EN | 2 | 578.6 | 731.9 | 425.3 | 7 | 332.2 | 471.9 | 198.5 |
| | LU | 4 | 513.5 | 695.8 | 328.4 | 20 | 162.3 | 406.2 | 23.3 |
| | MA | 6 | 626.4 | 1264 | 360.9 | 14 | 253.4 | 511.7 | 83.6 |
| | OE | 1 | 428.2 | 428.2 | 428.2 | 12 | 202.7 | 418.4 | 73 |
| | SH | 7 | 613.9 | 871.8 | 400.5 | 14 | 238 | 401.7 | 113 |
| | SI | - | - | - | - | 11 | 328 | 523.6 | 156.8 |
| | TE | 5 | 555.7 | 968 | 380.2 | 21 | 205 | 450.9 | 33.6 |
| **Total** | | | 541.4 | | | | 239.4 | | |

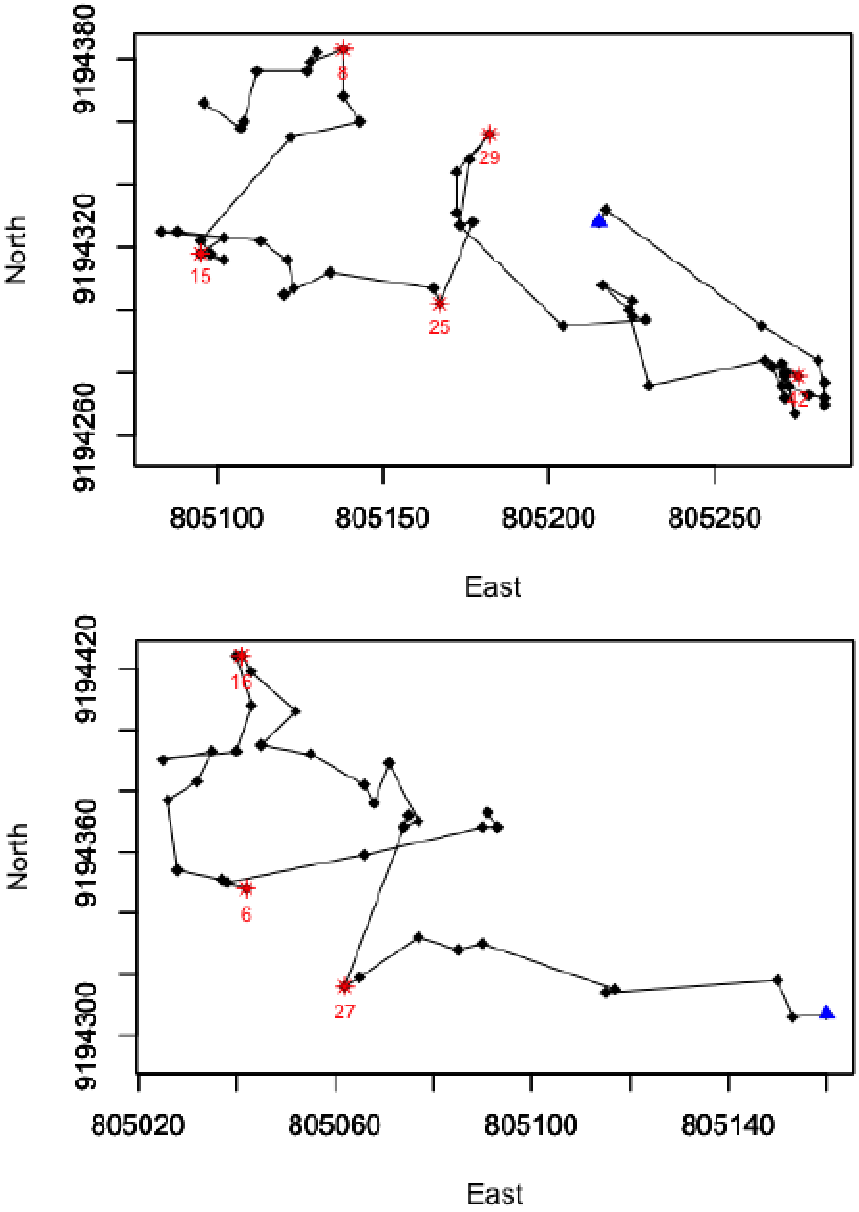


**Figure 6.2:** Travel routes in one male (AL) and one female (LU), where red stars denote change points and the blue triangle represents the putative goal in the Javan slow loris (*Nycticebus javanicus*) in Cipaganti.

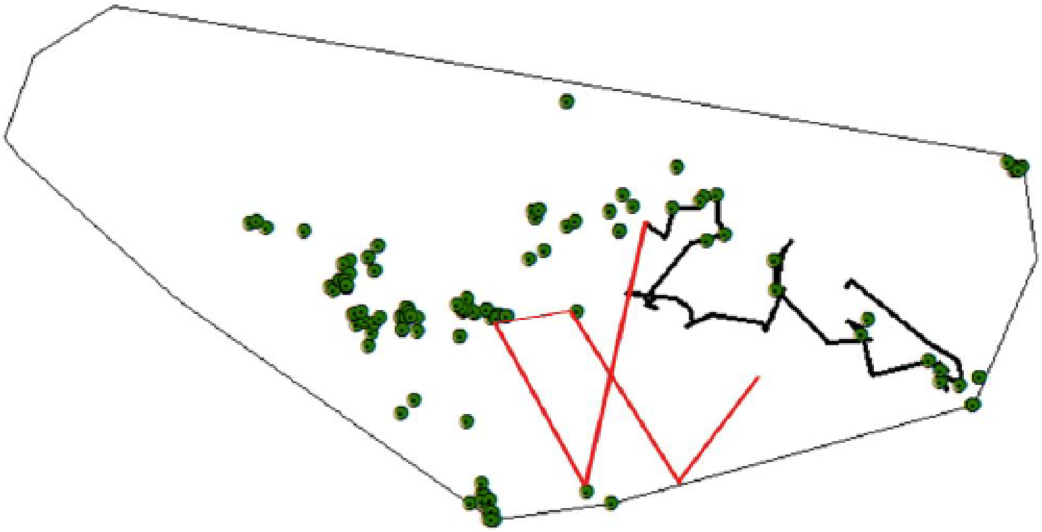


**Figure 6.3:** Map of key locales in one Javan slow loris (*Nycticebus javanicus*), AL's home range, displaying the same route presented in Figure 6.2, as well as, as the heuristic model for the five-meter detection radius.

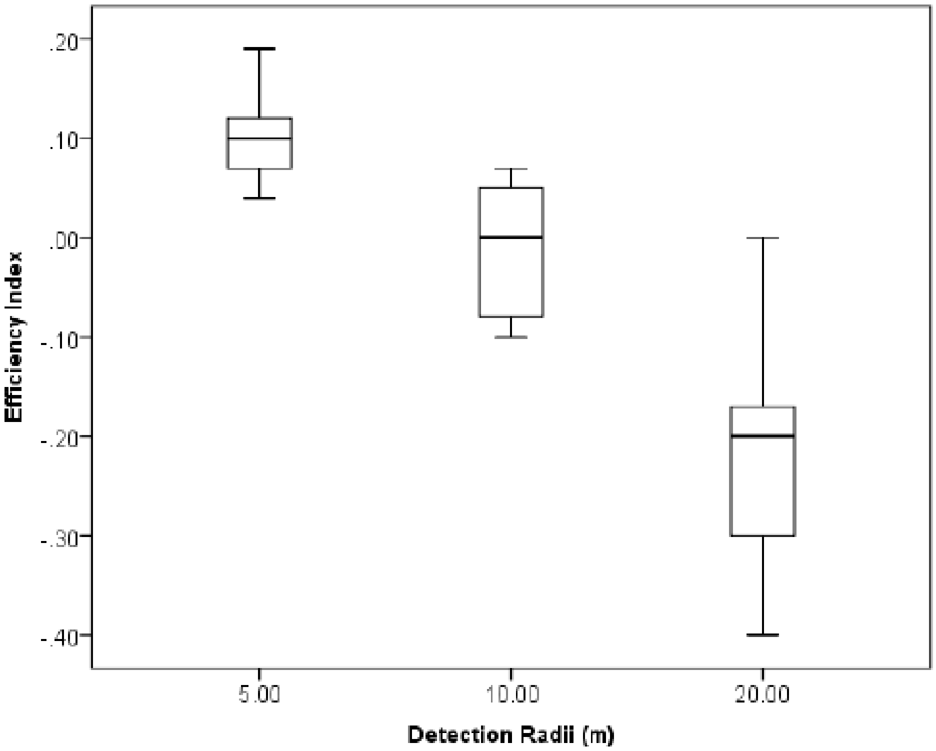


**Figure 6.4:** Boxplots displaying the calculated efficiency indices at three detection radii (5 m ,10 m, 20 m) in the Javan slow loris (*Nycticebus javanicus*) at the Little Fireface Project in West Java, Indonesia.

### 6.4 Discussion

These findings show that the Javan slow loris: spends the majority of its feeding time consuming food items at immobile gum-producing trees, reuse routes while traveling between goal locales, utilize change-points to efficiently traverse their home range, and out preform random search model within a certain distance. Change-points were associated with feeding, sleeping and social locales. The Javan slow loris outperformed heuristic random search models at short detection radii, but underperformed at greater distances, thus it is unlikely that they use random searches to reach goal locations, especially as they approach their perceived visual detection range. Data presented here not only support the presence of spatial cognition during navigation in the Javan slow loris, but also suggests that a route-based or topological map best characterizes the form of cognitive map used by this species. It is clear based on the Javan slow loris' change point associations and time spent at gum and nectar producing trees that traveling to feeding locales acts as a framework for their nightly navigation. Asensio et al. (2011) also stated that the distribution of preferred feeding trees structured the daily travel for gibbons (*Hylobates lar*) as did, Cunningham and Janson (2007) in saki monkeys (*Pithecia pithecia*) and Joly and Zimmermann (2011) in the grey mouse lemur.

The Javan slow lorises in this population displayed route overlap comparable to other primates, (Mackinnon, 1974; Boonrata, 2000; Milton, 2000, Di Fiore and Suarez, 2007; Erhart and Overdorff, 2008; Presotto and Izar, 2010; Urbani, 2009; Hopkins, 2011) that use regular routes (Sigg and Stolba, 1981; Byrne, 2000; Noser and Byrne, 2007a; 2010). In primates these habitual routes often coincide with streams, ridges of hills and tracks located in their home range (MacKinnon, 1974; Di Fiore and Suarez, 2007) and the use of such landmarks for navigation are evidence of topological familiarity.

It is important to highlight that the comparable level of overlap seen here is the result of non-consecutive observations. Though these data span 12-months, each slow loris is typically observed twice per month, unlike the previously mentioned studies LFP does not complete multi-night observations, but focuses more on a longitudinal sampling method. Due to the infrequency of consecutive nightly observations, it is possible that the Javan slow loris actually uses a more robust route network, which was undetected in this study. Alternatively, the overlap could be linked to the ecological features of the study site. As an agroforest, the landscape in Cipaganti can be restricting to movement along the same routes on a nightly basis. Howard et al. (2015) emphasized that studies analysing goal-directed travel in primates should consider how the landscape influences travel. Prior to this study the introduction of a new crop (labu), became popular in the area and elicited the construction of large bamboo frames over existing crops (Nekaris et al., 2017). They effectively increased connectivity between the already dispersed tree lines, making the landscape more accessible, as slow lorises regularly travelled through them.  Given that linearity is a common measure of efficiency in regards to traveling, we should allow for the possibility that a lack of linearity is not synonymous with inefficiency but instead, could suggest spatial knowledge of available routes dictated by the landscape.

The Javan slow lorises uses change point locales to make travel decisions or to reinforce them, the presence of change points, at, before, or after goal locales supports this conclusion. When looking at map formation and use in animals, change-points are seen as nodes, which Di Fiore and Suarez (2007) said were locales in topological/network cognitive maps, where decisions are made. This principle is a main assumption in justifying the importance of change points in navigation by Byrne et al. (2009) through the development of the Change Point Test Statistic (CPT). Having a detailed topological map with several change-points, and established routes aids in successful nightly movement and efficient resource exploitation. In addition to the presence of change points in a topological map, the navigator needs the cognitive ability to integrate changing phonological data, and have a sense of time to accurately access, and exploit changing resources.

To account for this needed additional cognitive capacity, it is important to rule out the possibility that animals are just using a random search model or happen upon needed resources (Janson, 1998). The varying results produced by the efficiently index offer support towards rejecting the null hypothesis, of random search methods. The Javan slow lorises, outperformed the model in efficiently reaching feeding resources within a 5 m detection radius, but the model outperformed the real routes once the detection radius reached 20 m. Nearly identical results were reported in mouse lemurs, where they were most efficient at the five m detection radius, were indistinguishable to the model at 10 m and surpassed by the model at the greater distance of 20 m (Joly and Zimmermann, 2011). The perceptual range in *Nycticebus* species is still unknown, thus we were unable to assess to what degree visual, olfactory, or auditory cues, may aid in reaching goal locales. Following Joly and Zimmermann's (2011), it is unlikely that these small nocturnal primates have a visual range as far as larger diurnal primates (about 20 m), even with their specialization for nocturnal navigation and theories suggesting that vision is a selection pressure for primate evolution. Their performance against the model at the 10 m detection radius, suggests that outside of 10 m it is unlikely they are able to visually identify resources. These results also lead to another question, regarding the way we interpret and perceive Euclidean spatial coding. The use of habitual routes and landmarks does not necessarily mean that there is a complete lack of Euclidean spatial representation.

Perceiving an environment using a Euclidean system is defined by flexibility and efficiency of behaviour and is therefore considered as the more advanced navigation mechanism. Because a prominent feature of evolution is the emergence of increased behavioural flexibility, it follows that Euclidean maps may play a crucial role in the onset of more complex behaviours displayed by higher vertebrates (Poucet, 1993). Poucet (1993) hypothesized that when travelling in small-scale space animals make use of Euclidian metrics, but when travelling across greater distances as they may use a route-based navigational mechanism. Normand and Boesch (2009) hypothesized that chimpanzees might be limited by the distances they could precisely remember, using a Euclidean map in less familiar areas. Poucet's theory has received some support from studies involving tamarins (Garber, 1989; 2000), howler monkeys (Garber and Jelink, 2005) and capuchin (Urbani, 2009), which all showed the use of a route based maps in large-scale space and suggested the use of a Euclidean maps in small-scale environment. It is highly likely that at shorter distances sensory cues, particularly olfactory and visual cues, play a major part in navigation and that this might be an alternative explanation for the highly efficient travel seen at shorter distances.

The findings presented in this chapter, lend support to theories that encephalisation is related to the demands of processing ecological information (Barton, 2000). If these nocturnal, small-bodied, solitary foragers are representative of early primates, their evident reliance on spatial cognition suggests that it could be an important selective pressure. That being said, there are a number of criticisms related to spatial memory as a selection pressure, namely the invariable size of the hippocampus across mammalian taxa (Kappeler, 2000), which is responsible for storing memories. Joly and Zimmermann (2011), concluded that spatial cognition may have evolved independent of sociality, citing results similar to those presented here in the Javan slow loris, a behaviourally and ecologically similar animal. Clearly, further research is needed to fully understand the complex relationship between, ecological and social pressures in regards to primate brain size and evolution.

### 6.5 Chapter summary

In this Chapter, I identify the use of spatial cognition and cognitive maps as tool to revisit goal locations, specifically gum producing trees and sleep sites. The temporal spatial distribution of resources throughout a home range can help individuals create a map of their environment. A route based cognitive map, which is what we identified in this population of Javan slow lorises, relies on a series of landmarks to guide individuals towards desired locations. Not only are they capable of relocating resources, they possess the ability to be flexible in a dynamic environment. In this chapter, I focused on the cognitive and evolutionary aspects of successful nightly movement and spacing (Figure 6.5). Understanding how *Nycticebus* is about to perceive their environment can facilitate a more accurate interpretation what they need prior to release and what they need successfully settle within a new area. In this chapter I focused on the cognitive and evolutionary aspects of successful nightly movement and spacing (Figure 6.5).

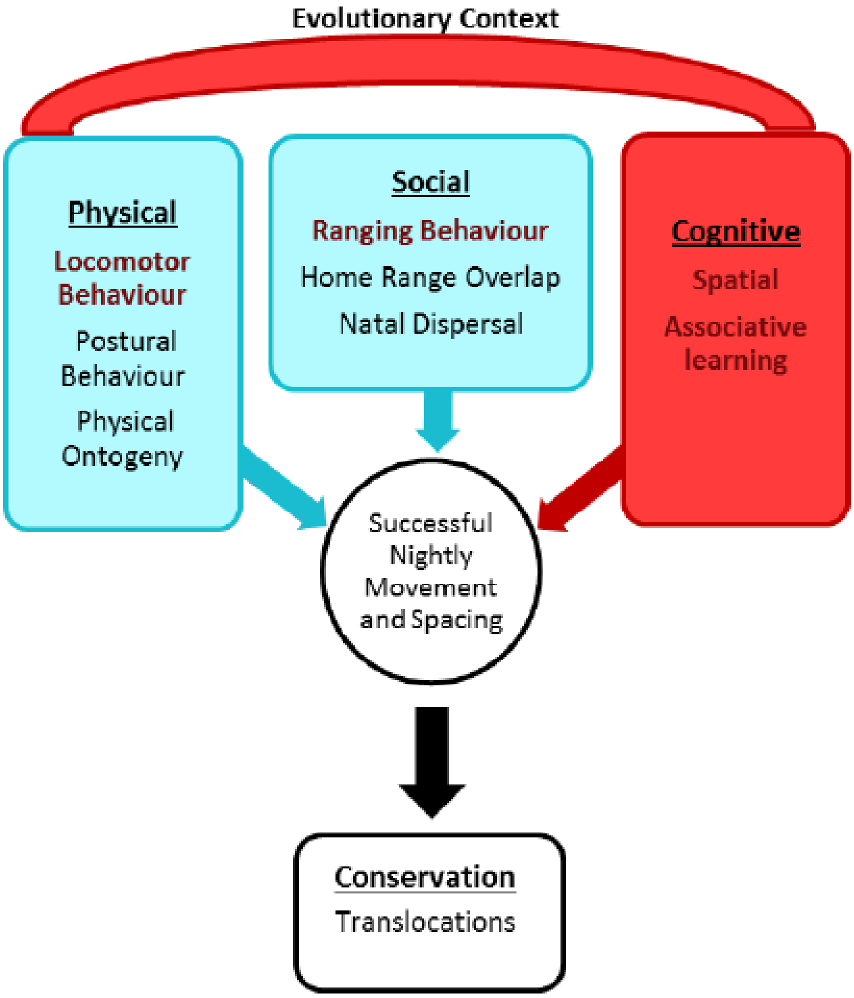


**Figure 6.5:** Visualisation of the framework of the thesis highlighting how the data and conclusions presented in chapter 6, fit into the context of the entire thesis. Topics in red are the focus of the chapter, topics in blue are related though not explicitly discussed.

# Chapter 7: The evolution of social organisation in lorisiformes.

**Figure 7.1:** Two Javan slow lorises (*Nycticebus javanicus*) together in a tree at the Little Fireface Project in West Java, Indonesia. Photo provided by the Little Fireface Project.

## 7.1 Introduction

Following an evaluation of the evolution of primate social organisation, Opie (2012) concluded that social organisation evolved from a solitary state at the primate last common ancestor (LCA) to multi-male/multi-female social organisation at the LCA of the anthropoids and the LCA of the Indriidae and Lemuridae in strepsirrhine. Typically classified as solitary, pair-living, or group-living (Crook and Gartlan, 1966; Kappeler and van Schaik, 2002), primate social organisations are rarely mutually exclusive making comparative analysis difficult. Despite a slew of publications examining primate social organisation evolution (e.g. Lukas and Clutton-Brock, 2012; Opie et al., 2012, 2013; Kamilar and Cooper, 2013; Lukas and Huchard, 2014;), there is more to uncover, especially in the more basal Lemuriformes and Lorisiformes. An assumption about the evolution of social organisation implicit to socio-ecology is that social organisation increases in complexity through time (Dunbar, 2000, Nunn, 2000). According to this view, social organisation evolved from solitary individuals early on in primate evolution, followed by small groups, which lead into larger complex group structures. Other forms of social living evolved later in primates. It was not until the LCA of the Colobine that the multi-female/uni-male social organisation first emerged followed by the Cercopithecines. Dispersed family groups (monogamous pairs) emerged at a similar time at the LCA of the Callitrichids. All other instances of a dispersed family group emerge later: in the Hylobatidae; *Avahi, Hapalemur*; *Aotus* and *Callicebus* (Opie, 2012).

Prior to Opie's (2012) analysis, Müeller and Thalmann (2000) evaluated the origin and evolution of primate social organization. They concluded that the dispersed harem (multi-female/uni male) social organisation proposed by Martin (1972, 1981, 1995) was unlikely to be representative of the ancestral social organisation in primates, based on data from cheirogaleids and one report of a wild slender loris' social organisation. Instead, they suggested that a dispersed multi-male/uni-female social organisation derived from the mammalian promiscuous social organisation, best characterizes the ancestral condition in primates. Among the primate species included in this review, there was a dearth of information regarding the diverse social and spacing systems present in Asian and African lorisids (Müeller and Thalmann, 2000; Müeller et al., 2007).

In the interest of uncovering the evolution of primate social organisation, researchers have noted that small nocturnal primates, namely Madagascar's dwarf and mouse lemurs and the Afro-Asian galago and lorisids are particularly important as extant primates that best resemble the ancestral euprimate state (Charles-Dominique and Martin, 1970; Martin, 1972). Mouse and dwarf lemurs (Cheirogaleidae), galagos (Galagidae) and lorises and pottos (Lorisidae) are behaviourally similar, and are sister taxa, with galago and lorises included in infraorder Lorisifomes and the mouse and dwarf lemurs falling in infraorder, Lemuriformes (Yoder, 1994; Müeller, 1999a; Rasmussen and Nekaris, 1998; Sussman and Nekaris, 2011; Poindexter and Nekaris, 2017). Instead of a steady progression from small and simple to large and complex structures, the social organisation of Lorisiformes may be rooted in a dispersed family group that later evolved into multi-female/uni-male organizations and multi-male/multi-female organisation.

Both theoretical and empirical research on the evolution of and current social organisations have been heavily biased towards group-living species in primates and in other mammals. This is partly due to some socially dispersed species being elusive or cryptic, thus difficult to study, and partly due to a misconception regarding their lack of social complexity. Most communication in nocturnal prosimians is temporally delayed or inaudible to human observers, contributing to the underrepresentation of their sociality (Charles-Dominique, 1977b; Bearder, 1987; Bearder and Nekaris, 2006; Gursky-Doyen, 2010; Gursky, 2015). Despite the difficulties in studying socially dispersed species and in recognizing their social units, research over the last few years has revealed a wide variation in the social systems of solitary foragers (Macdonald 1983; Müller and Thalmann 2000; Kappeler and van Schaik 2002; Dalerum 2007; Lacey and Sherman 2007). The social organisation of most nocturnal primates should be described as 'dispersed' instead of 'solitary' (Eisenberg et al., 1972; Martin, 1981; Dixson, 1997; Müeller and Thalman, 2000). I define social organisation following Müeller (1999b) including the dispersed family group, multi-female/uni-male, and multi-female/multi-male (Table 7.1)

**Table 7.1:** Definition of social organisations reprinted from Müeller (1999b; p 5).

| Distribution of Ranges | Cohesive Groups | Social Network | Solitary |
|---|---|---|---|
| **Male range coincides with female range (A)** | Gregarious family group or monogamy | Dispersed family group or monogamy | Spatial monogamy |
| **Male range overlaps several female ranges and vice versa (B)** | Gregarious multi-male group (polyandry) | Dispersed multi-male multi-female system | Promiscuity |
| **Male range overlaps several female ranges (C)** | Gregarious harem | Dispersed harem | Spatial harem |
| **Female range overlaps several male ranges (D)** | Gregarious polyandry | Dispersed polyandry | Spatial polyandry |

In regards to tracing evolutionary pathways and reconstructing the ancestral state, van Schaik and van Hooff (1983) stated that social organisation should be seen as a characteristic, a collection of behaviours that cannot fossilize like a tangible physical feature, making it increasingly difficult to infer changes over evolutionary time. Varying selective pressures have affected the evolution of social organization leading to the diversity of social organisation we see today. What selective pressures and how they affected the evolution of social organisation is considered unclear and contested.

In this chapter, I will first present lorisids data previously unknown on lorisid home range size, including three slow loris and two slender loris species. These data are the result of radio tracking studies that were not previously published. Then I will present data on lorisiform group size and social organisation, followed by a cladistics analysis of these social organisations with tree shrews acting as an outgroup. I hypotheses that the ancestral state for Lorisiformes is the dispersed family group which is the predominant social organisation in the Afro-Asian lorisids.

## 7.2 Methods

**See sections:**

2.2.1 Little Fireface Project (LFP)
2.3.1 Collaring and release
2.3.2 Nightly observations
2.3.5 Comparative data
2.4.2 Home range and overlap analysis
2.4.6 Phylogenetic tree
2.4.7 Statistical analysis

## 7.3 Results

### Lorisine home range size:

Home range size trends differed within and across each lorisiform species. The pygmy slow loris had the largest home range (M: 22.2±10.3 ha, F: 12.1±1.7 ha) followed by the Javan slow loris (M: 9.3±4.1 ha, F: 4.5±1.1 ha), the grey slender loris (M: 6.6+5.6 ha, F:4.4+4.4 ha), with the red slender loris maintaining the smallest home range size (M: 2.3+1.2 ha, F: 3.1 +1.5 ha) (Table 7.2).

### Lorisiform group size and current social organisation:

As a result of the comparative study, which included 36 studies between 1977 and 2016. I conclude that of the seven included genera, the group size ranges between one and 10 individuals (Figure 7.2). *Galagoides* had the largest reported range of 1-10 individual with a mean of 7 individuals. *Loris* and *Nycticebus* had the smallest range from 3-5 individuals.

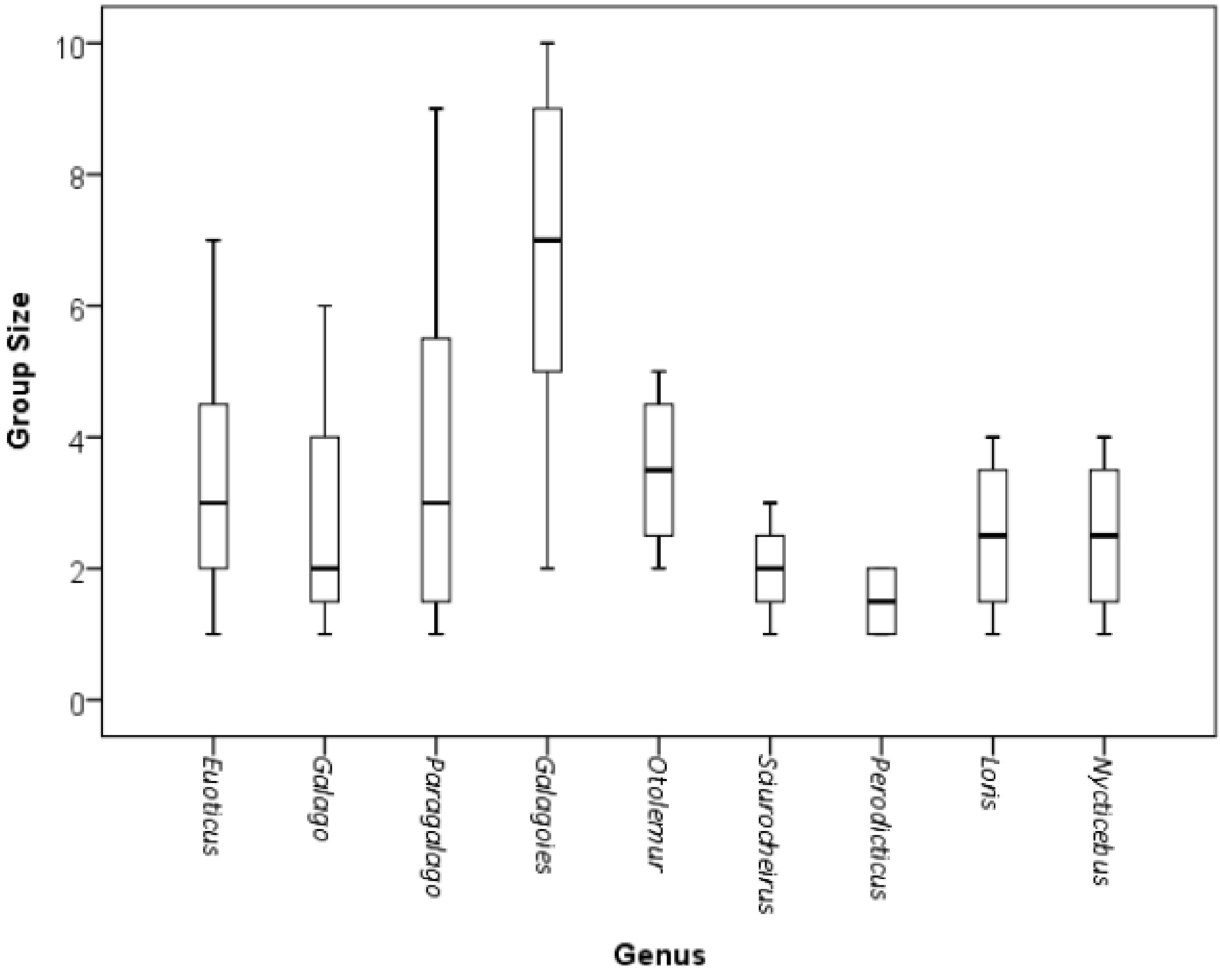


**Figure 7.2:** Boxplot representing reported group sizes in seven lorisiform genera, data were collected from published and unpublished sources*. The middle bar represents the mean group size the whiskers, represent the maximum and minimum reported group size.

****Euoticus:*** Jewell and Oats, 1969; Charles–Dominque, 1977; Ambrose, 1999; ***Galago:*** Smithers, 1971; Izard and Nash, 1988; Pullen, 2000; Butynski and de Jong, 2004; Bearder et al., 2008 ***Galagoides:*** Kingdon, 1971; 1997; Charles –Dominque, 1977; Ambrose, 1999; Olson and Nash, 2002-2003; ***Paragalago:*** Harcourt and Nash, 1986; Bearder et al., 2003; Butynski et al., 2006; ***Otolemur:*** Bearder, 1974; Doyle, 1979; Nash et al., 1990; Perkin, 2004; Bearder, 2007 ***Sciurocheirus*****:** Pimley, 2002 ***Arctocebus:*** Jewell and Oates, 1969a; 1969b; Charles-Dominique, 1977; ***Perodicticus:*** Pimley, 2002; Pimley et al., 2005; Pimley and Bearder, 2013; ***Loris:*** Nekaris, 2000; Nekarsi, 2003; Nekaris and Jayewardene, 2003; Kar Gupta, 2005; Kar Gupta and Katti, 2007; ***Nycticebus:*** Gupta, 2001; Wiens, 2002; Nekaris and Bearder, 2006; Pilosungnoen et al., 2010; Nekaris and Bearder, 2007.

**Table 7.2:** Known spatial overlap of Lorisiformes, detailing the male-male overlap, male-female overlap, and female-female overlap. Where possible the Social Organisation is identified. Data were collected from published resources, including books and articles listed in Figure 7.2*

| **Species** | **Male HR** | **Female HR** | **Social Organisation** |
|---|---|---|---|
| **Lorisinae** | | | |
| ***Loris lydekkerianus lydekkerianus*** | 3.6 | 1.59 | Dispersed Family Group |
| ***L. tardigradus tardigradus*** | - | - | Dispersed Family Group |
| ***Nycticebus coucang*** | 0.8-22 | 2.1- 10.4 | Dispersed Family Group |
| ***N. pygmaeus*** | 22.2 | 12.1 | Multi-female/Uni-male |
| ***N. javanicus*** | 9.3 | 4.5 | Dispersed Family Group |
| ***N. bengalensis*** | - | - | Dispersed Family Group |
| **Perodicticinae** | | | |
| ***Perodicticus potto edwardsi*** | 30.6 | 31.5 | Dispersed Family Group |
| ***P. p. edwardsi*** | 17.8 | 7.5 | Dispersed Family Group |
| **Galaginae** | | | |
| ***Euoticus elegantulus*** | - | - | Multi-female/Uni-male |
| ***E. pallidus*** | - | - | Multi-female/Uni-male |
| ***G. gallarum*** | - | - | Dispersed Family Group |
| ***G. moholi*** | 4.6-14 | - | Dispersed Family Group |
| ***Paragalago cocos*** | 1.8-5.1 | 1.3-2.6 | Multi-female/Uni-male |
| ***Galagoides demidovii*** | 0.8 | 0.5 | Multi-female/Uni-male |
| ***P. granti*** | - | - | Promiscuous |
| ***P. rondoensis*** | - | - | Promiscuous |
| ***Gd. thomasi*** | - | - | Promiscuous |
| ***P.zanzibaricus*** | - | - | Dispersed Family Group |
| ***Otolemur crassicaudatus*** | - | - | Promiscuous |
| ***Sciurocheirus alleni*** | 1.97-2.8 | - | Multi-female/Uni-male |

**Ancestral state at the root of Lorisiformes:**

The last common ancestor (LCA) of the lorisiforms split into two distinct subfamilies 40 Mya during the Eocene (Pozzi, 2016). The phylogenetic tree produced reconstructing the ancestral social organisation proposes that the most likely social organisation in the LCA for all lorisiforms was a dispersed family group (dispersed monogamy). The multi-female/uni-male social organisation has a `one-quarter likelihood of being the ancestral state, while the promiscuous social organisation has a negligible likelihood (Figure 7.3).

**Disperse family group/monogamy social organisation:**

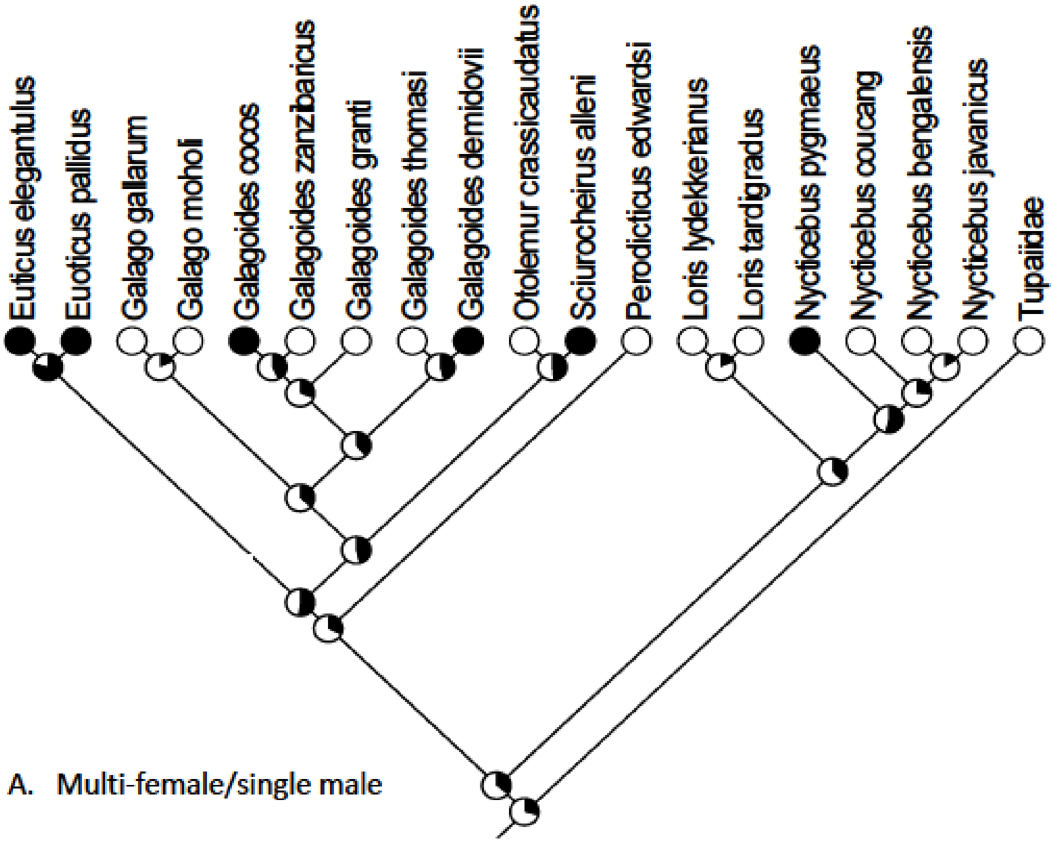
At the node where *Perodicticus* and galago split 30 Mya, the dispersed family group was still the most likely social organisation, but the likelihood is largely diminished at the node where *Euoticus* splits from *Paragalgo*, *Galagoides*, *Galago*, *Otolemur*, and *Sciurocheirus*. The dispersed family group remerges in *Paragalago zanzibaricus and Galago gallarum* between 5 Mya and the present. In Asia the dispersed family group remains the predominate social organisation among the lorisines. The pygmy slow loris and slender lories are an exception as they display a mulit-female/uni-male social organisation. The node where *N. javanicus*, *N. bengalensis* and *N. coucang* split from *N. pygmaeus* about 9 Mya during the Miocene, show that the LCA at this point had a one-quarter likelihood of not displaying the dispersed family group (Figure 7.3).

### Promiscuous social organisation:

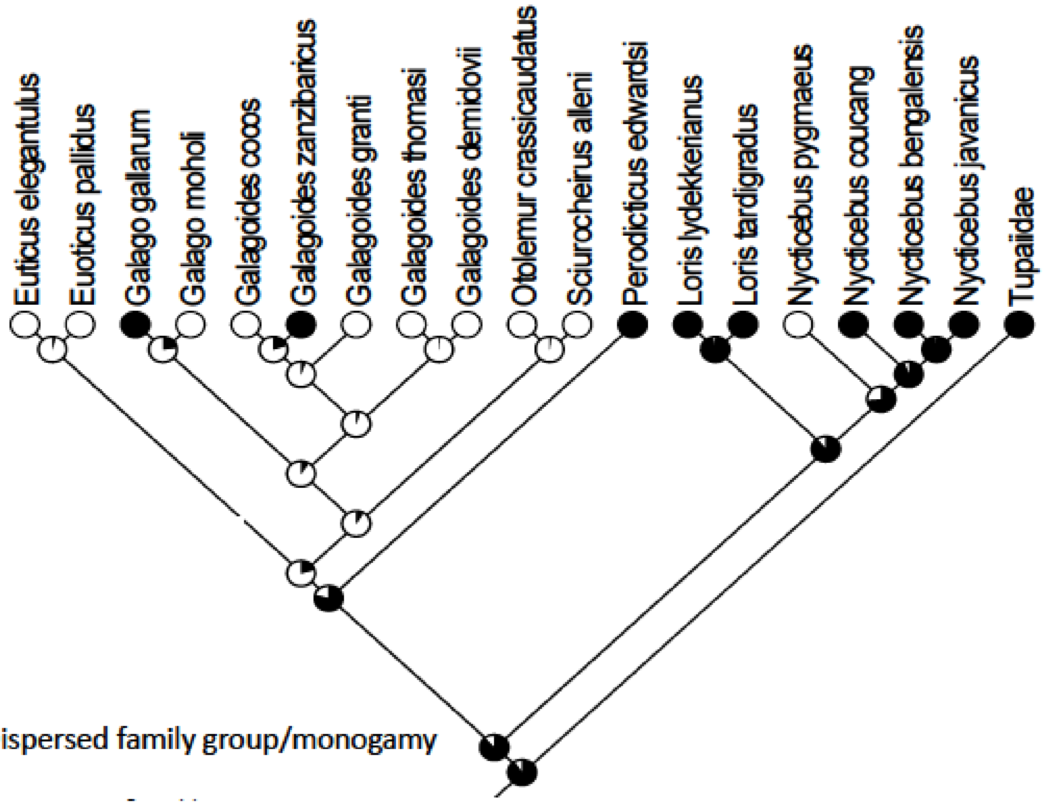
A promiscuous social organisation is unlikely at the node where Asian and African lorisiforms split 40 Mya, as well as, the point where pottos split from galago 30 Mya. It is not until 25-20 Mya that this social organisation displays a noticeable likelihood at the node where *Paragalogo coco, P. zanzibaricus, P. granti, Galago gallarum, G moholi, Otolemur crassicaudatus* and *Sciurocheirus alleni* last shared a common ancestor with *Gd. demidovii* and *Gd. thomasi*. Present today in *G moholi, O. crassicaudatus, P. granti*, and *Gd. thomasi*, a promiscuous social organisation has an increased likelihood at the node where *P. coco* and *P. zanzibaricus* share an LCA with *P. granti*, approximately 8 Mya; at the node where *G gallarum* and *G moholi* split 5-0 Mya, at the node where *O. cassicaudatus* and *S. alleni* split 15 Mya, and finally at the node where *Gd. demidovii* and *Gd. thomasi* split (Figure 7.3).

### Multi-female/uni-male social organisation:

The multi-female/uni-male social organisation in lorisiforms displays a one-quarter likelihood at the node where the Asian and African lorisiforms split during the Eocene. Thirty Mya the likelihood increase to more than half, where *Euoticus* and the other galagos share a common ancestor. In the Asian lorisines about 9 Mya the likelihood of this social organisation being present is slightly more than half (Figure 7.3).



A. Multi-female/single male



B. Dispersed family group/monogamy

1924)

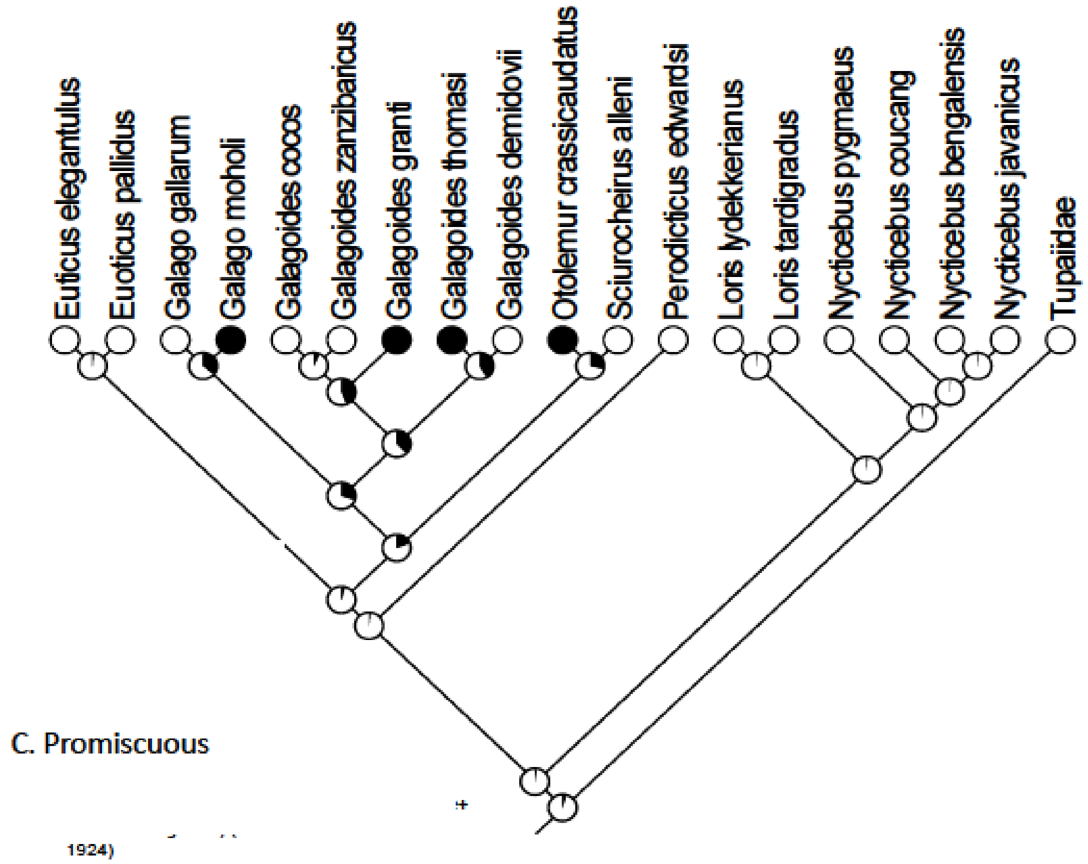

C. Promiscuous

**Figure 7.3:** Phylogenetic reconstruction of lorisiform social organization using the reconstructed character states function in Mesquite 3.3. Each tree shows one of three social organisations, including Multi-female/ single-male (A), Dispersed family group/monogamy (B), and Promiscuous (C). The dispersed family group/monogamy is the most likely state at the root of the lorisiform tree. Galagoides coco, Gd. Zanzibaricus and Gd. Granti, were changed to Paragalago after this tree was created, but the topography remains the same.

### 7.4 Discussion

After incorporating previously unavailable data on lorisine spatial systems and reported social organisations, I believe that early primates may have displayed a dispersed family group/monogamous social organisation. In this chapter, I categorised known lorisiform social organisations into three groups, multi-male/multi-female (promiscuous), a dispersed family group (monogamy), and multi female/uni-male. I found that the most prominent social organisation is the dispersed family group in the lorisids, while the multi-female/uni-male and promiscuous systems are more prominent in the galagos. Based on the phylogenetic analysis here the dispersed family group is the most likely ancestral state in all lorisiforms. Promiscuity and multi-female/uni-male are seemingly derived traits, potentially emerging 25-20 Mya and 30 Mya, respectively. The promiscuous social organisation is recorded in *Paragalago*, *Galagoides*, *Otolemur*, *Sciurocheirus*, and *Galago*, while the multi-female/uni-male emerged at the node of the LCA for all African lorisiforms.

Müeller and Thalmann (2000), already noted that a dispersed harem was not the ancestral state in primates. The dispersed harem social organisation was originally believed to be the ancestral states in primates based on the belief that Malagasy mouse and dwarf lemurs and the Afro-Asian galago and lorises displayed a dispersed harem social organisation. New data have debunked this belief and the results present here provide further support to Müeller and Thalmann's (2000) argument.

Among nocturnal strepsirrhines, individuals not only overlap spatially, but there is an observed paired movement and social associations among males, females and their offspring highlighting the presence of not only a social network, but also a family group (Chapter 4; Charles-Dominique and Petter, 1980; Harcourt and Nash, 1986; Fietz, 1999; Müeller, 1999b; Rasoloharijaona et al., 2000; Thalmann, 2001 Schulke, 2003). Despite observations of spatial overlap and social associations in the wild it can still be hard to confidently identify this social organisation; especially when pairs are do not consistently associated during their active hours or do not always sleep at the same sleeping site. These species may represent examples of independent transitions from a solitary to a monogamous social organization (Kappeler, 1999). There is a growing list of strepsirrhine displaying some form of monogamous association.

Seeing how prevalent the dispersed family group/monogamy social organisation is among lorisiforms, led me to wonder what are the benefits of this social organisation compared to other organisations? In general, social and solitary lifestyles have costs and benefits, where one or the other prevails if the benefits of that particular lifestyle outweigh the costs (Alexander, 1974). Alexander (1974) identified some of the defining factors that determine whether sociality is present, citing the availability of resources, the probability of disease transmission, and predation risk. Alternatively, there are cost associated with not being social, namely the reduced access to mating opportunities (Andrewartha and Birch, 1954), while one benefit is a reduced food competition. These pressures are also believed to have elicited the evolution of dispersed social groups, like the ones seen in *Nycticebus* and *Loris* species (Sterling and Richard, 1995; Gursky, 2002). Comparing the costs and benefits of any scenario can be difficult, in that a certain level of cohesion needs to be apparent to members within group as well as those outside of the group for the benefits to outweigh the costs.

There are a number of benefits to employing a dispersed family group compared to both promiscuity and a dispersed multi-female system. Arguably, monogamy or a reduced level of promiscuity played an important role in favouring the evolution of cooperative breeding and eusociality (Leggett et al., 2012). The number of males that a female mates with is thought to have pushed solitary animals in to more complex societies (Cornwallis et al., 2010). In the wild, an individual can disperse early to either secure independent breeding opportunities or spend an extended amount of time within their natal group and aid sibling development. Considering both of these decisions, there are varying benefits. If the potential disperser comes from a dispersed family group then the relatedness between the two siblings and the offspring they may have in the future is the same (Leggett et al., 2012). In this scenario, there is a negligible difference between the two options, in regards to passing your genes on. Thus, ecological factors will have a greater influence on what the most advantageous option is for each species. The alternative scenario is that the mother of the potential disperser has multiple mates, and then the likelihood of relatedness between siblings is decreased compared to the relatedness to their own offspring. In the interest of ensuring that genes pass from one generation to the next, the dispersed family group/monogamous social traits provide security in the likelihood of passing genes either through offspring or through the offspring of siblings.

### 7.5 Chapter summary

In this Chapter, I re-evaluated the ancestral state in lorisiforms regarding their social organisation. Since 2007, the prevailing hypothesis stated that promiscuity was the ancestral mammalian social organisation, which then evolved into a dispersed multi-female system in basal primates. I concluded that among lorisiforms the presumed promiscuous ancestral state in mammals, then evolved into a dispersed family group. In this chapter I used data on spacing and movement to discuss social organization in an evolutionary context (Figure7.4). These data highlight just how underrepresented the social complexity can be in nocturnal and dispersed species.

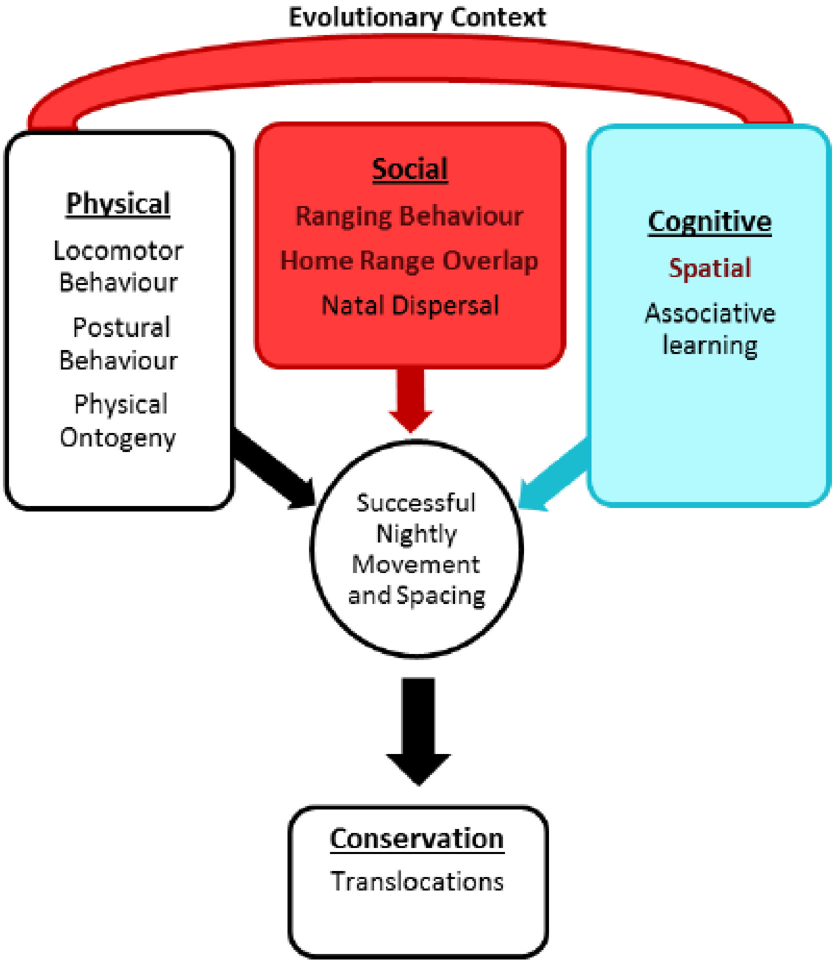


**Figure 7.4:** Visualisation of the framework of the thesis highlighting how the data and conclusions presented in Chapter 7, fit into the context of the entire thesis. Topics in red are the focus of the chapter; topics in blue are related though not explicitly discussed.

# Chapter 8: General discussion emphasising applications to conservation

**Figure 8.1:** Two Bengal slow lorises (*Nycticebus bengalensis*) displaying irregular active hours at a rescue centre in Chonburi, Thailand.

## 8.1 Introduction

Ranging patterns, natal dispersal, physical ontogeny, spatial cognition, and social organisation are all influential factors guiding the way *Nycticebus* species move each night and form home ranges. Based on data presented in this thesis and current literature it is clear that in order to successfully conceive and execute conservation efforts, researchers and practitioners must understand the evolutionary history as well as the ecology of their species. I have taken a multifaceted approach to learning more about *Nycticebus* species as a whole and individual populations; this approach echoes the call of many conservation agencies and regional practitioners. In this chapter, I will discuss the varying impacts data presented in this thesis can have on conservation practices and goals.

In 2010 the Convention for Biodiversity(CBD) created the 'Strategic Plan for Biodiversity 2011-2020', along with the five strategies presented in this plan, the Aichi Biodiversity Targets task force was created to support the implementation of the CBD strategies. Throughout this thesis I provide data that can be used in support of two targets specifically; targets 12 and 13 of strategy C. This strategy was created "to improve the status of biodiversity by safeguarding ecosystems, species, and genetic diversity". Target 12 states that "By 2020 the extinction of known threatened species has been prevented and their conservation status, particularly of those most in decline, has been improved and sustained." Target 13 states that "By 2020, the genetic diversity of cultivated plants and farmed and domesticated animals and of wild relatives, including other socio-economically as well as culturally valuable species, is maintained, and strategies have been developed and implemented for minimizing genetic erosion and safeguarding their genetic diversity."

In addition to the CBD and the Aichi targets, the IUCN reintroduction specialist group offers guidelines on how to approach release site selection and release strategy (Box 8.1).

**Box 8.1:** Direct quotes of recommended guidelines for release site selection and captive management.

A release site should:

- Meet all practical needs for effective release with least stress for the released organisms,
- Enable released organisms to exploit the surrounding release area quickly,
- Be suitable for media and public awareness needs, and any community involvement.

A release area should:

- Meet all the species' biotic and abiotic requirements,
- Be appropriate habitat for the life stage released and all life stages of the species,
- Be adequate for all seasonal habitat needs,
- Be large enough to meet the required conservation benefit,
- Have adequate connectivity to suitable habitat if that habitat is fragmented,
- Be adequately isolated from suboptimal or non-habitat areas which might be sink areas for the population.

Central release strategies are as follows:

- The life stage and season of release should be optimised with respect to the species' natural dispersal age or season, considering whether dispersal after release is to be encouraged or discouraged,
- The age/size, sex composition and social relationships of founders may be optimised for establishment and the population growth rate stated in the objectives,
- Translocation success increases with the numbers of individuals released (which is often enhanced through multiple release events across more than one year), but this needs to be balanced against impacts on source populations,
- Releases, either simultaneously or sequentially, at multiple sites may serve to spread out the released organisms, with several potential benefits,
- Minimising stress during capture, handling, transport and pre-release management will enhance post-release performance,
- Various management interventions and support before and after release can enhance performance.

Regarding slow loris captive management, according to an online Loris husbandry guide a section on inadequate cage furnishing states that:

- Vertical trunks and branches with a large diameter do not allow a safe grip; Tree trunks can be improved by inconspicuously attaching some wire mesh or lianas for climbing up and down.

They also note the importance of providing cage designs that encourage physical training.

- … cages mainly equipped with the preferred, comfortable horizontal substrate apparently promote indolence and adiposity in some individuals; some substrate gaps which promote bridging, feeding places or lookouts which can only be reached with some effort, longer passages outside cages or between two cages providing a view on the surroundings, or two cages connected by a longer passage may promote locomotion.

In an effort to contribute to evidence based conservation actions, I summarize these findings with recommendations for release site selection, release strategy, and captive management.

## 8.2 Chapter 3- Translocation

In regards to the pygmy slow lorises released in Cuc Phuong National Park, the release team and myself concluded the Cuc Phuong National Park's former botanical garden is no longer suitable for future pygmy slow loris releases. It became increasingly apparent that this area was not large enough to support multiple translocated male pygmy slow lorises. The post release movement of animals is an important consideration for the success of a translocation program. There is evidence that dispersing individuals have a higher mortality rates compared to non-dispersers and males that disperse longer distances from the release site are unlikely to contribute to the intended translocated population (Bright and Morris, 1994; Steen, 1994).

Having seen the post-release dispersal in the 2014-2015 release and the lack of a viable re-established population after the 2004 release, it is clear that some needed resources in this area are missing, or that the reintroduced individuals were not prepared to handle the added stressors associated with translocations. Beyond the former botanical gardens, Cuc Phuong National Park may have a flourishing population of pygmy slow lorises. Following population, predator, and forest structure surveys, it is necessary to find a more suitable release site for future translocations. Though it was not particularly successful in this study, it is evident in the successes seen in Cat Tien National Park (Kenyon et al., 2015) that translocations should still be considered a valuable conservation strategy for the pygmy slow loris. Learning from both successful and unsuccessful translocation programs is vital to improving practices for individual release candidates and for the species as a whole.

Another crucial aspect to improving translocation and our general approach to slow loris conservation is the understanding that anything we learn in the wild and in captivity should be shared so others can learn from one another. As I emphasis throughout this thesis there is still much to uncover about the behaviour, sociality, cognition, ontogeny, and morphology in slow lorises in the wild.  These data will help conservation practitioners to give dwindling species the best chance at overcoming the human-mediated obstacles to their survival. The difficulty in this is that the results of many studies are unavailable in the scientific literature partially because scientific journals are reluctant to publish studies with low statistical power and a small sample size, but in actually these should be encouraged in order to facilitate detailed analyses and reviews (Moseby et al., 2014). This also supports the World Wildlife Fund's (WWF) Protected Area for a Living Planet (PA4LP) goal of 'Informing global decisions by sharing lessons learned and expertise gained on the ground.'

### 8.3 Chapter 4- Natal Dispersal

In Chapter 4, I present the social interactions between both mothers and social fathers during the development of juveniles while in the natal home range. The period of time young Javan slow lorises spend within their natal home range is evident in the spatial data as well as the *ad libitum* data collected at LFP. During future translocations, practitioners should acknowledge the likelihood that all slow loris acquire a great deal of information while within the natal range. Not just ecological and behavioural competencies but social competencies as well. If practitioners continue to release adult slow lorises depending on the amount of time spent out of their natal area, there is the risk that no release sites will sufficiently fulfil their prior understanding of what an appropriate environment looks like. As Kenyon et al. (2015) suggested following a series of pygmy slow loris translocations, sub-adults are the most ideal age class for release. Their suggestion primarily based on survivorship and detailed documentation during translocations, can be further explained based on the information presented in Chapters 4 and 6. During a slow loris' period of dependence, needed information is presumably transferred from older conspecifics to maturing conspecifics. In any instance where information is presented to an immature individual there is an understanding that this information is correct especially when the informant is within the same familiar unit. Sub-adults are at a natural point where the information provided throughout development is applied during the search for a new home range for settlement. They are sufficiently independent in securing resources, but must also be appropriately malleable in what they consider acceptable as they enter novel areas during periodic forays. Practitioners should take care to create a similar process of leaving and returning to some type of home base, which can act as a proxy for the natal range in translocated individuals, and not just for food provisioning, but for a sense of familiarity. Some practitioners deemed food provisioning unnecessary, which may well be true during the wet season when all of the known slow loris food options are available, thus evaluating the need for a soft release cage, or food provisioning should not be measured based how much of the provisioned food remains. Translocated slow lorises may not return for food specifically but they may seek a familiar area, while establishing a new home range.

### 8.4 Chapter 5- Ontogeny

The physical and behavioural competency in wild individuals should act as a baseline goal for those being rehabilitated for translocations. Similar to much larger primates, including humans, juvenile must gain the appropriate competencies before leaving the natal group and home range (Beck, 2010). Due to their small body size this fact can often be overlooked during rehabilitations and when assessing preparedness before release. Reports of rescued infants or juveniles from wildlife markets, who are then released into the wild within 12 months, are ignoring key aspects of how these primates develop and survive into adulthood. Though some of these factors are poorly documented others are well known, yet still ignored. In Chapters 4 and 5. I stated how immature slow lorises spend more time than previously believed within their natal home range and that they are not fully proficient in all needed behaviours until they reach adulthood. These data speak to the fact that some form of social learning occurs between mature and immature conspecifics. It is well known among other primate species that there is a level of socially based learning between mature and immature individuals (Fragaszy and Visalberghi, 2004). In the case of confiscated juvenile slow lorises, imagine that they are first removed from their natal range, with an unknown level of behavioural and ecological independence. At this point it is unclear if they possess the ability to identify the function of specific resources, independent of simple associations gained through observing their mother. Next they are transported an unknown distance to join other animals for sale at a market, while being kept in improper conditions with improper food items. Then they are transported again an unknown distance to a rescue centre where many are at capacity and/or understaffed. There are indeed opportunities for non-related slow lorises to interact and develop social bonds in their centres, they are rarely specifically prepared for the rigors of living in a wild habitat. Once 'old' enough these individuals may be deemed ready for release and taken, yet again to an unknown place, an unknown distance from their natal home ranges, comprised of potentially unfamiliar vegetation. There may be a period where the released individual is monitored in a soft release cage at the release site, but this is not always the case. These soft release cages can help mediate any shock from being in a new place, but there is still the concern regarding what they were familiar with prior to their initial capture. There are no direct solutions to these problems, but practitioners can take care during rehabilitation and soft releases. The condition in which an individual develops, their dispersal performance and behaviour will likely create dispersal asymmetries (Benard and McCauley, 2008). In just acknowledging that there is a wide range of information shared between individuals, could influence housing arrangements at the rescue centres and pairing prior to release.

Finally, in Chapter 5, I highlighted the important role that gums and vertical substrates play in the physical and ecological ontogeny of the Javan slow loris. When selecting a release site or constructing captive enclosures, gum-producing trees should be present to elicit vertical clinging and gouging in slow lorises of all ages. The importance of gum and vertical substrates for slow lorises in captivity has already been established (Poindexter, 2013; Cabana and Plowman, 2014; Gray et al., 2015). Cabana and Plowman (2014) found that once they presented captive pygmy slow lories with a more natural diet including exudate that they displayed a more diverse range of normal behaviours and time spent engaging in stereotypies reduced.

In other gum feeding primates this is already a common practice (McGrew et al., 1986; Huber and Lewis, 2011) suggesting that the capacity to fulfil this natural dietary and physical need is there, but the importance is not widely accepted in these species yet.

### 8.5 Chapter 6- Cognitive Map Use

The recommendations derived from the data presented in Chapter 5, focused in the need for a longer rehabilitation and soft release period, as well as the need for gum-producing trees to elicit vertical clinging and gouging. In addition to the presence of gum producing tree, data in Chapter 6, show the added importance of the distribution of these resources. Though highly flexible in their use and ability to manoeuvre their dynamic environment, the Javan slow loris relies on landmarks to navigate to goal destinations. We as humans may see a forest, survey it for variation and deem it suitable to sufficiently support a wild population, but practitioners must remember to see the environment as the released animal will see it. Not only should practitioners thoroughly assess the vegetation in potential release sites, they should incorporate an aspect of measuring the spatial distribution of key trees.

The degree to which individual trees are aggregated or dispersed, is crucial to how a species uses resources. Spatial patterns are important in regards to tropical ecology, because high diversity in the tropics is typically indicative of low densities (Condit et al., 2000). If releasing multiple males, there should be a wide spread distribution of gum producing trees to ensure that each male can settle within an inclusive home range that does not overlap with another male.

Based on the number of times individuals at LFP revisited a single cluster of trees, I recommend that the trees considered appropriate as a gum resource be in good health and likely to withstand a high level of gouging. Similarly, the relative frequency for the area changing should be considered. As a route-based cognitive make user, landmarks are a key aspect of the way these primates envision their environment. If the potential release site is a part of an ever-changing environment, the translocated slow lorises may have difficulty creating a complete mental representation from which to build their cognitive map.

## 8.6 Chapter 7- Evolution

Species-specific social organisation should be incorporated in the rehabilitation and release plan for all lorises. No release should take place until there is a clear understanding of what species you have and what their natural behaviours they display especially in regards to spacing and social interactions. In Chapter 7, I present published and unpublished data that further highlight the diversity of sociality seen in Lorisiformes. Species-specific social organisations have a direct influence on the way that animals move and interact with conspecific in the wild and in captivity. Despite the reoccurring assertion that *Nycticebus* spp. are social animals that live in dispersed family groups, they are regularly housed as single animals. They are also released alone, or in randomly assigned pairs. Ignoring what we know about these animals to suit our sense of what is “right” for conservation and the individual is a disservice. In larger animals, especially primates, such as, great apes this approach to translocations is considered unacceptable. As such, these practises are not appropriate for any animal and smaller primate translocations should be held to the same standard as great apes. Sociality is one of the key aspects of living in the wild, especially if you maintain a social network. In Chapter 3, 4, 6, and 7, I acknowledge the complex nature of *Nycticebus* sociality, which can greatly affect the way practitioners approach translocations and captive housing.

Another applicable conclusion from Chapter 7, is the importance of proper spacing between translocated individuals. The variable Male-Male and Female-Female overlap reported in Chapter 7, emphasize the relations between not just males and females, but also same sex interactions. Social interactions between conspecifics as well as other animals within the environment can have unexpected effects on translocation project, Kenward and Hodder (1998), found during a red squirrel (*Sciurus vulgaris*) release that they were reluctant to enter traps used by the grey squirrels (*Sciurus carolinensis*) also present at the release site. In general, all of these interactions contribute to the way a slow loris or any animal will move in a natural setting and practitioners should consider this while creating a naturalistic environment or selecting an ideal release site.

### 8.7 Conclusion

Throughout the World, primates are facing an impending extinction crisis, where approximately 60% of the 504 primate species are threatened with extinction and approximately 75% have declining populations (Estrada et al., 2017). While completing my body of doctoral work I have made a conscientious effort to maintain a balance between focusing on research by addressing big questions across space and time in addition to the practical applications of what I uncover. Within each chapter presented in this thesis, I have reported novel data and analysis as well as noting how they directly correspond to international conservation goals and initiatives (Figure 8.2). In light of the many threats causing primate population decline, it is important to always consider the fate of these animals while we look to answer questions about their evolutionary history, ontogeny, behaviour, and ecology.

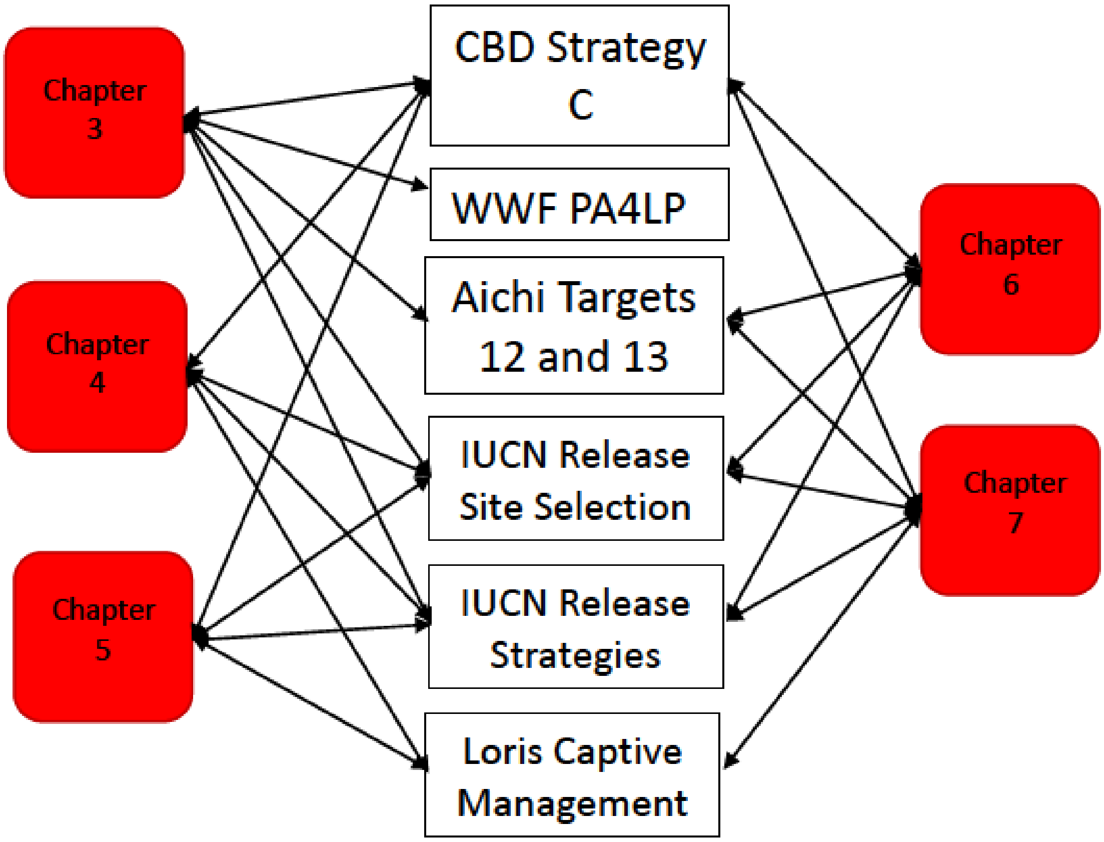


**Figure 8.2:** Visualisation of how each chapter supports various conservation initiatives and goals. Arrows connect each chapter to the goal that relate to them.

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Yoder, A.D., 1994. Relative position of the Cheirogaleidae in strepsirhine phylogeny: a comparison of morphological and molecular methods and results. *American Journal of Physical Anthropology*, 94(1), pp.25-46.

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# Appendix I- Thesis Publications and Collaborations during the PhD

## CHAPTER 3

Published in Vietnamese Journal of Primatology
Poindexter, S.A., Khoa, D.D., and Nekaris, K.A.I., 2017. The ranging patterns of reintroduced pygmy slow lorises (*Nycticebus pygmaeus*) in Cuc Phuong National Park, Vietnam. *Vietnamese Journal of Primatology*. 2(5), 37-49

## CHAPTER 5

Published in Mammalian Biology-Zeitschrift für Säugetierkunde
Poindexter, S.A. and Nekaris, K.A.I., 2017. Vertical clingers and gougers: Rapid acquisition of adult limb proportions facilitates feeding behaviours in young Javan slow lorises (*Nycticebus javanicus*). *Mammalian Biology-Zeitschrift für Säugetierkunde*.

## COLLABORATIONS DURING PhD

Nekaris, K.A.I., **Poindexter, S.**, Reinhardt, K.D., Sigaud, M., Cabana, F., Wirdateti, W. and Nijman, V., 2017. Coexistence between Javan slow lorises (Nycticebus javanicus) and humans in a dynamic agroforestry landscape in West Java, Indonesia. *International Journal of Primatology*, *38*(2), pp.303-320.

**Poindexter S** and Nekaris KAI. 2016. Sanctuaries-Asia. In: The International Encyclopedia of Primatology. Wiley Blackwell. Hoboken: New Jersey. 10.1002/9781119179313.wbprim0441

Nekaris KAI and **Poindexter S**. *Nycticebus hilleri*. The IUCN Red List of Threatened Species 2016. *In Press*

Nekaris KAI, **Poindexter S**, and Streicher U. *Nycticebus coucang*. The IUCN Red List of Threatened Species 2016. *In Press*

**Poindexter S** and Nekaris KAI. 2015. Lorisiformes. In: The International Encyclopedia of Primatology. Wiley Blackwell. Hoboken: New Jersey. 10.1002/9781119179313.wbprim0131

# Appendix II- Publication Reprints

Details of and links to the six publications incorporated in the bound copy of this thesis are given below:

**1 Lorisformes**

STEPHANIE POINDEXTER and K.A.I NEKARIS Oxford Brookes University, United Kingdom
The International Encyclopedia of Primatology Edited by Agustín Fuentes. © John Wiley & Sons, Inc. Published 2017 by John Wiley & Sons, Inc. https://onlinelibrary.wiley.com/doi/10.1002/9781119179313.wbprim0131

**2 Sanctuaries - Asia**

STEPHANIE POINDEXTER and K.A.I NEKARIS
Oxford Brookes University, United Kingdom
The International Encyclopedia of Primatology Edited by Agustín Fuentes. © John Wiley & Sons, Inc. Published 2017 by John Wiley & Sons, Inc. https://onlinelibrary.wiley.com/doi/10.1002/9781119179313.wbprim0441

**3 The ranging patterns of reintroduced pygmy slow lorises (Nycticebus pygmaeus) in Cuc Phuong National Park, Vietnam**

Vietnamese Journal of Primatology (2017), vol. 2 (5), 37-49
Stephanie Poindexter (Corresponding author)1, Do Dang Khoa2 and K. Anne-Isola Nekaris1, Oxford Brookes University, Nocturnal Primate Research Group, Department of Social Sciences, Faculty of Humanities and Social Sciences, Gibbs Building, Gipsy Lane, Oxford OX3 0BP, UK1, Endangered Primate Rescue Center, Cuc Phuong National Park, Ninh Binh Province, Vietnam2
http://www.primate-sg.org/vietnamese-journal-of-primatol/
https://www.researchgate.net/publication/317345452_The_ranging_patterns_of_reintroduced_pygmy_slow_lorises_Nycticebus_pygmaeus_in_Cuc_Phuong_National_Park_Vietnam

**4 Vertical clingers and gougers: Rapid acquisition of adult limb proportions facilitates feeding behaviours in young Javan slow lorises (Nycticebus javanicus)**
Mammalian Biology, Volume 87, November 2017, Pages 40-49
Stephanie A. Poindexter, K.A.I.Nekaris, Nocturnal Primate Research Group, Oxford Brookes University, Oxford, United Kingdom https://doi.org/10.1016/j.mambio.2017.05.007

**5 Poindexter S. (2017) Prosimian Cognition.** In: Vonk J., Shackelford T. (eds) Encyclopedia of Animal Cognition and Behavior. Springer, Cham
DOI: https://doi.org/10.1007/978-3-319-47829-6_468-1

**6 Poindexter S. (2017) Prosimian Navigation.** In: Vonk J., Shackelford T. (eds) Encyclopedia of Animal Cognition and Behavior. Springer, Cham
DOI: https://doi.org/10.1007/978-3-319-47829-6_453-1

The content of pages 225-260 in the bound copy of this thesis consists of full-text publications subject to copyright. These have been redacted from the electronic version and the resulting blank pages removed.

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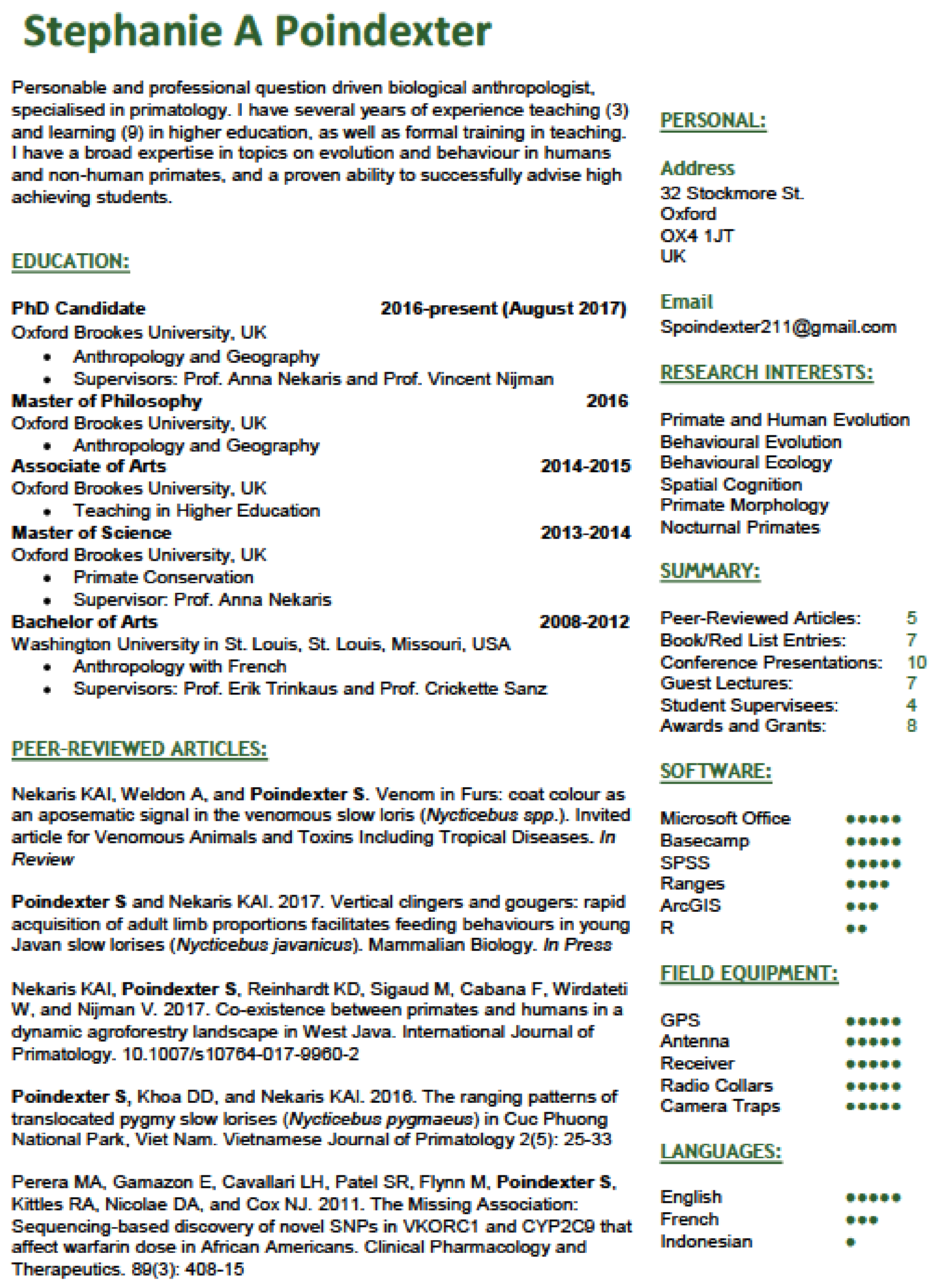
# Appendix III- Academic CV



## Stephanie A Poindexter

Personable and professional question driven biological anthropologist, specialised in primatology. I have several years of experience teaching (3) and learning (9) in higher education, as well as formal training in teaching. I have a broad expertise in topics on evolution and behaviour in humans and non-human primates, and a proven ability to successfully advise high achieving students.

### EDUCATION:

**PhD Candidate** **2016-present (August 2017)**
Oxford Brookes University, UK
- Anthropology and Geography
- Supervisors: Prof. Anna Nekaris and Prof. Vincent Nijman

**Master of Philosophy** **2016**
Oxford Brookes University, UK
- Anthropology and Geography

**Associate of Arts** **2014-2015**
Oxford Brookes University, UK
- Teaching in Higher Education

**Master of Science** **2013-2014**
Oxford Brookes University, UK
- Primate Conservation
- Supervisor: Prof. Anna Nekaris

**Bachelor of Arts** **2008-2012**
Washington University in St. Louis, St. Louis, Missouri, USA
- Anthropology with French
- Supervisors: Prof. Erik Trinkaus and Prof. Crickette Sanz

### PEER-REVIEWED ARTICLES:

Nekaris KAI, Weldon A, and **Poindexter S**. Venom in Furs: coat colour as an aposematic signal in the venomous slow loris (*Nycticebus spp.*). Invited article for Venomous Animals and Toxins Including Tropical Diseases. *In Review*

**Poindexter S** and Nekaris KAI. 2017. Vertical clingers and gougers: rapid acquisition of adult limb proportions facilitates feeding behaviours in young Javan slow lorises (*Nycticebus javanicus*). Mammalian Biology. *In Press*

Nekaris KAI, **Poindexter S**, Reinhardt KD, Sigaud M, Cabana F, Wirdateti W, and Nijman V. 2017. Co-existence between primates and humans in a dynamic agroforestry landscape in West Java. International Journal of Primatology. 10.1007/s10764-017-9960-2

**Poindexter S**, Khoa DD, and Nekaris KAI. 2016. The ranging patterns of translocated pygmy slow lorises (*Nycticebus pygmaeus*) in Cuc Phuong National Park, Viet Nam. Vietnamese Journal of Primatology 2(5): 25-33

Perera MA, Gamazon E, Cavallari LH, Patel SR, Flynn M, **Poindexter S**, Kittles RA, Nicolae DA, and Cox NJ. 2011. The Missing Association: Sequencing-based discovery of novel SNPs in VKORC1 and CYP2C9 that affect warfarin dose in African Americans. Clinical Pharmacology and Therapeutics. 89(3): 408-15

### PERSONAL:

**Address**
32 Stockmore St.
Oxford
OX4 1JT
UK

**Email**
Spoindexter211@gmail.com

### RESEARCH INTERESTS:

Primate and Human Evolution
Behavioural Evolution
Behavioural Ecology
Spatial Cognition
Primate Morphology
Nocturnal Primates

### SUMMARY:

| | |
|---|---|
| Peer-Reviewed Articles: | 5 |
| Book/Red List Entries: | 7 |
| Conference Presentations: | 10 |
| Guest Lectures: | 7 |
| Student Supervisees: | 4 |
| Awards and Grants: | 8 |

### SOFTWARE:

| | |
|---|---|
| Microsoft Office | ●●●●● |
| Basecamp | ●●●●● |
| SPSS | ●●●●● |
| Ranges | ●●●● |
| ArcGIS | ●●● |
| R | ●● |

### FIELD EQUIPMENT:

| | |
|---|---|
| GPS | ●●●●● |
| Antenna | ●●●●● |
| Receiver | ●●●●● |
| Radio Collars | ●●●●● |
| Camera Traps | ●●●●● |

### LANGUAGES:

| | |
|---|---|
| English | ●●●●● |
| French | ●●● |
| Indonesian | ● |

## BOOK AND RED LIST CONTRIBUTIONS:

**Poindexter S**. Prosimian Morphology. In: Encyclopedia of Animal Cognition and Behavior. Springer Nature. New York: New York. *In Press*

**Poindexter S**. Prosimian Cognition. In: Encyclopedia of Animal Cognition and Behavior. Springer Nature. New York: New York. *In Press*

**Poindexter S**. Prosimian Navigation. 2017. In: Encyclopedia of Animal Cognition and Behavior. Springer Nature. New York: New York. *In Press*

**Poindexter S** and Nekaris KAI. 2016. Sanctuaries-Asia. In: The International Encyclopedia of Primatology. Wiley Blackwell. Hoboken: New Jersey. 10.1002/9781119179313.wbprim0441

Nekaris KAI and **Poindexter S**. *Nycticebus hilleri*. The IUCN Red List of Threatened Species 2016. *In Press*

Nekaris KAI, **Poindexter S**, and Streicher U. *Nycticebus coucang*. The IUCN Red List of Threatened Species 2016. *In Press*

**Poindexter S** and Nekaris KAI. 2015. Lorisiformes. In: The International Encyclopedia of Primatology. Wiley Blackwell. Hoboken: New Jersey. 10.1002/9781119179313.wbprim0131

## CONFERENCE PRESENTATIONS:

**Poindexter S**and Nekaris KAI. 2017. Lateralization in the slow loris (*Nycticebus* spp.) Venom Pose. Poster accepted at the American Association of Physical anthropologists Meeting, New Orleans LA USA.

**Poindexter S** and Nekaris KAI. 2016. Cognitive map use in the Javan Slow Loris (*Nycticebus javanicus*). Oral presentation at the International Primatological Society Meeting, Chicago IL USA.

**Poindexter S**, Nadler T, and Nekaris KAI. 2016 Pygmy slow loris (*Nycticebus pygmaeus*) translocation in Cuc Phuong National Park, Vietnam. Oral presentation at the Spring Primate Society of Great Britain Meeting, York UK.

**Poindexter S**, Warditeti, and Nekaris KAI. 2015. Age differences in locomotor behaviour in the Javan slow loris (*Nycticebus javanicus*). Oral presentation at the Spring Primate Society of Great Britain Meeting in Roehampton UK.

Reinhardt KD, **Poindexter SA**, and Nekaris KAI. 2015. Husbandry of pygmy, Bengal and Javan slow lorises: Implications for re-introduction. Oral presentation at the Spring EAZA Prosimian TAG Meeting in Prague Czech Republic.

**Poindexter SA**, Reinhardt KD, and Nekaris KAI. 2014. The influence of morphometrics on behaviour and habitat use in the Javan slow loris (*Nycticebus javanicus*). Poster presentation at the Winter Anatomical Society and the Primate Society of Great Britain Meeting in Birmingham UK.

**Poindexter S** and Nekaris KAI. 2014. Promoting wild postures: the use of gum-based enrichment in increasing the natural behaviors of rescued slow lorises (*Nycticebus bengalensis, N. pygmaeus and N. coucang*) in Thailand. Poster presentation at the American Society of Primatologist Meeting in Atlanta GA USA.

**Poindexter S**. 2012. The Holly Project 2012: The effects of sensory integration disorder on a chimpanzee (*Pan troglodytes*). Oral presentation at the Saint Louis Zoo.

**Poindexter S**. 2010. Adaptive vocalizations: training roloway guenons (*Cercopithecus roloway*) to recognize imitation calls. Oral presentation at Washington University in St. Louis.

**Poindexter S**. 2008. Doctor-patient interaction in Internal Medicine at the University of Chicago Hospitals. Poster presentation at the Collegiate Scholars Program Meeting.

## GUEST LECTURES AND INVITED TALKS:

2016. "The Little Fireface Project: what do we know about the slow loris?" Oral presentation at Brookfield Zoo for senior keepers, Chicago IL USA

2016. "Slow loris nutrition" Lecture presented during the Captive Management and Rehabilitation module for MSc in Primate Conservation students, Oxford UK

2016. "Primate morphology" Lecture presented during the Captive Management and Rehabilitation module for MSc in Primate Conservation students, Oxford UK

2016. "Collaborations and data management" Lecture presented during the Methods and Analysis module for MSc in Primate Conservation students, Oxford UK

2015. "Pygmy loris reintroductions in Cuc Phuong National Park" Oral presentation at Dao Tien's Endangered Asian Species Trust for government official, Ho Chi Minh City Vietnam

2015 and 2017. "Social learning" Lecture presented during the Humans and Other Primates module for BSc Biological Anthropology students, Oxford UK

2015. "Adaptability in changing environments: the case of slow loris" Presented at the MSc in Primate Conservation Seminar Series, Oxford UK

## WORK IN PROGRESS:

**Poindexter S**, Weldon A, and Nekaris KAI. Dispersal patterns in the Javan slow loris (*Nycticebus javanicus*).

**Poindexter S**, Reinhadrt KD, and Nekaris KAI. Lateralization in unimanual tasks and a bilateral posture in *Nycticebus* species.

**Poindexter S** and Nekaris KAI. Cognitivemap use in the Javan slow loris (*Nycticebus javanicus*).

**Poindexter S** and Nekaris KAI. Evolution of social systems in Lorisiformes.

O'Hagan RP, Marsh C, **Poindexter S,** Reinhardt KD, and Nekaris KAI. Translocation of Javan slow lorises (*Nycticebus javanicus*) in West Java, Indonesia.

## RESEARCH EXPERIENCE:

**Little Fireface Project, Indonesia** **Jan. 2015/Sept-Nov 2015**
Visiting Researcher: I used radio telemetry to track and observe wild Javan slow lorises (*Nycticebus javanicus*) in a high altitude agro forest. I managed the five-year dataset, by cleaning and sorting data. In collaboration with Prof. Anna Nekaris

**The Endangered Primate Rescue Center, Vietnam** **April-Sept. 2015**
Visiting Researcher: I oversaw the post release monitoring of six translocated pygmy slow lorises (*Nycticebus pygmaeus*) and completed vegetation structure surveys. I trained local staff in geographical data collection/organization and created their current vegetation and animal survey methodology. In collaboration with Tilo Nadler and Sonya Posser

**Bang Phra Research Center, Thailand** **May-Aug. 2014**
Visiting Researcher: I conducted nightly observations of 10+ rescued slow lorises (*Nycticebus bengalensis* and *N. pygmaeus*), while introducing various food-based environmental enrichment for my Master's thesis, and developed a husbandry guide, which was translated to Thai for local practitioners. In collaboration with the Department of Nature and Parks and Love Wildlife Thailand

**Saint Louis Zoo, St. Louis MO** **June 2011-Dec. 2011**
Behavioural Research Intern: I completed live and video observations of the Channel Island Fox (*Urocyon littoralis*) and Somali Wild Ass (*Equus africanus somaliensis*) resulting in an independent report. Supervised by Dr. Cheryl Asa and Dr. Fiona Marshall

**University of Chicago Hospital, Chicago IL** **2007-2010**
Research Assistant: I interviewed patients, extracted data from charts, and entered data. Supervised by: Dr. Minoli Perera and Dr. Vineet Arora.

## TEACHING EXPEREINCE:

2016-present. Associate Lecturer - Department of Anthropology and Geography, Oxford Brookes University

Spring 2017. Graduate Level Teaching Assistant – Primate Population Genetics

Spring 2017. Undergraduate Level Teaching Assistant – Humans and Other Primates

Spring 2015/2016. Graduate Level Teaching Assistant – Captive Management and Rehabilitation

Fall 2014/2015. Undergraduate Level Teaching Assistant – Methods and Analyses in Biological Anthropology

### Undergraduate Dissertation Co-Supervisees:

2016. Asia Bee: Database development and management for the Little Fireface Project, West Java Indonesia. BSc Thesis Computer Science, Oxford Brookes University

Present. Mathew Gardiner: Slow loris (*Nycticebus* spp.) saliva and its effect on human cancer cells. BSc Thesis Biological Anthropology, Oxford Brookes University

Present. Lucy Holland: What environmental factors influence the use of human-made substrates by the Javan slow loris (*Nycticebus javanicus*). BSc Thesis Biological Anthropology, Oxford Brookes University

Present. Shahroz Ahmed: Data visualization for the long-term dataset at the Little Fireface Project, West Java Indonesia BSc Thesis Computer Science, Oxford Brookes University

### Student Feedback:

"Stephanie is such a friendly and approachable person and I am very grateful to Stephanie for supporting me throughout my dissertation. Not only did she help me to overcome challenges in areas I did not feel comfortable with such as statistics, Stephanie's positive, smiley and calm attitude was very much appreciated during times I felt I was struggling. Stephanie is a wonderful teacher and I would very much love to be taught by Stephanie in the future." –**Lucy Holland**

"Stephanie was able to explain challenging concepts in engaging and accessible ways. Her style of teaching was adaptable, and appropriate to the module subject and level. Whether it was explaining statistical analysis or helping with osteological identification - or anything in-between - Stephanie was enthusiastic, informative and vital to my academic experience."-**Mathew Gardiner**

## ADMINISTRATIVE EXPERIENCE:

**Little Fireface Project, Oxford UK** **Jan 2014- present**
Administrative Assistant: I managed the field site database, assisted with public outreach across the UK and managed the inventory/order fulfillment of the Etsy Shop.

***Canopy* Journal, Oxford UK** **Sept. 2013-2014**
Editor: I worked with five other MSc students to organise and produce the in-house journal for the MSc in Primate Conservation course. I assisted in conceptualising the issue theme, selecting, editing, and formatting articles.

**The School Council of Arts and Sciences, St. Louis MO** **May 2011-2012**
President: I oversaw weekly council meetings regarding student concerns, successfully planned an awards ceremony recognising excellence in teaching and completed a council wide restructuring. As the president I was the student representative on ad hoc committees for new course approvals, mitigating circumstance approvals, and special major approvals.

**The Congress of the South Forty, St. Louis MO** **Aug. 2009-May 2010**
Academic Chair/Treasurer: I worked on a board of 12 planning events such as concerts, movie screenings, and lectures series. I specialised in academically focused events and managed a 20,000 USD budget to organise these events.

**Washington University in St. Louis Anthropology Department, St. Louis MO** **Jan. 2010-Aug. 2010**
Administrative Assistant: I maintained the office of Dr. Fiona Marshall, by replying to professional emails, creating class calendars, making copies, PDFs, formatting scientific articles.

### AWARDS AND GRANTS:

2015 Disney Conservation Fund (Participating Recipient): **25,000 USD**
2015 Margot Marsh Biodiversity Fund (Participating Recipient): **15,000 USD**
2015 People's Trust for Endangered Species (Participating Recipient): **10,000 USD**
2010 Washington University in St. Louis Career Development Grant (Principal Recipient): **2,000 USD**
2016 Primate Society of Great Britain Research Grant (Principal Recipient): **750 GBP**
2016 European Human Behavior and Evolution Association (Principal Recipient): **500 EUR**
2015 Graduate College Online Conference Prize Winner: **50 GBP**
2014 Finalist in the ASP Student poster competition

### PROFESSIONAL MEMBERSHIPS:

| | |
|---|---|
| Lambda Alpha:Anthropology Honors Society | 2011-present |
| Primate Society of Great Britain | 2013-present |
| International Primatological Society | 2013-present |
| American Society of Primatologists | 2013-present |
| Association of Black Anthropologists | 2014-present |
| Nocturnal Primate Research Group | 2014-present |
| European Human Behaviour and Evolution Association | 2015-present |
| American Association of Physical Anthropologists: | 2016-present |

### AD HOC REVIEWER:

Folia Primatologica
Asian Primates
Elsevier